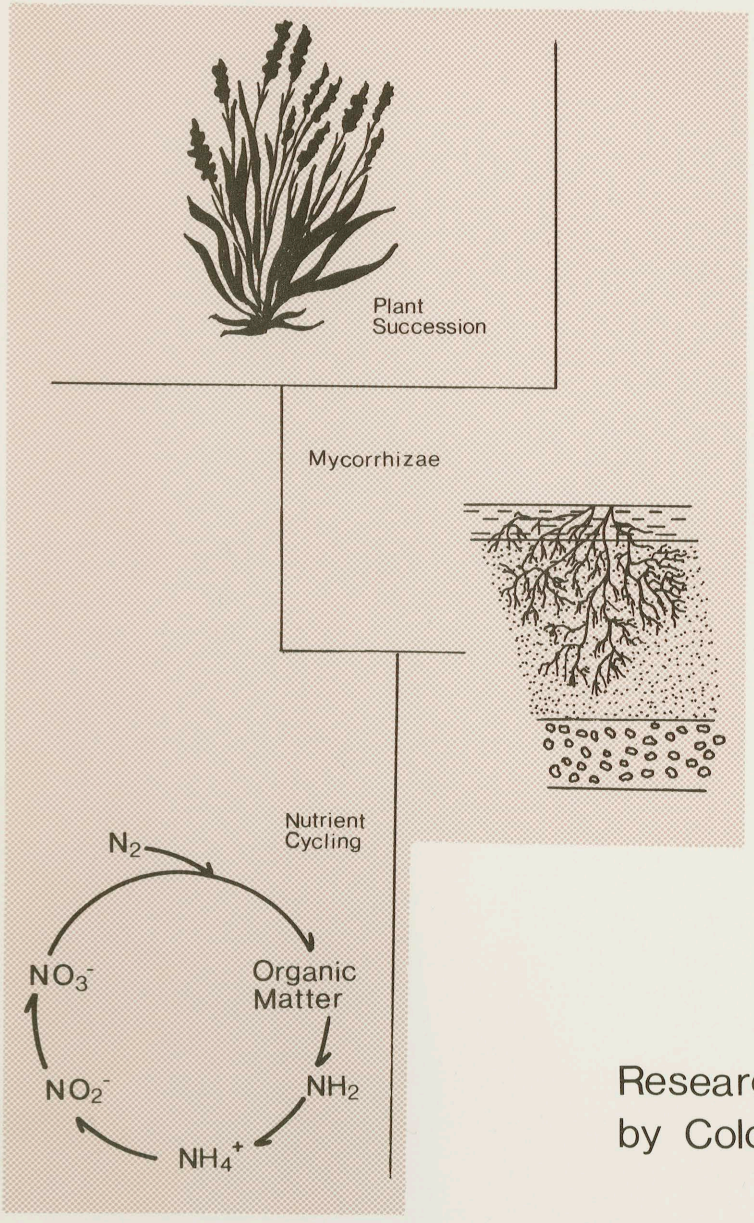
DOE/EV/04018-9

Structural and Functional Changes in Early Successional Stages of a Semiarid Ecosystem



February 1986

Research Report
by Colorado State University

Report Submitted to
U.S. Department of Energy

DOE/EV/04018-9

Structural and Functional Changes in Early Successional Stages of a Semiarid Ecosystem

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Submitted

February 1986

Prepared for

U.S. Department of Energy

Under Contract No. DE-AC02-76EV04018

ABSTRACT

The objective of our research is to study structural and functional changes that occur within and between ecosystem compartments during secondary succession in disturbed semiarid environments. This information not only will assist in better understanding fundamental aspects of these processes, but should lead to more effective management of these disturbed semiarid environments.

First year data clearly showed an increase in resource abundance after disturbance which produced not only alteration of the soil surface but a decrease in available organic matter. In addition, marked increases in NO_3^- and soil water potentials were evident at all depths in the disturbed sites as compared to the undisturbed community. Potential N mineralization rates, a measure of plant-available N, primarily from microbial biomass did not differ, but actual mineral N levels were higher because of higher soil moisture. Water use efficiency also varied with the early successional species being more efficient than late successional species. However, the late successional species were able to effectively use water under lower soil water potentials. These results are consistent with available information showing that "climax" species are less efficient in producing biomass at high levels of resource availability but able to sustain growth under conditions of nutrient (including water) stress.

Soil disturbance as well as manipulation of the microflora compartment by fumigation had a significant impact on microflora structure and function, and could have a long term impact on resource availability which will be important in understanding microbial contributions to the early development of plant-soil systems. Soil enzymatic activity, phosphatase, dehydrogenase and especially N fixation, ammonium and nitrite oxidation were still markedly reduced by disturbance and fumigation. This reduction of nutrient cycling, together with the elimination of plants, resulted in a sharp decline in fungal species diversity, with the saprobic community being dominated by pioneering species like Penicillium, Phoma, and Cladosporium. The mycorrhizal population was also drastically reduced by disturbance and fumigation. With plant community development, the level of mycorrhizal inoculum potential (MIP) was lower with ruderal (R) and competitive-ruderal (C-R) plants while higher MIP values occurred when the plant community was dominated by stress tolerant plants (S). MIP was also inversely correlated with the level of non-rhizosphere microbial activity. A preliminary study of rhizosphere vs. non-rhizosphere microbial development was conducted in the field in this first growing season where cheatgrass (Bromus tectorum) and western wheatgrass (Agropyron smithii) responses, with and without fertilization, were evaluated. The rhizosphere of both plants had consistently higher microbial populations, enzymatic activity, and fungal diversity than the non-rhizosphere. The rhizosphere of cheatgrass showed higher microbial population and enzymatic activities and lower diversity than the rhizosphere of western wheatgrass. These preliminary studies conducted with an annual versus a perennial plant will be examined in greater detail in comparison with other perennial plant responses in the coming year.

The floristic composition of the primary producers on the disturbed site was highly correlated with the propagule supply, with composition of the seed bank being the main driving force. Resource competition was not important at this stage in determining species composition because plant density was low and N, P, and water resources were abundant. Total aboveground net primary production (NPP) was similar in undisturbed and disturbed plots but the structure of primary producers was significantly different. The disturbed sites were dominated by plants with an R and CR strategy while the undisturbed sites were dominated by plants with an S strategy, indicating strong relationships between plant composition and soil resource abundance.

Competition studies between bluebunch wheatgrass (Agropyron inerme), western wheatgrass, big sagebrush (Artemisia tridentata), and winterfat (Ceratoides lanata) showed that these four species were able to coexist under a wide range of water availability conditions. This appeared to be related to differences in carbon allocation to shoots, roots, and stems and an ability to control water losses among these plants. The grasses showed a faster rate of growth and root expansion than shrubs during the establishment phase and as a result, competition between grasses was more intense than between shrubs or grasses and shrubs, leading to a decline in biomass production. Competitive relationships of mature species in the natural community were in some instances different than those found in greenhouse experiments. For instance, winterfat competed better with western wheatgrass than with another winterfat because winterfat could use water deeper in the profile, which was not available to the grass. Under field conditions, the water status of all plants was more favorable on deeply disturbed soils, than on shallowly disturbed soils and varied carbon allocation patterns, stomatal conductance, and transpiration rates were also evident.

The final phase of an experiment designed to determine the effects of retorted shale recarbonation on plant uptake of toxic trace elements was completed. Plants grown on recarbonated retorted shale had significantly lower concentration of B, Ba, and Sr and higher Mo levels than plants grown in non-recarbonated shales. In contrast, As, Cr, F, and Ni uptake was below toxic levels with and without recarbonation. The Cu:Mo ratio in plants was not influenced by recarbonation, being below the recommended levels for utilization by ruminants. This represents a potential source of toxicity which will not be influenced by the recarbonation process.

These initial studies, in summary, indicate that both plant community characteristics and the presence of a functioning belowground community will be important in secondary succession processes which occur in disturbed semiarid environments. Rhizosphere and nonrhizosphere microflora structure and dynamics as well as plant competition strategies, as influenced by nutrient resource availability, will be critical factors influencing the successional process.

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.

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INTRODUCTION

Succession, defined as ecosystem development over time (MacMahon 1980), has been described by many ecologists, and a variety of hypotheses to explain succession have been formulated. Some traditional hypotheses are that succession is driven by autogenic processes (Weaver and Clements 1938), or that succession results from the individual tolerances and chance dispersal of organisms (Gleason 1926; Whittaker 1975; Glenn-Lewin 1980). Successional theories also have been based on population dynamics (Peet and Christensen 1980), species' life histories (Grime 1979), species' vital attributes (Noble and Slatyer 1980), and changes in soil nutrient ratios (Tilman 1982). These theories focus on the aboveground components of terrestrial ecosystems (MacLean 1974) and as a result largely ignore belowground components. To understand changes and functions in ecosystems, integrated studies that examine both primary production and decomposition must be devised (Parkinson 1979).

Our studies over the past several years have dealt primarily with stand establishment and early succession in disturbed native ecosystems of western Colorado. Recently we began a basic study on characteristics of ecosystem development. Our previous research has documented important relationships among vegetation changes, soil biological activity, and abiotic factors during the course of natural and induced succession (Redente et al. 1982; Klein et al. 1982, 1985; Reeves et al. 1982; Slauson and Ward 1982; Slauson 1983; Schmidt and Reeves 1984; Bonham et al. 1984; Biondini et al. 1984, 1985; Stark and Redente 1985; Reeves 1985; Biondini and Redente 1986; Kiel and Reeves 1986). From these observations, we have developed a research project to study secondary successional changes in semiarid ecosystems. Our research addresses fundamental structural and functional changes that occur during ecosystem development. These changes are integrated in a model designed to clarify the mechanisms that cause and control succession (Fig. 1).

Our research emphasizes (1) the structure and function of the (belowground) microflora as they relate to (aboveground) species tolerances and autogenic processes, (2) the role of competition, resource partitioning, and initial species composition in ecosystem development, and (3) the influence of plant life history strategies on secondary succession processes. Our approach can be linked to modern theories of succession based on resource availability (Tilman 1982), plant strategies (Grime 1979), and competition and tolerance models (Connell and Slatyer 1977). The advantage of our approach is that it examines many interactions within the ecosystem that are believed responsible for directing secondary succession. A test plot (Ecosystem Development Plot) was constructed in 1984 in the Piceance Basin of northwest Colorado to address our specific research objectives. This report presents first year data from this study.

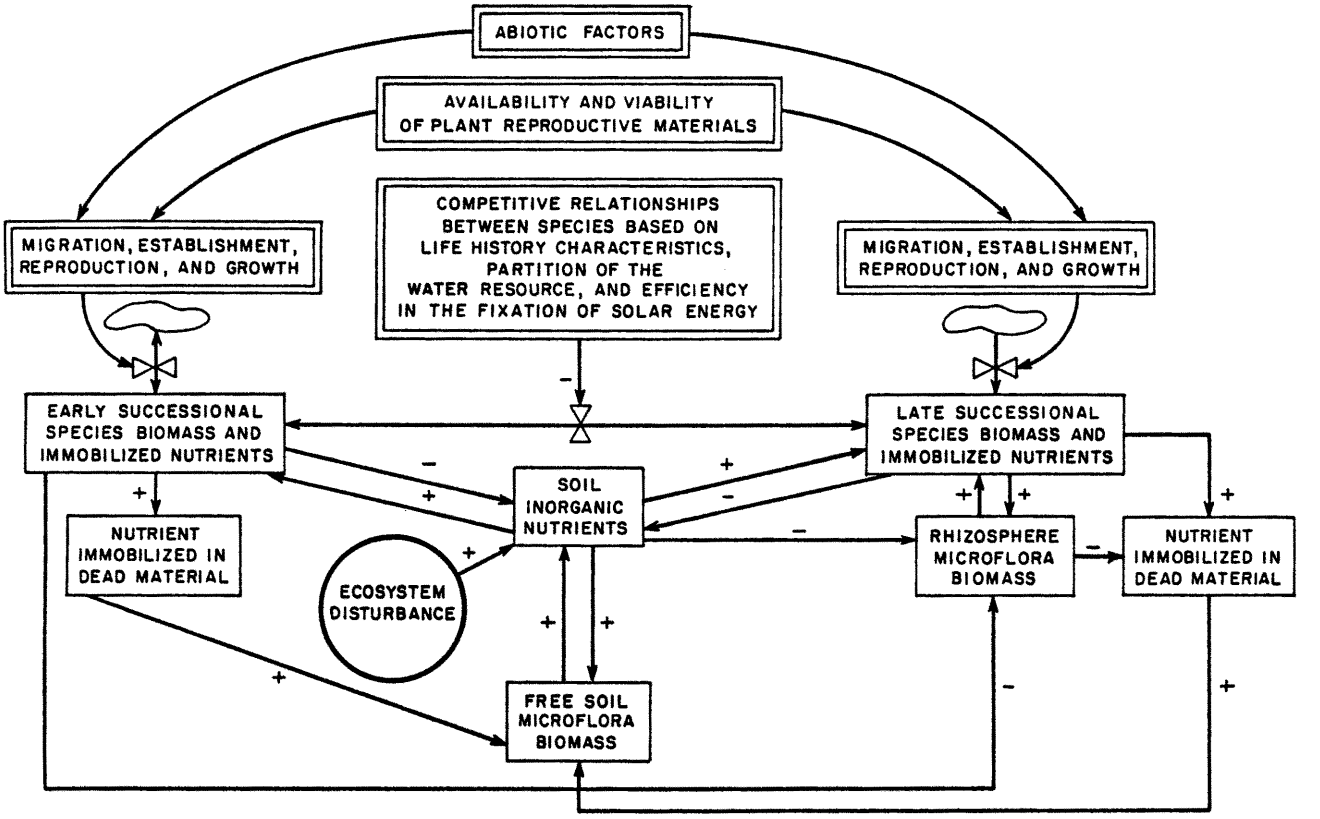

Figure 1. A model that integrates the changes in the primary producers, the microflora, and the abiotic environment during succession. The single rectangles represent the ecosystem components that are being addressed in this research. The double rectangles represent the main controlling variables which regulate the interrelationships between the ecosystem compartments that will be addressed in this research. **The circle represents an ecosystem disturbance that initiates secondary succession. Interpretation of the model should begin at this point.** The arrows represent interrelationships between both ecosystem compartments and controlling variables. A sign on an arrow indicates how the state of an ecosystem compartment affects the state of another ecosystem compartment (a "-" sign represents an inverse relationship, a "+" sign represents a positive relationship). The symbol ☁ represents a source and the symbol ⋈ represents a flow rate control.

RESEARCH APPROACH AND OBJECTIVES

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 successional changes.

Field studies are located in the Piceance Basin of northwest Colorado in close proximity to the Intensive Study Site established in 1976. A new field plot was constructed in 1984 in a mid-elevation big sagebrush community on a site with uniform soil and topographic conditions. The main study plot was prepared by mechanically removing the vegetation and thoroughly mixing the topsoil and subsoil to a depth of 35 cm. This ecosystem disturbance has set the stage for secondary succession. In order to study the changes of different ecosystem compartments during succession four treatments were applied: **(1)** Fertilization experiments are being used to study the role that inorganic nutrient availability plays in controlling structural and functional changes in primary producers and the microflora during succession. **(2)** Fumigation experiments, to initially control microbial populations, are being used to study the role that the microbial compartment plays in the regulation of succession. **(3)** Seeding experiments, and **(4)** Weeding experiments are being used to determine the role that primary producers with different life history strategies play in the advance of succession.

Besides the Intensive Study Site, other sites in the Piceance Basin and vicinity, which have been disturbed at various times in the past, are serving as field laboratories to test objectives concerning availability and viability of plant reproductive material and life history strategies of major primary producers during succession. These field laboratories also provide a means for studying longer successional sequences to further compare above- and belowground ecosystem components.

Laboratory and greenhouse studies are being conducted in facilities at Colorado State University. These studies include nutrient cycling, competition, and mycorrhizal dependency experiments that are best conducted under controlled environmental conditions.

The specific objectives addressed in this report are listed below:

1. To monitor the effect of disturbance and fertilization on resource availability and determine how resource availability changes during succession.
2. To determine the effect of disturbance, increased nutrient availability, and reduced microbial community functioning on net primary production by various vascular plant groups.
3. To monitor the vascular plant community and determine if changes in species composition can be explained by changes in resource availability, distribution, and processing patterns.
4. To test alternate successional theories, such as the Facilitation Model of Connell and Slatyer (1977), against the model proposed in this study.
5. To determine the characteristics of nitrogen (N) mobilization and immobilization by the microflora, as well as effects on carbon (C) allocation and flows in the ecosystem during plant community development in relation to variations in fertilizer, fumigation, and initial plant community.
6. To determine structural patterns and diversity of the soil microflora during ecosystem development, with special emphasis on microbial dynamics in the rhizosphere and rhizoplane.
7. To provide background information for C allocation and plant root exudate studies planned for future investigation, where early and late successional plants will be compared.
8. To determine the influence that vesicular-arbuscular mycorrhizal (VAM) fungi have on secondary succession in semiarid ecosystems.
9. To determine the mycorrhizal dependency and colonization of major primary producers by mycorrhizal fungi and the relationship of this process to changes in microbial populations and to ecosystem development.
10. To describe the changes in the saprobic fungal community associated with disturbance and to compare this community with that present in undisturbed communities.
11. To determine the availability and viability of plant reproductive material and to determine how life history strategies differ as the composition of the major primary producers change during ecosystem development.

12. To evaluate the effects of inter- and intra-specific competition on the physiological responses in late successional plant species under field conditions.

13. To characterize seasonal patterns of transpiration and stomatal conductance in late successional plant species growing under different soil disturbance and competition conditions.

14. To elucidate the role of water relations in the physiological responses of primary producers.

15. To determine biological and physiological responses of primary producers to competition and water stress during ecosystem development.

16. To determine the dynamics of net primary productivity (NPP) and C allocation to different plant parts of late successional species during ecosystem development.

In addition to these above objectives, which are related to the present study, information from previous research concerned with the following objectives also is included in this report.

17. To develop an effective method for the recarbonation of retorted shales.

18. To examine the uptake of trace elements by plants growing on recarbonated shales.

RESEARCH PLAN

ENVIRONMENTAL SETTING

The study site is in the Piceance Basin of northwest Colorado. The elevation at the site is 2020 m, mean annual precipitation is approximately 28.2 cm, and mean annual temperature is 6.8°C. An ecological climate diagram showing the distribution of temperature and precipitation at the site is included in Appendix Figure 1. The study plots are located exclusively on Yamac loams (fine-loamy, mixed, Borollic Camborthids). These deep soils normally support a big sagebrush (Artemisia tridentata var. tridentata) shrubland, while shallower, rockier entisols in the area support a pinyon-juniper woodland. The species composition of the big sagebrush community and a description of the Yamac soil series are given in Appendix Tables 1 and 2.

FIELD PLOT ESTABLISHMENT

Test Plot Design

The Ecosystem Development Plot has a randomized complete block design with ten treatments and four blocks. Figure 2 shows the arrangement of treatments within one of the four blocks. The ten treatments are 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 continually removed from site by hand-weeding
Fumigated	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 seeding or fertilization
Nonfumigated	
Climax	Broadcast seeded and transplanted with late successional plant species (Table 1)
Ruderal	Broadcast seeded with early successional plant species (Table 1)
Control	No seeding or fertilization

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

PLOT CONSTRUCTION

Four areas (blocks) of approximately equal size were selected for the study site. In early August 1984, the native vegetation and top 3-4 cm of soil were mechanically stripped from the four sites. The soil was then plowed to a depth of 30 cm using the tilted blade of a road grader. Following plowing, the sites were harrowed to break up large clods and to smooth the surface. Each of the four blocks was divided into ten 500 m^2 subplots, using 1 m buffer zones between subplots. Near the center of each subplot five psychrometers were placed at depths of 5, 15, 30, 50, and 80 cm. In addition, a 120 cm 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 as a barrier against subterranean microbial invasion. In late September 1984, the areas were covered with plastic tarps and approximately 3 kg of methyl bromide was injected beneath the tarp at 5 m intervals giving an application of 45 kg of methyl bromide per subplot. The tarps were left for 24 hours to insure an adequate reduction of microbial populations.

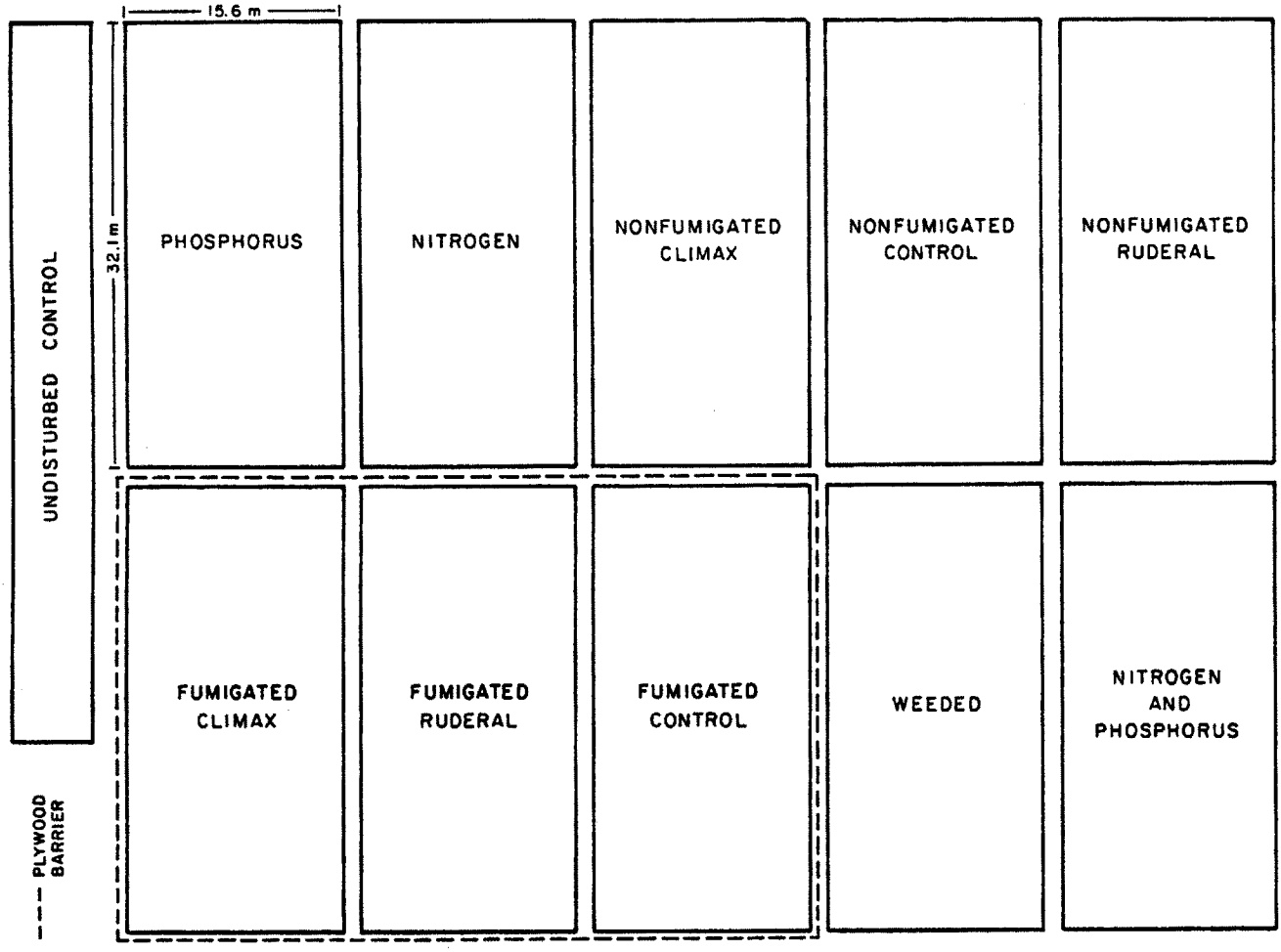

Figure 2. Experimental design representing one of the blocks.

In mid-October, big sagebrush seedlings were transplanted at a density of approximately 0.3 seedlings per m^2 into the subplots seeded to climax species. In early November, climax and ruderal subplots, were broadcast seeded with the appropriate seed mixtures (Table 1) and the subplots were lightly hand-raked to 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 P application, ammonium nitrate was broadcast on the N + P and N subplots at a rate of 100 kg/ha. Nitrogen and P were applied three times in 1985 to study high nutrient levels throughout the growing season. One-third of the fertilizer was applied at the beginning of June, another third in mid-August, and the final application was made in mid-October.

METHODOLOGY FOR INDIVIDUAL STUDIES

Soil Data on Ecosystem Development Plot

Soil N + P Pools

Soil cores were collected following disturbance in late fall (12/84), early spring (4/85), and late summer (8/85) on the undisturbed control, control, N, P, and N+P subplots. The soil core samples were collected by taking two cores to a depth of 60 cm and two cores to a depth of 20 cm within a single subplot. The cores were divided into 0-10, 10-20, 20-40, and 40-60 cm depth intervals and samples from a single depth interval were composited. The composited samples were homogenized and divided into two subsamples. One subsample was kept cool and at field moisture content and analyzed for mineralizable N (Keeney 1982), while the other was air-dried and analyzed for total N and KCL extractable NH_4^+ (Kjeldahl method), and NH_4HCO_3-DTPA extractable NO_3^- and P (Soltanpour and Schwab 1977). Organic matter was also determined by the Walkley-Black procedure on samples collected 12/84.

Table 1. List of species seeded on climax and ruderal subplots, Piceance Basin November 1984.

Common Name	Scientific Name	PLS+/m²	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	*Gutierrezia 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%).

\+ PLS = Pure Live Seed.

Psychrometer Soil Water Potential Data

Psychrometers were placed at 5, 15, 30, 50, and 80 cm depths in all subplots except fumigated ruderal subplots. Water potentials were taken at approximately two-week intervals on all treatments from 6/1/85 to 8/24/85, and on selected treatments until 10/5/85.

Vegetation Data on Ecosystem Development Plot

Aboveground Net Primary Production (NPP)

On each of three sampling dates (mid-June, mid-July, and mid-August) ten 50x100 cm quadrats were randomly located in each disturbed subplot. To minimize disturbance, only five quadrats were used per sample date in the undisturbed control subplots. Within each quadrat, all current year growth was clipped either at ground level or at the point of entry into the quadrat volume. This material was separated by species, oven-dried for 72 hours at 60°C, and weighed.

The sampling dates used during 1985 were chosen to coincide with biomass peaks of major plant groups. The data indicated that the biomass of annual grasses and annual forbs peaked in mid-July on disturbed sites, while biomass of all other species peaked in mid-August. The biomass values determined for these dates were used as NPP, since this was the first growth on the plots.

For the analysis of NPP data, plant species were divided into functional forms based on morphological and physiological differences that are ecologically important. The first group of forms was based on the degree of perenniation of plant parts. Plant species were separated into (1) annuals and biennials, (2) perennial herbaceous species, (3) perennial woody deciduous species, and (4) perennial woody evergreen species. A second group was based on the degree of formation of symbioses with mycorrhizal fungi and N-fixing bacteria. This included groups of (1) non-mycorrhizal species, (2) mycorrhizal annuals or biennials, (3) mycorrhizal perennials, and (4) mycorrhizal perennial N-fixers. Finally, a third group was based on Grime's (1979) plant strategies: (1) stress tolerators (S), (2) competitors (C), (3) ruderals (R), (4) stress-tolerant competitors (C-S), (5) competitive ruderals (C-R), (6) stress-tolerant ruderals (S-R), and (7) C-S-R strategests. Appendix Table 3 lists the plant strategy groupings used for each plant species.

Belowground Root Standing Crop

In late August, two soil cores (10 cm in diameter) were taken to a depth of 60 cm in the undisturbed control, control, climax, and ruderal subplots. The cores were divided into 0-15, 15-30, 30-45, and 45-60 cm depth intervals. These samples were washed in a hydropneumatic elutriation system to separate the mineral fraction from the coarse organic fraction, and the coarse organic fraction was then separated by hand into live roots and dead organic matter. The root and organic matter samples were oven-dried at 60°C for 72 hours, weighed, ashed in a muffle furnace, and reweighed.

Test of the Facilitation Model

The weeded subplots were used to test the facilitation model of Connell and Slatyer (1977). Throughout the growing season all annuals and biennials were continually removed from the subplots. Then twice during the season, all of the perennials that had become established were removed. As each of the established perennials was removed, a record was kept as to the number of plants of each species that were removed. Plants were considered established if they appeared healthy and vigorous and either (1) were as large as they usually are on undisturbed sites or (2) were over 20 cm tall. The height criterion allowed removal of shrubs and other large species before they could substantially modify the environment.

Soil Microbial Data on Ecosystem Development Plot

Nutrient Cycling Measurements

Soil Sampling

Triplicate soil samples were collected from each subplot in mid-June and mid-July, 1985 using 3 five-fold replicate samples at 5-10 cm depth in each of the subplots of the Ecosystem Development Plot. The soil was passed through a 2 mm mesh sieve without drying, and stored at 6°C in ziplock plastic bags.

Analytical Procedures

The soil samples were analyzed for the following: organic matter (Nelson and Sommers 1982), mineralizable N (Keeney and Nelson 1982), phosphatase activity (Tabatabai and Bremner 1969), dehydrogenase activity with and without added glucose (Klein et al. 1971; Sorensen et al. 1981; Tabatabai 1982), glucose-amended acetylene reduction activity (Hersman and Klein 1979), and ammonium and nitrate oxidation potential (Robertson and Vitousek 1981; Belser and Mays 1980).

Rhizosphere Development Analyses

Three of the four blocks were sampled for this study, which included sampling the rhizosphere (0 to 7 cm from the plant root) and 30 cm from the plant stem (non-rhizosphere) for an early successional species (Bromus tectorum) and a late successional species (Agropyron smithii) growing in each subplot. The rhizosphere soil was collected by carefully excavating the plants and

placing the roots and clinging soil in a sterile plastic bag (Fresquez and Lindemann 1982). The 30 cm distance non-rhizosphere samples were collected with a soil spade to a depth of 13 cm; the samples were immediately cooled in an ice chest. Samples were then passed through a 2 mm sieve, and stored at 4°C. A composite sample from each treatment was analyzed at the New Mexico State University Soil and Water Testing Laboratory. All methods of chemical analyses are described by Fresquez and Lindemann (1983).

Rhizosphere microbial populations were estimated by methods similar to those described by Lochhead (1940) and Starkey (1958), and have been described previously (Fresquez and Lindemann 1982). Also, methods used for determining the populations of aerobic heterotrophic bacteria, Streptomyces, fungi, aerobic asymbiotic nitrogen-fixing bacteria (Azotobacter), and ammonium oxiziders have been described by Fresquez and Lindemann (1982). All values are reported on an oven-dry weight soil basis.

Fungal genera were isolated by evenly distributing 1 ml of a 10^{-3} dilution (from a 10 g oven-dry weight equivalent soil sample) over the surface of solidified rose bengal-streptomycin agar. Six plates were inoculated for each composited site sample and incubated at 30°C for 7 days (Fresquez et al. 1985a). Fungal genera were identified using the taxonomic guides of Barnett and Hunter (1972), and Gilman (1968). Population structure and distribution patterns of the fungal community were analyzed using Shannon's index of species diversity (Zar 1974) and Sorensen's Similarity Coefficient (SPCC) (Mueller-Dombois and Ellenberg 1974).

All microbial and soil enzyme measurements in the rhizosphere study were completed within 5 weeks of collection. Dehydrogenase activity was determined by procedures described by Klein et al. (1971) and Sorensen et al. (1981). Nitrogenase activity was assayed by the acetylene reduction technique similar to that used by Stewart et al. (1967), and described by Fresquez et al. (1985b). Urease activity was determined by the general method of Pancholy and Rice (1973), except that a 2.5 M KCl-Ag_2SO_4 solution (Tabatabai and Bremner 1972) was used, and the amount of evolved ammonia was measured by Nessler's method, as described by Allen (1957). Invertase activity was measured by the method of Ross (1965), with the reducing sugar of the filtrate determined by Nelson's method (Clark 1969). Phosphatase activity was measured using the method of Tabatabai and Bremner (1969). Variations in functional patterns of bacterial isolates from these same samples were accomplished using procedures described by Mills and Wassell (1980) and more specific applications described by Metzger (1985) and Klein et al. (1986)

Saprobic and Mycorrhizal Fungi Data

Saprobic Fungi

Three 10 g soil samples (10 cm deep) were removed from each of four replicates of 11 plots (132 samples in all). Using sterile water, each soil sample was initially sieved through two sterile screens of decreasing mesh (1.0 and 0.25 mm), and soil which collected on the 0.25 mm screen was washed again 40 times with sterile water through three sterile screens (0.11, 0.7, and 0.4 mm) to remove spores and disrupt the soil particles (Bissett and Widden 1972). The soil and organic particles that collected on the 0.4 mm screen were plated on 6 Gochenaur's medium petri plates (Gochenaur 1978), with each plate receiving 20 soil particles. The plates were incubated in the dark at 20°C for 5 days, and hyphal tips were selected from each particle to establish 40 pure cultures on 2% malt agar. Pure cultures were allowed to grow for 2 weeks and sorted into presumptive species and recorded. Subcultures of presumptive species were maintained for identification. Contrasts among treatments were calculated using Sorensen's Similarity Coefficient (Mueller-Dombois and Ellenberg 1979).

Mycorrhizal Inoculum Potential (MIP)

In each of the four blocks of the eleven subplots three equally spaced soil samples were taken along a transect near the middle of each subplot to a depth of 15 cm before fumigation in 1984, and after fumigation in 1984 and 1985. Each soil sample was sieved through a 1 cm screen to disrupt soil particles and remove rocks. Soil was placed in 3.5 x 21 cm plastic tubes ("Conetainers", Ray Leach Co., Canby, OR), seeded with pregerminated corn seedlings (NC+ 1341 hybrids), and placed in a growth chamber. A 30-day bioassay (Moorman and Reeves 1979) of each sample was completed. After 30 days roots from each container were harvested, washed, fixed, and stained. For each plant, total root length and percent root length colonized with VAM fungi were calculated. Mean percent root length colonized is expressed as the MIP of that soil. For each soil sample triplicate MIP values were made, i.e., the MIP value for each treatment is the mean of 36 separate soil subsamples.

All of the subplots have been analyzed for MIP for 1984. All samples for 1985 have been bioassayed, but data for 1985 are based on analyses of approximately half of the bioassay plants. Thus comparisons of 1984 and 1985 data are indicative of changes, but are not final.

Mycorrhizal Dependency

The mycorrhizal status of most of the species have been reported (Allen 1984; Lindsey 1984; Miller 1979; Pendleton and Smith 1983; Reeves et al. 1979; Trappe 1981). For those species in which the mycorrhizal status is equivocal, i.e., sometimes reported to be mycorrhizal and sometimes reported to be non-mycorrhizal, we have assigned "half-credit" to that species. We then calculated the percent of mycorrhizal vs. non-mycorrhizal species in each life history category for the Piceance Basin species listed in Appendix Table 3.

Propagule Supply Data

Seed Rain and Seed Bank

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 yet effective seed trap that protects seeds against predation, moisture, and wind. Filter paper sprayed with Tanglefoot™ is laid in polystyrene petri dishes (150 x 15 mm) to provide a receptive surface. The dishes are fixed to the ground by a galvanized nail. Holes in the bottom of the dish provide for water drainage. We have modified this method by using mylar, secured to plywood squares, which holds the adhesive longer and does not buckle with repeated wetting and drying. We also have increased the trap size (30 x 30 cm) to provide a larger catching surface. To aid seed identification a seed herbarium has been started.

The seed supply in the soil (seed bank), was sampled at the end of the growing season by excavating soil from a 10 x 40 cm metal frame pressed 2 cm into the ground. Samples were randomly taken from 6-8 places per site, bagged separately and returned to the laboratory for cold storage. After cold storage, 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.

Seed rain and seed bank samples were taken from the non-fumigated-ruderal and climax seeded subplots and the undisturbed control subplot of the Ecosystem Development Plot. In addition, propagule supply was sampled in a subset of "field succession study sites" that have experienced various kinds of prior disturbance, and in associated undisturbed big sagebrush vegetation. Field succession sites now include eight pipelines of different ages and associated undisturbed vegetation, two abandoned roads, and one buried telephone cable.

These plots are located away from the Intensive Study Site, but generally occur in comparable shrub and woodland vegetation. Individual sites are homogeneous with respect to soil, topography, and vegetation cover. Soil microbial and MIP measurements are also being made on some of these sites.

Plant Community Composition

Community structure of the field succession sites was measured by estimating plant cover by species in 0.5 x 0.5 m quadrats systematically placed within each site. Preliminary sampling using 40 quadrats per site revealed that adequate estimates of cover for all but the rarest species were obtained with 12 to 15 quadrats. Adequacy was defined as having a mean cover value within 10% of the value estimated by 40 quadrats and generally 20 quadrats were used per site. For the shrub species, the number of individuals in each quadrat was recorded to calculate density and the maximum height of each shrub species in each quadrat was measured to the nearest 0.1 m.

Life History Strategies

The life history strategies of prominent Piceance Basin species were initially determined by using a key presented by Grime (1984). An analysis to quantitatively assign life history strategies to approximately 80 species is underway. Vascular plant phenotypes are seen as approximating one of three primary life history strategies adapted to the extremes of stress and disturbance afforded by different environments (Grime 1979). Stress is an environmental condition that contrains the production of biomass; disturbance is any environmental condition that can destroy plant biomass. Plants adapted to perform well in benign, productive habitats are competitors (C); plants adapted to exist in productive yet periodically disturbed habitats are ruderals (R); and plants adapted to persist in unproductive, stressful, but stable habitats are stress tolerators (S).

Competitors are large, fast-growing plants able to occupy space and gather resources in the presence of rivals. Ruderals are small, fast-growing plants that produce abundant seed in short, productive flushes between disturbances. Ruderal seeds usually have well developed dormancy and are dispersed widely over the landscape. Stress tolerators use time and space in another way; they are small, slow-growing, resource-sequestering organisms that can survive long-term environmental stress and grow and reproduce when the environment becomes more moderate.

In basically productive habitats which are periodically disturbed, plants have developed traits intermediate to competitor and ruderal (C-R). Similarly, other plant species can be classified as competitive-stress tolerator (C-S), competitive ruderal (C-R), or the competitive stress-tolerant ruderal (C-S-R), giving seven categories of plant life history strategies.

Plants in each category (of the two-dimensional continuum) not only occupy different parts of the productive-disturbed-stressed habitat continuum, but also possess special life history features. Important for our purpose is the putative relation of the various life history features related to succession. The relations of the seven life history strategies to each other, to their respective environments, and to successional position, as conceived by Grime (1979), are summarized in Figure 3.

Grime (1984) gives a dendrogram representing the life history strategies of plant species based on their growth form, physiology, and reproduction. Below is our translation of this into a key for identifying the life history strategies of Piceance Basin species. Our modification of Grime is indicated parenthetically. Our tentative placement of Piceance Basin species into these seven categories is given in Appendix Table 3.

Annual plants (or winter annuals)

- Fast-growing (and large)
  - Precocious flowering — R
  - Delayed flowering — C-R
- Slow-growing (and small) — S-R

Biennial plants (or monocarpic)

- Fast-growing (potentially large) — C-R
- Slow-growing (small) — S-R

Perennial plants

- Vernal geophytes (and vernal cryptophytes and hemicryptophytes) — S-R
- Non-vernal geophytes (cryptophytes and hemicryptophytes)
  - Rapid leaf turnover
    - Rapid proliferation of shoots — C-R
    - Shoots not proliferating rapidly
      - Shoots tall and laterally extensive — C
      - Shoots short or creeping — C-S-R
  - Slow leaf turnover
    - Shoots tall and laterally extensive — C-S
    - Shoots short and not laterally extensive — S

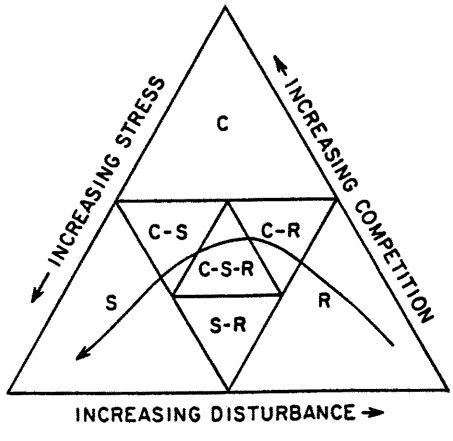

Figure 3. Triangular arrangement of life history strategies showing their relation to environmental disturbance and stress. The arrow represents the place of strategies in succession. R = ruderal; C = competitor; S = stress tolerator. Adapted from Grime (1979).

Competition for Water and Allocation of Fixed Energy

Greenhouse Study

Soil from the Intensive Study Site was sifted, air-dried, and mixed and 10-cm pots were filled with 3500 g of soil. A two-factor randomized complete block design was used. Factor 1 represented species: western wheatgrass (Agropyron smithii), bluebunch wheatgrass (A. inerme), big sagebrush (Artemisia tridentata), and winterfat (Ceratoides lanata) in pure and paired cultures. Two individuals of a species occurred together as pure culture and one individual of each of the two species made up a mixed culture. Factor 2 represented three watering regimes. All pots were watered daily to 80% of field capacity for six weeks during the germination and seedling stages. After six weeks, plants were subjected to a dry cycle treatment according to that used by Marjerus (1975) with soils brought to field capacity at one-week (wet regime), two-week (moist regime), or at three-week (dry regime) intervals. Each treatment was replicated six times.

Plants were grown in a greenhouse with 28-32°C day and 10-15°C night alternating temperatures and an artificially extended 15-hr day. Relative humidity was maintained at 20-40%. This environment corresponded to the mean climatic conditions during the months of July and August in the Piceance Basin. Plants were harvested 120 days after the drying cycle treatment was started.

Stomatal conductance and transpiration of plants were measured with a LI-1600 LICOR steady state porometer. Measurements were made on all plants in each treatment, on the upper and lower surface of the leaf. Gravimetric soil water for minimum and maximum moisture was determined at the end of the experiment. Half of the plants were harvested before the usual watering time and soil samples weighed, while the remaining plants were harvested when the soil was at field capacity. Soil samples were dried at 110°C for 24 hours to determine soil moisture as percent of dry weight and harvested plants were separated into roots, stems, and leaves for dry weight determination.

Data for each species growing in pure or mixed culture under three water treatments were combined giving 15 treatment groups (Table 2). These groups were subjected to a stepwise discriminant analysis to find variables which were significant in discriminating among treatment groups. Table 2 is to be used as a legend for group identification for Figures 16-27. Only significant variables are discussed in the Results section and shown in bar diagrams by treatment groups. Test of equality of group means for each pair of groups was carried out using the F-matrix of the stepwise discriminant analysis (Jennrich and Sampson 1983). Significant differences between all possible pairs of means for the 15 treatment groups of each species are shown in the form of matrices.

Canonical analysis of the biological data (stem, leaf and root biomass) and physiological data (soil moisture at the end of the drying cycle,

Table 2. Treatment group identification numbers for winterfat, big sagebrush, bluebunch wheatgrass, and western wheatgrass in relation to co-species combination and water regime. Example is given for bluebunch wheatgrass only.

Water Regime	Co-Species in Combination				
	Winterfat	Big Sagebrush	Bluebunch Wheatgrass	Bluebunch Wheatgrass	Western Wheatgrass
Bluebunch Wheatgrass					
Dry	1	2	3	4	5
Moist	6	7	8	9	10
Wet	11	12	13	14	15

transpiration and stomatal conductance, both from upper and lower leaf surfaces) was completed to compare the 'niche response' of species in the presence of other species and according to water levels.

Field Studies

A study of physiological and morphological responses of winterfat, bluebunch wheatgrass, and western wheatgrass to soil disturbance was 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, represented intensive disturbance. The Shallowly Disturbed Successional Study plot represented a surface disturbance. This plot had been scraped free of existing vegetation and the soil was scarified to a depth of 30 cm to simulate minor disturbances. Both disturbed sites were seeded with mixtures of native and introduced grasses, forbs, and shrubs (Redente et al. 1982, 1984).

Selected intra- and interspecific neighboring plant pairs of winterfat, bluebunch wheatgrass, and western wheatgrass were randomly chosen in May 1985 in each of the disturbance treatments. An individual of a species and its nearest neighbor were randomly chosen in sets for combinations to specifically test the effects of competition (Table 3). Nearest neighbors selected were within 20 cm of each other. Each combination for each level of disturbance was replicated six times.

Table 3. Combinations of species for study of the effects of competition and soil disturbance on the physiological and morphological response of primary producers, 1985.

Winterfat - Winterfat
Winterfat - Bluebunch wheatgrass
Winterfat - Western wheatgrass
Bluebunch wheatgrass - Bluebunch wheatgrass
Western wheatgrass - Western wheatgrass

Physiological measurements were made seven times during the growing season: 7 June, 27 June, 9 July, 27 July, 15 August, 9 September, and 3 October. Measurements of the physiological response of plants were taken with a LI-1600 LICOR steady state porometer. Measurements included ambient temperature, leaf temperature, stomatal conductance, and transpiration. Physiological measurements were taken between 10:00 am and 4:00 pm MST during maximum plant activity. Individual leaves of plants were measured with a small aperature (4.8 mm x 1.37 cm). The two uppermost, fully expanded leaves from each plant were sampled and both surfaces (upper and lower) were measured independently. Measurements were averaged for each treatment effect.

Gravimetric soil moisture (%) was determined for three depths (0-20, 20-40, and 40-60 cm) at each of the sampling dates. Soil samples for each depth were taken to the laboratory and calibrated using pressure plates at 0.3, 1, and 15 bars to determine soil matrix potential at each depth. Gravimetric samples were then calibrated to MPa matrix potential.

Internal water potential of each plant species was measured with a Sholander type pressure chamber (Waring and Cleary 1967) on 9 July, 27 July, 15 August, 6 September, and 3 October. Water potential was measured between 11:00 am and 2:00 pm MST. One stem from each winterfat plant and one leaf from each bluebunch and western wheatgrass plant were measured. Winterfat stems were used because its leaves were too small for the pressure chamber. Measurements were made with six replications for each combination on each level of soil disturbance.

Excavation of root transects and diagrams of root systems were made for each combination on each soil disturbance. Trenches were dug parallel to a line passing through the center of the two plants in the pair. Soil was removed from around roots in a transect 10 cm wide as described by Bohm (1979). Root systems were diagrammed as the roots were exposed. Two diagrams were made for each combination on each level of soil disturbance. Aboveground measurements included height, cover area and basal area of plants (except for western wheatgrass where the number of stems was noted). Measurements of root systems included maximum rooting depth, lateral spread of roots, number of axillary roots (for winterfat only), and depth, diameter and area of the zone of root concentration. Root diagrams of individual winterfat and bluebunch wheatgrass

plants also were made in an undisturbed control plot and used to help assess the differences due to soil disturbance.

Recarbonation of Retorted Oil Shale and Plant Uptake of Toxic Elements

Recarbonation of Retorted Oil Shale

A Lurgi-Ruhrgas (Lurgi) processed shale was used in this study. Raw oil shale for this process was provided from the Federal Prototype Oil shale Tract C-a. During processing, this raw shale was heated at 800°C. To examine the solubility of trace elements, 30 g of Lurgi retorted shale was equilibrated with 60 ml distilled H_2O for 24 hrs on a mechanical shaker. The suspensions were filtered and the clear filtrates were used to measure pH, EC, and trace elements. The pH was measured with a glass-calomel combination electrode and EC was measured with a conductivity bridge. The trace elements Fe, Mn, Zn, Cu, Mo, Cd, B, Ba, Cr, Sr, As, and Se were determined with inductively coupled plasma optical emission spectrometery (ICP-OES). Fluoride was measured with a specific F-ion electrode.

To lower pH of the retorted shale, a carbon dioxide pressure system shown in Figure 4 was developed. The reaction vessel consisted of a 30-cm diameter by 30-cm length PVC cylinder. A filter paper overlying a metallic screen was placed inside the cylinder to support the sample. The gas inlet was connected to a distilled water flask through which the entering CO_2 was water-saturated and bubbled into the sample. The gas outlet was connected to a mercury manometer to measure the pressure inside the cylinder. Approximately 300 ml of distilled H_2O was placed at the bottom of the PVC cylinder to provide moisture for recarbonation. Approximately 800 g of retorted Lurgi shale was spread over the filter paper. Before connecting the gas outlet tube to the manometer, $CO_2(g)$ from a tank was slowly bubbled through the distilled H_2O flask and the PVC cylinder. Approximately 0.40 bar pressure above atmospheric pressure was applied to the sample during recarbonation. Samples were removed after four days. A total of 3.0 kg of Lurgi retorted shale was recarbonated and placed into a plastic box.

Sufficient distilled H_2O was added to the recarbonated shale to prepare a saturated paste that was allowed to equilibrate with the air. Each day the pH of this saturated paste was measured using a combination glass-calomel electrode. After 14 days of equilibration the pH remained unchanged at 8.6. The recarbonated shale was then air-dried and used in a greenhouse experiment and for solubility measurements.

Plant Uptake of Toxic Elements

To measure the solubility of trace elements in the recarbonated samples, 15 g were equilibrated with 30 ml distilled H_2O for 24 hr on a mechanical shaker. The suspensions were filtered and clear filtrates were used to measure pH, EC, and trace elements as described above. To examine

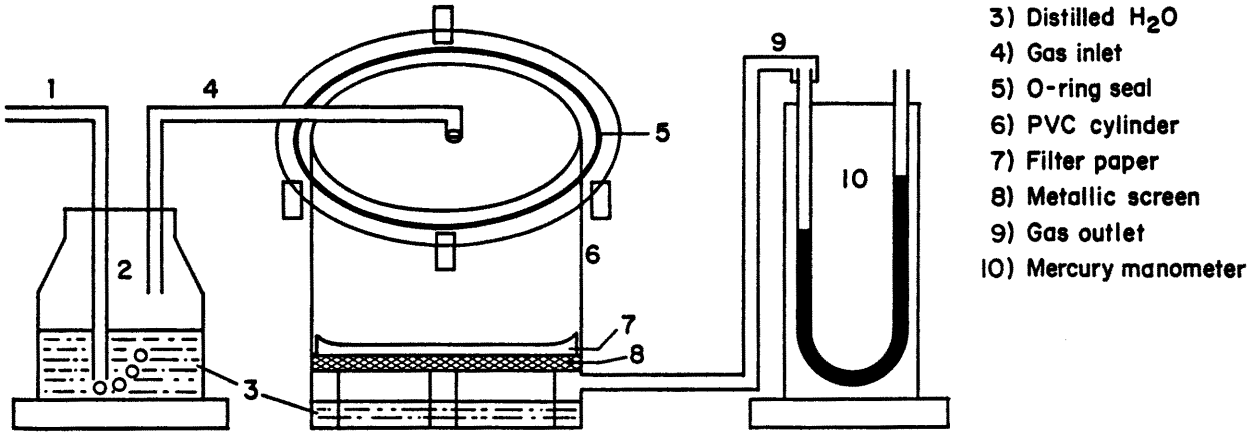

Figure 4. The $CO_2(g)$ pressure system used to recarbonate retorted shale.

the uptake of trace elements by plants growing on recarbonated shale, a greenhouse experiment was conducted using tall wheatgrass (Agropyron elongatum). Four treatments were included: (1) a control consisting of soil, (2) Lurgi retorted shale, (3) Lurgi retorted shale covered with soil (150 g of shale under 150 g of soil), and (4) recarbonated Lurgi shale covered with soil (150 g of recarbonated shale under 150 g of soil). The soil used in this experiment was a Weld loam with pH 6.7 and O.M. 0.74%. A total of 12 plastic pots each of 0.5 l capacity were used. Each pot received 300 g of recarbonated shale or soil, in three-fold replications using a completely randomized block design. The soil and shale materials were fertilized with N and P at a rate of 15 ppm N and 20 ppm P as $NH_4H_2PO_4$.

The soil and shale materials were moistened to saturation percentage with deionized water and allowed to air-dry to half saturation before seeding. Fifteen tall wheatgrass seeds were placed in each pot. After emergence, the seedlings were thinned to 10 plants per pot. Seeds did not germinate in the Lurgi retorted shale treatment. During the experiment, soil moisture was kept at field capacity by adding weighed amounts of distilled water. After 30 days of growth, another 15 ppm of N and 20 ppm of P was added to each pot. Plant tops were harvested after 70 days and were washed several times with dilute HCl and distilled H_2O to remove surface contaminants. The washed plant samples were dried at 70°C for 48 hr, weighed, and ground in a stainless steel Wiley-mill to pass a 20-mesh sieve. Plant samples were analyzed for trace elements after a nitric-perchloric acid digestion (Havlin and Soltanpour 1980), using inductively coupled plasma optical emission spectrometry (ICP-OES). Plant fluoride content was determined using ion selective technique (Villa 1979). The data were subject to analysis of variance to study the effect of recarbonation of retorted shales on the uptake of trace elements compared to unrecarbonated retorted shale.

RESULTS

RESOURCE AVAILABILITY

Nutrient Pools

Effect of Disturbance

Disturbance and fertilization generally increased the size of readily available nutrient pools, while either slightly reducing or having no measurable effect on total pool sizes.

Table 4 shows that disturbance significantly reduced the organic matter content in the top 10 cm of soil, while total N was not significantly affected. This indicates that the organic matter lost had a high C:N ratio and thus was relatively undecomposed. Most of this material was probably very near the soil surface and removed when the vegetation was scraped from the site. The fact that both organic matter and total N still decrease steadily with depth in the disturbed sites indicates that soil mixing was somewhat incomplete. Ideally, at least the upper two depth intervals should show the same contents.

Table 4. Effect of disturbance on soil nitrogen and organic matter. For a given depth, values followed by the same letter are not significantly different ($P \leq 0.05$).

Depth (cm)	Total N		Organic Matter	
	U[1]	D	U	D
	- - - - - - - - % - - - - - - - -			
0-10	.119 a	.112 a	2.2 a	1.8 b
10-20	.106 a	.106 a	1.9 a	1.6 a
20-40	.076 a	.088 a	1.3 a	1.3 a
40-60	.063 a	.068 a	1.0 a	1.0 a

1 U = Undisturbed; D = Disturbed.

Figures 4-7 show the effect of disturbance on more readily available nutrient pools. Although disturbance had no discernable effect on either NH_4^+ or mineralizable N pools, the NO_3^- pool increased continuously during the months following disturbance. During April and August following disturbance, the disturbed control

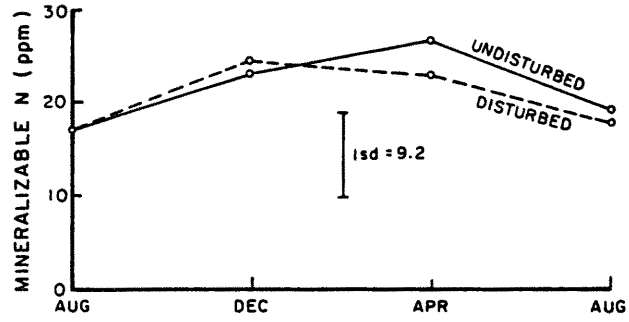

Figure 4. Mineralizable nitrogen concentration in the 0-60 cm soil layer of the disturbed and undisturbed control. LSD is for $P \leq 0.05$.

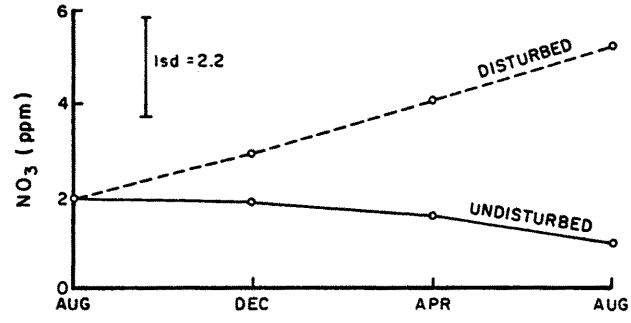

Figure 5. Nitrate concentration in the 0-60 cm soil layer of the disturbed and undisturbed control. LSD is for $P \leq 0.05$.

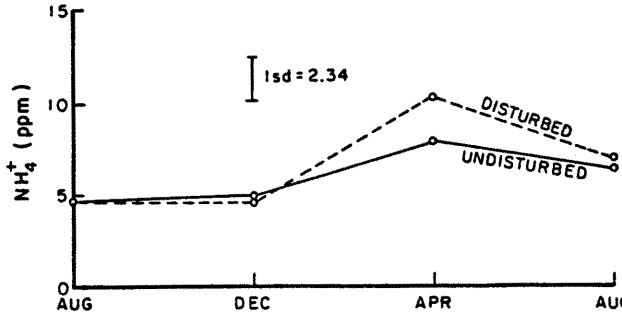

Figure 6. Ammonium concentration in the 0-60 cm soil layer of the disturbed and undisturbed control. LSD is for $P \leq 0.05$.

subplots had significantly higher NO_3^- pools than undisturbed subplots. This increase presumably occurred because populations of nitrifying microorganisms recovered rapidly and continued to produce NO_3^-, but since the disturbed sites remained relatively bare during the first year, vascular plants were not able to deplete the NO_3^- pool as they were on the undisturbed sites.

Disturbance had no significant effect on extractable P pools (Fig. 7). It may be that since P pools are highly dependent on chemical equilibrium relationships with the Ca minerals present, reduction of biological activities by disturbance has little lasting effect on extractable P pool sizes.

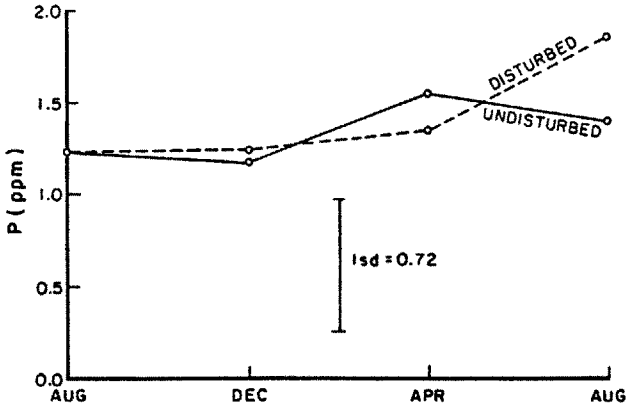

Figure 7. Phosphorus concentration (NH_4HCO_3-DTPA extractable) in the 0-60 cm soil layer of the disturbed and undisturbed control. LSD is for $P \leq 0.05$.

Effect of Fertilization

Fertilization had no significant effect on total N (Table 5). This is not surprising since the application of 100 kg N/ha should just barely increase total N by a detectable amount in the top 60 cm of soil. Fertilization significantly increased NO_3^- pools at all depths sampled. Nitrate concentrations were 2-4 times higher in fertilized subplots than in control subplots. Fertilization increased NH_4^+ pools primarily in the top soil layer. Because of its tendency to be adsorbed on cation exchange sites, NH_4^+ is considerably less mobile in soils than NO_3^-. In spite of its effect on soil mineral N pools, fertilization had no significant effect on mineralizable N.

Phosphorus pools were significantly increased by fertilization at all soil depths (Table 5). The limited mobility of P resulted in most of the fertilizer P remaining in the 0-10 cm layer, however, the P contents of the lower layers were also increased considerably.

Table 5. Effect of fertilizer on nitrogen and phosphorus abundance - Piceance Basin, 1985.

Depth (cm)	Treatment			
	Control	N	N+P	P
	TOTAL NITROGEN (%)			
0-10	.087	.110	.100	.104
10-20	.106	.106	.095	.104
20-40	.088	.097	.075	.083
40-60	.035	.066	.065	.068
	NO_3^- (ppm)			
0-10	5.68	22.77**	22.23**	4.82
10-20	5.25	11.73**	9.23*	4.05
20-40	3.83	8.50**	7.92*	3.82
40-60	4.85	12.27**	13.42*	4.88
	NH_4^+ (ppm)			
0-10	7.23	17.57***	18.43***	9.00
10-20	9.42	10.58	12.07	7.75
20-40	8.35	8.48	9.50	7.93
40-60	5.23	8.33	11.42*	5.23
	MINERALIZABLE N (ppm)			
0-10	28.0	34.9	30.5	26.4
10-20	30.0	30.6	25.8	26.0
20-40	22.1	24.2	20.0	23.7
40-60	15.4	16.3	20.6	15.9
	PHOSPHORUS (ppm)			
0-10	1.42	1.88	35.46***	41.16***
10-20	1.38	1.73	7.13**	6.12**
20-40	0.69	1.58	6.12**	3.69*
40-60	0.75	1.44	6.98*	6.37*

* Significantly different than the control ($P<.10$)
** Significantly different than the control ($P<.05$)
*** Significantly different than the control ($P<.01$)

Soil Moisture

Figures 8 and 9 show how soil water potentials change with depth during the summer on disturbed subplots (control, N, P, and N + P) and undisturbed control subplots. The soil surface of both disturbed and undisturbed sites showed the most variation over time. This is probably due to the interaction between strong evaporative forces and small precipitation events that occur during the summer months. In the subsoil, the disturbed sites showed almost no change in water potential, while the undisturbed sites showed a progressive decline in water potential from June through August. These results demonstrate that availability of the water resource was considerably higher throughout the profile on disturbed sites than on undisturbed sites.

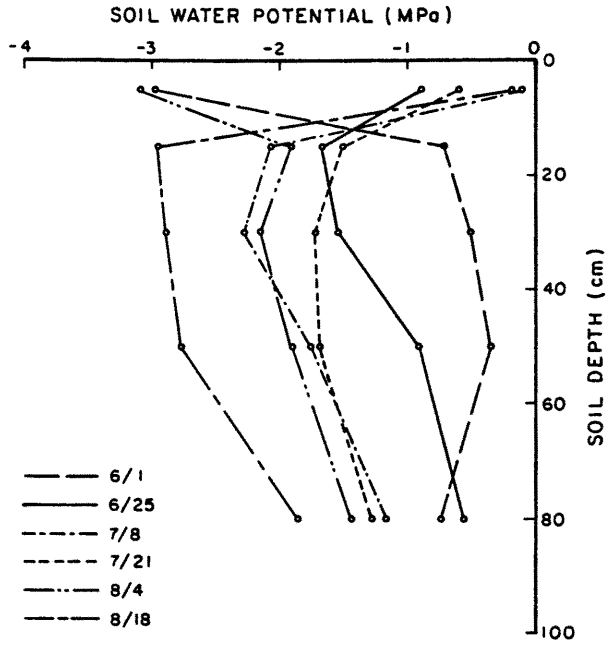

Figure 8. Mean soil water potentials in profiles of the undisturbed control treatments - Piceance Basin, June-August, 1985.

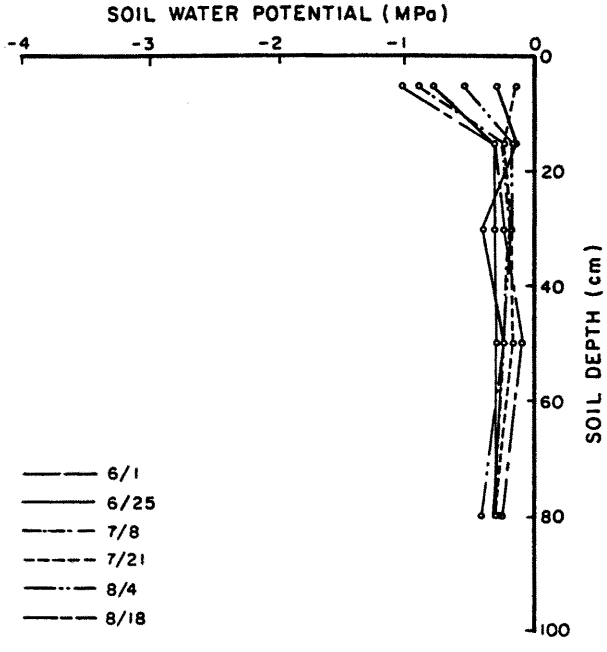

Figure 9. Mean soil water potentials in profiles of disturbed nonseeded treatments (control, N, P, and N + P) - Piceance Basin, June-August 1985.

Figure 10 shows more clearly how water potential changed on a variety of treatments throughout the growing season. While water potential in undisturbed and ruderal treatments decreased as the growing season progressed, disturbed nonseeded (control, N, P, and N + P), climax, and weeded treatments showed virtually no change in water potential. The ruderal treatment initially had water potentials equal to those in the other disturbed treatments. In late July, however, they began to decline and by mid-August they reached a minimum that was significantly lower than the other disturbed treatments. Water potentials on the undisturbed treatment were lower than all of the disturbed treatments throughout the measurement period and they continued to decline through the end of the season. The low water potential in early June on the undisturbed treatment was primarily a result of low water potentials in the 5 cm soil depths. At this time subsoil water potentials were very similar to those in the disturbed treatments. These results indicate that the late successional plant community on the undisturbed sites began using water earlier and continued using later in the growing season than any of the early successional communities. In addition, plants in the late successional community apparently can withdraw moisture at much lower soil water potentials than plants in the early successional community. Absolute minimum water potentials recorded for the undisturbed and ruderal treatments were -7.48 and -3.29 MPa, respectively, with both of these values from a 5 cm depth. Minimum subsoil water potentials were -5.32 MPa for the undisturbed treatment and -3.02 MPa for the ruderal treatment (both occurred at 30 cm depths).

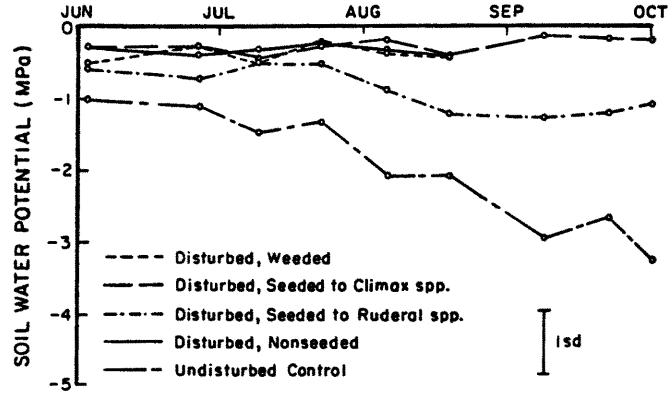

Figure 10. Soil water potentials averaged across all depths of the undisturbed control, disturbed nonseeded, ruderal, climax, and weeded treatments - Piceance Basin, 1985. LSD is for $P \leq 0.05$).

MICROFLORA STRUCTURE AND FUNCTION

Bacteria, Fungi, and Enzymatic Activity

Microbial responses to N and P fertilization are shown in Table 6. Nitrogenase activity (acetylene reduction) in plots that received N, with or without P, was significantly lower than for plots that were not fertilized with N. No other microbial responses were affected by the presence of N fertilizer. In addition, P fertilization had no effect on any microbial responses. However, an interaction between N and P in relation to nitrite oxidation potential was significant. On plots where N was added, the addition of P suppressed nitrite oxidation potential, while on plots that were not fertilized with N, the presence of P fertilizer apparently increased nitrite oxidation rates. Some microbial responses in plots used to measure fertilizer effects also exhibited a seasonal effect, with phosphatase activity and ammonium oxidation potential being significantly higher in the July sampling than in the June sampling.

The effects of fumigation on microbial responses were still evident nine months after the application of methyl bromide to selected plots (Table 7). Except for phosphatase activity, all microbial responses, especially nitrification, were significantly lower in the fumigated plots, compared to the non-fumigated plots. Zymogenous dehydrogenase, phosphatase, and nitrogenase (acetylene reduction) activity also were influenced by season, with higher values occurring in July than in June. In addition, the seasonal responses of zymogenous dehydrogenase, phosphatase, and nitrogenase activity were directly correlated with the soil water content, which was significantly higher in July than in June.

A preliminary study was initiated to evaluate the above- and belowground development in communities older than those growing on the Ecosystem Development Plot. Four high elevation sites (2250 m) and two low elevation sites (2040 m) disturbed by pipeline construction 2-27 years ago were compared with undisturbed native controls. Aboveground community properties that showed relationships to belowground features included percent litter cover, percent plant cover and percent relative cover of three life history classes (R, C-S-R, C-S). Above- and belowground results, summarized in Table 8, indicate that distinct relationships between above- and belowground responses are evident at both high and low elevation sites.

The major points of interest are the distinct direct relationships observed between increases in soil organic matter, phosphatase, and mineralizable N which occurred in relation to plant community age. In a similar manner, the older sites had higher rates of nitrification, which may be related

Table 6. Soil water content and nutrient cycling responses as affected by fertilization and sampling date, Piceance Basin, 1985. Treatment manipulation or sample date means with different letters within a parameter are significantly different ($P \leq 0.05$).

Parameter (unit)	Fertilizer Treatment				Sample Date	
	Nitrogen		Phosphorus		11 June	19 July
	Yes	No	Yes	No		
Soil water content ($g\ 100\ g^{-1}$)	14.1 a	13.7 a	14.5 a	13.3 a	12.8 b	15.0 a
Phosphatase ($\mu g\ PNP\ g^{-1}\ hr^{-1}$)	182.0 a	170.0 a	160.0 a	192.0 a	118.0 b	234.0 a
Autochthonous dehydrogenase (μg formazan g^{-1} 24 hr^{-1})	9.0 a	11.0 a	9.0 a	11.0 a	9.0 a	11.0 a
Zymogenous dehydrogenase (μg formazan g^{-1} 24 hr^{-1})	9.0 a	11.0 a	10.0 a	10.0 a	9.0 a	11.0 a
Acetylene reduction (nmoles $C_2H_4\ g^{-1}\ hr^{-1}$)	0.02 b	0.16 a	0.09 a	0.09 a	0.04 a	0.14 a
Ammonium oxidation potential ($\mu g\ N\ g^{-1}\ hr^{-1}$)	0.02 a	0.03 a	0.02 a	0.02 a	0.01 b	0.03 a
Nitrite oxidation potential ($\mu g\ N\ g^{-1}\ hr^{-1}$)	0.03 a	0.02 a	0.02 a	0.02 a	0.01 a	0.04 a

Table 7. Soil water content and nutrient cycling responses as affected by fumigation and sampling date, Piceance Basin, 1985. Treatment manipulation or sample date means with different letters within a parameter are significantly ($P \leq 0.05$).

Parameter (unit)	Treatment		Sample Date	
	Fumigated	Control	11 June	19 July
Soil water content ($g\ 100\ g^{-1}$)	13.9 a	13.4 a	13.1 b	14.2 a
Phosphatase (μg PNP $g^{-1}\ hr^{-1}$)	172.0 a	195.0 a	129.0 b	237.0 a
Autochthonous dehydrogenase (μg formazan g^{-1} 24 hr^{-1})	7.0 b	10.0 a	8.0 a	8.0 a
Zymogenous dehydrogenase (μg formazan g^{-1} 24 hr^{-1})	9.0 b	12.0 a	8.0 b	14.0 a
Acetylene reduction (nmoles $C_2H_4\ g^{-1}\ hr^{-1}$)	0.06 b	0.19 a	0.06 b	0.25 a
Ammonium oxidation potential (μg N $g^{-1}\ hr^{-1}$)	0.01 b	0.03 a	0.01 a	0.02 a
Nitrite oxidation potential (μg N $g^{-1}\ hr^{-1}$)	0.001b	0.02 a	0.001a	0.03 a

Table 8. Above- and belowground responses, natural plant community development at high and low elevation sites - Piceance Basin, 1985.

Parameter	High elevation site, yrs				Low elevation site, yr	
	2	4	27	Native	23	Native
pH	8.36	7.72	7.35	6.70	8.54	7.13
% moisture	24.8	25.8	27.7	31.6	23.1	19.8
% organic matter	0.95	1.49	1.04	2.66	0.53	0.93
Phosphatase (μg PNP g $soil^{-1} hr^{-1}$)	193.0	467.0	690.0	781.0	70.0	377.0
Mineralizable N (μg NH_4-N g^{-1} soil)	47.4	63.7	62.7	91.9	29.2	46.1
Nitrification						
NH_4-N μg $soil^{-1} hr^{-1}$)	0.14	0.51	0.33	0.54	0.04	0.26
NO_3-N μg $soil^{-1} hr^{-1}$)	0.1	0.23	0.16	0.22	0.05	0.16
Dehydrogenase (μg formazan g $soil^{-1}$ 24 hr^{-1}						
Control	37.1	17.7	11.5	13.6	13.7	3.8
Glucose	25.3	25.89	9.8	15.4	13.9	8.0
Litter cover (%)	2	0	47	63	6	4
Total Plant Cover (%)	19	20	60	67	38	20
Relative cover of R species	85	10	0	0	1	0
Relative cover of C-S-R species	10	35	7	7	87	35
Relative cover of C-S species	1	20	72	70	7	44

to the increased level of soil organic matter or the decreased pH in these older soils. In contrast, the dehydrogenase activities showed trends of decreasing activities in the older sites. These results contradict, in part, our previous findings (Biondini et al. 1985; Klein et al. 1985) as well as other published information by Pancholy and Rice (1973), Kapustka and Rice (1976), and Uhl and Jordan (1984) and may be related to the fact that some of the areas that were sampled have been heavily grazed. The reduction of dehydrogenase activity on old successional plots, however, was consistent with our previous findings and Titlyanova's (1982) findings of a reduction in soil biological activity as the ecosystem approaches maturity.

Rhizosphere Development

Chemical Responses

Some chemical properties of the treatment plots are given in Table 9. In general, P, NH_4^+-N, NO_3^--N, EC, and sodium absorption ratios (SAR) were lower in the control plots compared to the fertilized plots. Cheatgrass contained higher Na, Ca, Mg, K, P, organic matter, EC, pH, and SAR values in its rhizosphere than western wheatgrass had in its rhizosphere. Soil N values (NH_4^+-N, NO_3^--N and total N), however, were higher in the rhizosphere of western wheatgrass compared to the rhizosphere of cheatgrass.

With fertilization, some soil properties (particularly Ca, K, NH_4^+-N, total N, and organic matter) were higher in the rhizosphere than outside the rhizosphere of both plant species. The rhizosphere zone of cheatgrass, compared to the nonrhizosphere zone, appears to have higher Ca, Mg, K, P, NH_4^+-N, NO_3^--N, total N, organic matter, and EC values, and a lower SAR. In the control plots, there appears to be no differences in most chemical parameters in both plant types between rhizosphere and nonrhizosphere zones.

Microbial Population Dynamics

Microbial populations generally increased in the fertilizer treatments compared to the control (Table 10). Cheatgrass tended to have higher populations, especially in the rhizosphere, a response which was largely independent of fertilizer presence.

Western wheatgrass had lower levels of fungal propagules (Table 10) but a higher fungal diversity than occurred in the rhizosphere of cheatgrass in the control plots (Table 11). In contrast, more fungal propagules, but a lower fungal diversity occurred in the rhizosphere of cheatgrass compared to the rhizosphere of western wheatgrass. Similar rhizosphere fungi found in both species in the control plots included Acremonium, Aspergillus, Chaetomium, Fusarium, Mortierella, Pencillium, and Trichoderma. Western wheatgrass contained a Gliocladium sp., in its rhizosphere, where this organism is completely absent from the rhizosphere of cheatgrass. Fertilization generally increased the diversity of fungal genera in both plant type rhizospheres compared to the rhizospheres in the control treatments. Fungal genera isolated from the rhizospheres of both species growing in the control and in the fertilized plots show high percent similarities of 82 and 84%, respectively (Table 12).

Bacterial community structural responses in the rhizosphere were evaluated using API procedures during 1985, to provide information on bacterial diversity without the intensive labor requirements involved in replica plating procedures.

These procedures, which involved measurements of 23 characters for the bacterial isolates from each of these samples, indicated that distinct shifts in the functional characteristics of the bacterial populations had occurred in relation to plant type and fertilization. The major changes are summarized in Table 13. Fertilization and plant type effects were distinctly evident, especially related to hydrogen sulfide production and urea hydrolysis (decreased with fertilizer presence). With fertilization, the frequency of utilization of carbohydrates shifted, suggesting that major changes in the structural-functional characteristics of the microbial communities had occurred in relation to the field site treatments used in this study.

Nutrient Cycling

The enzymatic analyses, which were carried out as a part of this study, indicated that cheatgrass tended to have higher dehydrogenase, nitrogenase, urease, and phosphatase activities in its rhizosphere compared to the rhizosphere of western wheatgrass (Table 14). A distinct fertilizer effect also was evident; cheatgrass showed increased C flow in the rhizosphere (dehydrogenase) and decreased nitrogen fixation potential with N and P present.

Table 9. Soil chemical characteristics in the rhizosphere and nonrhizosphere of Agropyron smithii (AGSM) and Bromus tectorum (BRTE) growing in a one-year-old disturbed soil - Piceance Basin, 1985.

Treatment	Soil Chemical Properties											
	Na	Ca	Mg	K	P	NH_4+-N	NO_3--N	Total N	O.M.	EC	pH	SAR
	- - - - - - - - - - - - mg g^{-1} - - - - - - - - - - - -								g kg^{-1}	dS m^{-1}		
Control												
AGSM												
R[1]	11.5	68.8	8.8	1.2	2.1	4.7	5.1	1273	18.1	0.47	7.43	0.35
NR	12.9	72.8	9.6	1.6	2.4	4.1	6.8	1136	16.0	0.48	7.61	0.38
BRTE												
R	13.8	87.3	9.9	2.7	3.2	3.6	4.7	1119	19.1	0.54	7.61	0.38
NR	22.3	135.1	16.4	4.3	2.9	4.1	6.8	1187	16.4	0.91	7.59	0.49
N + P												
AGSM												
R	71.3	63.7	16.4	3.1	30.5	5.5	17.7	1043	15.7	0.87	7.51	2.08
NR	119.8	57.3	16.8	2.0	49.4	5.1	28.6	1018	13.5	1.10	7.61	3.59
BRTE												
R	38.0	246.2	27.4	6.7	57.9	5.3	58.7	1052	19.7	1.81	7.44	0.62
NR	53.6	127.3	16.4	2.0	40.8	3.3	27.1	849	13.5	1.09	7.62	1.19

1 R = rhizosphere (0 to 7 cm from the root stem); NR = nonrhizosphere (30 cm from the root stem).

Table 10. Microbial populations in the rhizosphere and nonrhizosphere of Agropyron smithii (AGSM) and Bromus tectorum (BRTE) growing in a one-year-old disturbed soil - Piceance Basin, 1985.

Treatment	Aerobic Heterotrophic Bacteria	Streptomyces	Ammonium Oxidizers	Fungal Propagules
Control				
AGSM				
R[2]	10.14 c[3]	6.87 a	1.32 d	5.49 b
NR	7.04 e	6.74 a	2.02 c	4.42 c
BRTE				
R	11.25 a	7.11 a	2.59 ab	6.51 a
NR	7.30 de	6.80 a	1.73 cd	4.49 c
N + P				
AGSM				
R	10.48 b	6.97 a	2.75 a	6.54 a
NR	7.58 d	6.63 b	2.01 cd	4.71 c
BRTE				
R	11.08 ab	7.13 a	2.89 a	6.30 a
NR	7.54 d	6.76 a	2.56 a	4.71 c

1 All values are log base 10 per gram dry weight soil.

2 R = root region (rhizosplane + rhizosphere); NR = nonrhizosphere (30 cm from root stem).

3 Means within the same column followed by the same letter are not significantly different at the 0.05 level by the LSD test.

Table 11. Distribution and relative density of fungal genera in the rhizosphere and nonrhizosphere of Agropyron smithii (AGSM) and Bromus tectorum (BRTE) growing in a one-year-old disturbed soil - Piceance Basin, 1985.

Fungal Groups[1]	Control				N + P			
	AGSM		BRTE		AGSM		BRTE	
	R[2]	NR	R	NR	R	NR	R	NR
Absidia	3	6	1	5	6	5	3	13
Acremonium	10	0	5	0	6	1	28(2)	27
Alternaria	1	1	0	0	0	0	1	0
Arthrinium	0	1	0	0	4	2	0	0
Aspergillus	8(2)†	24(3)	7(2)	4	4(3)	4(2)	8(3)	24(3)
Chaetonium	5	19	16	11	20	13	17	7
Chrysosporium	0	20	0	0	35	0	81	5
Cladosporium	0	0	0	0	2	0	0	0
Cunninghamnella	0	1	0	0	0	0	0	0
Curvularia	1	1	0	0	0	0	0	0
Fusarium	15	16	55	24	17	15	46	23
Gliocladium	28	35	0	2	15(2)	14	8	11
Mortierella	18	9	5	0	6	4	7	4
Mucor	0	0	0	0	1	0	2	0
Mycelia sterilia	0	0	0	0	3	0	4	0
Myrothecium	1	8	13	0	1	7	1	8
Penicillium	100(5)	103(4)	179(3)	301(3)	115(4)	150(4)	140(4)	230(4)
Phoma	0	0	0	0	2	0	0	3
Rhizopus	0	0	0	1	0	2	1	0
Scholecobasidium	1	0	0	0	0	0	0	0
Trichoderma	22	6	42	38	9	28	21	10
Trichurus	0	0	0	0	0	0	0	0
Total isolates	213	250	323	386	246	245	360	365
Total genera	13	14	9	8	16	12	15	12
Diversity	0.77	0.84	0.61	0.37	0.82	0.63	0.80	0.64
Evenness	0.69	0.73	0.64	0.41	0.68	0.58	0.68	0.59

1 Relative density of isolates from ten 1:1000 soil dilution plates.

2 R = rhizosphere (0 to 7 cm from the root stem); NR = nonrhizosphere (30 cm from the root stem).

† Number in parentheses = number of fungal species identified.

Table 12. Sorensen's presence community coefficient for fungal populations in the rhizosphere and nonrhizosphere of Agropyron smithii (AGSM) and Bromus tectorum (BRTE) growing in a one-year-old disturbed soil - Piceance Basin, 1985.

	Community Coefficient (%)							
	Control				N + P			
	AGSM		BRTE		AGSM		BRTE	
	R[1]	NR	R	NR	R	NR	R	NR
Control								
AGSM								
R	82	82	67		69	80	79	80
NR		70	64		73	77	76	77
BRTE								
R			71		72	86	75	86
NR					58	80	70	70
N + P								
AGSM								
R						79	84	86
NR							82	83
BRTE								
R								82
NR								

1 R = rhizosphere (0 to 7 cm from the root stem); NR = nonrhizosphere (30 cm from the root stem).

Table 13. Frequency of selected positive character occurrences in Bromus tectorum (BRTE) and Agropyron smithii (AGSM) rhizosphere bacterial populations, in response to fertilization - Piceance Basin, 1985.

Parameters	Positive			
	BRTE		AGSM	
	NF†	F	NF	F
Lysine decarboxylase	56	47	40	36
Citrate utilization	42	53	29	49
H_2S production	2	11	0	13
Urea hydrolysis	60	38	51	44
Voges Proskauer Acetoin production	58	49	44	38
Gelatin hydrolysis	64	76	76	49
Glucose utilization	16	2	0	7
Mannitol utilization	9	13	9	27
Inositol utilization	2	7	2	13
Rhamnose utilization	22	4	0	9

† NF = nonfertilized; F = fertilized.

Table 14. Enzyme activities in the rhizosphere and nonrhizosphere of Agropyron smithii (AGSM) and Bromus tectorum (BRTE) growing in a one-year-old disturbed soil - Piceance Basin, 1985.

Treatment	Enzyme Activity				
	Dehydrogenase	Nitrogenase	Urease	Phosphatase	Invertase
	ug Formazan $g^{-1}d^{-1}$	nm $C_2H_4 g^{-1}d^{-1}$	ug NH_4^+-N $g^{-1}d^{-1}$	ug PNP $g^{-1}d^{-1}$	mg Glucose $g^{-1}d^{-1}$
Control					
AGSM					
R[1]	30 c[2]	6556 a	4489 b	1545 a	15.6
NR	22 d	187 c	4658 b	1199 b	12.1
BRTE					
R	43 b	8214 a	5261 b	1689 a	13.8
NR	24 cd	166 c	4634 b	1379 a	11.4
N + P					
AGSM					
R	24 cd	5021 ab	5400 b	1647 a	14.4
NR	18 de	50 d	3296 c	1412 a	10.7
BRTE					
R	84 a	1856 b	7232 a	1512 a	11.5
NR	16 e	47 d	1628 d	892 b	10.0

1 R = rhizosphere (0 to 7 cm from the root stem); NR = nonrhizosphere (30 cm from root stem).

2 Means within the same column followed by the same letter are not significantly different at the 0.05 level by LSD test.

Saprobic Fungi

Fungal isolates were sorted into 224 presumptive taxa. For the three major treatments of the Ecosystem Development Plot, viz. undisturbed, disturbed, and fumigated, there were, respectively, 99, 209, and 193 taxa. Since 1984 soil samples were taken before application of fertilizers or seedling establishment, there were 4 replicates of the undisturbed subplots, 28 replicates of the disturbed subplots, and 12 replicates of the fumigated subplots. Included in Table 15 is the relative density (isolates of a given species as a percentage of the total isolates) of taxa which exceeded 1%. Using Sorensen's index, undisturbed vs. disturbed = 73%, disturbed vs. fumigated = 60%, and undisturbed vs. fumigated = 53%.

Table 15. Relative density of major fungal taxa in Undisturbed (n=4), Disturbed (n=28) and Disturbed Fumigated (n=12) plots - Piceance Basin, 1984.

Species	Percent Occurrence		
	Undisturbed	Disturbed	Disturbed Fumigated
Aspergillus a	1.9		
Aspergillus h			1.8
Aspergillus n	1.9	3.2	3.1
Chrysosporium sp.	2.9	1.6	4.6
Cladosporium c	2.2	2.7	5.1
Cladosporium h	2.2	2.0	2.5
Fusarium d			1.1
Fusarium l	1.7		
Fusarium t			2.6
Mortierella sp.	1.7	3.0	2.3
Myxotrichum sp.	1.2		
Penicillium a	1.7	1.9	1.4
Penicillium c	2.4	1.2	2.8
Penicillium d	1.7	5.9	10.2
Penicillium g	1.9		
Penicillium h		1.5	1.5
Penicillium l	5.3	2.8	
Penicillium k	2.9	1.9	
Penicillium m	2.9	1.2	
Penicillium n	1.9		
Penicillium t			1.8
Penicillium w		1.2	
Penicillium x	4.1	1.1	
Penicillium hh	1.7		
Penicillium mm	2.2		
Penicillium ddd		1.1	
Phoma sp.	3.2	4.8	8.8
Sterile a	1.5	2.5	3.8
Sterile b	3.2	1.6	3.8
Sterile c			1.6
Sterile d	1.7	1.4	1.9
Sterile g	2.7		
Sterile h	3.4	2.4	2.6
Sterile j	2.7	1.6	2.1
Sterile l		1.6	
Sterile m	1.7	1.4	
Sterile u			1.2
Sterile w	2.4	2.4	
Sterile ee	2.7	1.2	1.5
Trichoderma h.		1.9	1.5

Clearly the saprobic fungi change in response to disturbance (Table 15). Although the Sorensen's index values are relatively high among the three treatments, there are several obvious changes in the population structure. Most obvious is the rapid rise in the dominance of Penicillium d (presumptive species d) and Phoma sp. in both the disturbed and fumigated subplots, and the decline and elimination of Penicillium l and x from the undisturbed to the disturbed to the fumigated subplots.

With the exception of Penicillium h, found in the disturbed and fumigated subplots, all other taxa occurred in all three treatments. However, several species had a relative denisty of less than 1%. Penicillium h was not detected in the undisturbed subplots.

Based on a limited analysis (approximately 800 of the 5280 cultures) of the saprobic fungi present in the plots in 1985 there does not appear to be major significant changes in the taxa present. Penicillium l and x are still the dominant species present in the undisturbed subplots, with sterile forms and Phoma sp. contributing to the dominants. In 1985 samples there appear to be significantly more Fusarium, Myrotheicium, and Mortierella species present than found in 1984.

In both the disturbed and fumigated subplots Penicillium d continues to dominate, with a major contribution by Chrysosporium and Phoma sp., and both species of Cladosporium. Because of the limited number of cultures analyzed to date, it is impossible to determine if there are effects of fertilization that can be correlated with changes in the saprobic fungal population.

Mycorrhizal Inoculum Potential (MIP)

The initial relative population levels of VA mycorrhizal fungi present in the Ecosystem Development Plot, including the MIP values of the fumigated subplots prior to fumigation (values in parentheses), in 1984 are summarized in Table 16. Table 17 gives the relative population levels of VA mycorrhizal fungi present in the plots in 1985.

In 1984 the undisturbed subplots had a mean MIP value of 28.4. We infer that this value is indicative of the MIP of the disturbance subplots prior to disturbance. After disturbance, MIP values decreased significantly in all of the subplots in 1984 (Table 16). Disturbed subplots had an average MIP value of 9.6; this value is in agreement with MIP values of the fumigated subplots which were disturbed in an identical manner prior to fumigation (Table 16). It is important to note that the disturbed subplots were effectively equivalent when the soil samples were taken since no plants had become established in 1984.

Fumigation with methyl bromide in 1984 effectively reduced the MIP values of the fumigated subplots. These plots had a mean MIP value of 0.8 which is significantly less than that found on the disturbed subplots and significantly less than the pre-fumigation mean MIP value of 7.6. No correlation between root length and percent colonization

Table 16. Mean root length and mycorrhizal inoculum potential (MIP) values of subplots - Piceance Basin, 1984.

	Root Length (cm)	MIP†
Undisturbed	864	28.4a
Disturbed		
P	674	10.1 b
N	759	10.3 b
N and P	748	9.0 b
Weeded	765	7.8 b
Ruderal	803	10.7 b
Control	768	9.0 b
Fumigated		
Control	830	0.6 c (8.0)*
Ruderal	821	0.7 c (8.0)
Climax	872	1.0 c (6.7)

† Columns with different letters indicate MIP values are significantly different at P = 0.05.

* Prefumigation MIP values of the fumigated soil treatments are given in parentheses.

Table 17. Mean root length and mycorrhizal inoculum potential (MIP) values of subplots - Piceance Basin, 1985.

	Root Length (cm)	MIP†
Undisturbed	863	38.0 a
Disturbed		
P	918	4.6 b
N	834	5.2 b
N and P	836	1.9 c
Weeded	*	*
Ruderal	*	*
Control	889	7.6 b
Fumigated		
Control	793	0.3 d
Ruderal	820	0.2 d
Climax	738	0.3 d

† Columns with different letters indicate MIP values are significantly different at P = 0.05.

* Data for the weeded and ruderal plots have not been analyzed.

by mycorrhizal fungi in the bioassay plants was evident when data for each of the three major treatments (undisturbed, disturbed, and fumigated) are examined separately.

The significant reduction in MIP values in the disturbed and fumigated subplots for 1984 is repeated in 1985 (Table 16). The 1985 data indicate that there has been an increase in the MIP value for the undisturbed subplots compared to 1984. However, this increase may not be significant when all the bioassay plants have been analyzed.

Data for 1985 (Table 16) suggest that there is a further reduction in MIP values on the disturbed subplots when MIP values for 1985 are compared with values for 1984. Because a larger total number of samples have been analyzed for the disturbed subplots for 1985 than for the undisturbed subplots, we are reasonably confident that the 1985 data represent an actual reduction in MIP values. However, this apparent reduction needs confirmation with analyses of all samples.

Mycorrhizal Dependency and Life History Strategies

Using Grime's (1984) life history categories as a base for comparison of percentage mycorrhizal and non-mycorrhizal species of semiarid soils, we found a strong correlation between the percentage of non-mycorrhizal species present in a category and the degree to which that category approaches the Ruderal (R) strategy (Table 18 and Fig. 11).

Table 18. Correlations of the percentage of mycorrhizal plant species present on semiarid soils and their life history strategy.

Category	%M+
1. Ruderals	25
2. Competitive-Ruderals	55
3. Stress-tolerant ruderals	83
4. C-S-R	91
5. Competitors	100
6. Stress-tolerant competitors	100
7. Stress tolerator	100

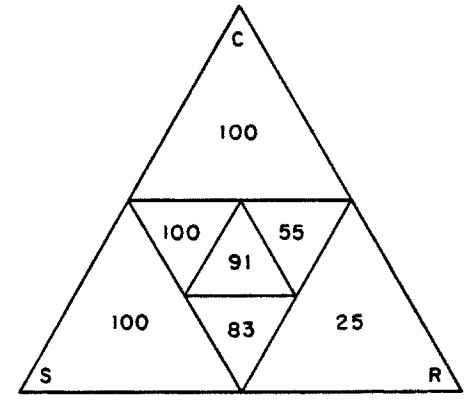

Figure 11. Percent mycorrhizal species in each life history strategy (strategies arranged as in Figure 3). R = ruderal; C = Competitor; S = Stress tolerator.

These data support the concept that semiarid ruderal species are primarily non-mycorrhizal. If non-mycorrhizal ruderal species are replaced in succession in a sequence suggested by Grime (1984) (Fig. 3), the probability that the replacement species will be a mycorrhizal species increases. Further, there is a relative increase in the percentage of mycorrhizal species as the stress-tolerant (S) category is approached (Table 17). Indeed, it appears that competitors (C) and beyond (C-S and S) will be mycorrhizal (Table 18). The mycorrhizal status of various semiarid species categorized into life history strategies is given in Appendix Table 3.

VASCULAR PLANT COMMUNITY STRUCTURE AND RESOURCE USE

Propagule Supply

Seed Rain

Three patterns involving seed rain on paired disturbed and undisturbed field succession study plots were found. Differences occurred in the seed rain of ruderals (small, non-competitive annuals); in the dispersal of pappus-bearing, or plumed members of the Asteraceae; and in the dispersal of certain species abundant in the landscape such as sagebrush and perennial grasses.

Large numbers of ruderals occurred in the seed rain of some disturbed sites, but only if large numbers of these plants were growing on the disturbed site. For example, approximately 50 seeds per m^2 of Lappula redowskii and Polygonum aviculare were trapped in one 2-week collection period in August. Few ruderal seeds were dispersed to nearby undisturbed sites, however, as these two species dispersed only about 3 seeds per m^2 to an undisturbed site only 5 m away. Further, few seeds dispersed to disturbed sites were derived from non-ruderal species common in the adjacent undisturbed sites, and ruderals were not consistently abundant in the seed dispersed to disturbed sites. Thus, disturbed and undisturbed sites differed in their seed rain, but disturbed sites also differed from one another in the kinds and quantities of seeds falling on them.

The pappus or plume of some fruits and seeds are thought to facilitate wind carry. In our samples several such species were represented in the seed rain but only dandelion (Taraxacum officinale) occurred in high numbers. In one collection from the first two weeks in July 280 seeds per m^2 were trapped. The number of species of this group dispersed to a site was correlated with the number of species already growing on the site. In a similar way, rabbitbrush is pappus-bearing and more aggressive in early establishment than sagebrush, perhaps because of greater dispersal ability.

Big sagebrush, although ubiquitous in the Piceance Basin landscape and growing within meters of our seed traps, was essentially absent from seed rain samples. Dispersal might occur later than our last trap collection in early October which would account for the lack of sagebrush seeds. However, little establishment of big sagebrush into the Intensive Study Site (ISS) from adjacent areas indicates big sagebrush dispersal is sometimes restricted in the Piceance Basin. Grasses, in general, also were conspicuously absent from the seed rain (the one exception is cheatgrass, a weedy annual). This was true even for sites that supported a substantial grass cover.

Seed rain on the new study plots was sampled by traps placed in the non-fumigated ruderal and climax seeded subplots and the undisturbed control of the Ecosystem Development Plot. Cheatgrass seeds dominated the ruderal subplot (73 seeds per m^2 trapped from 20 July to 13 August), but were not found in the climax seeded subplot during any collection period were present in low numbers in the undisturbed control. Plant species growing in the treatment subplots (with the exception of cheatgrass) were not represented in the seed rain of the undisturbed control indicating no or meager short distance dispersal.

Kochia (Kochia scoparia) and Russian thistle plants were common in the Ecosystem Development Plot, but only a few seeds of the former and none of the latter were trapped from seed rain. We do not conclude, however, that no or few seeds were dispersed. Because we observed many seeds of these species, we conclude that our traps were not effective in catching these species.

Seed Bank

Seed bank samples were collected from disturbed sites of different age and associated undisturbed vegetation. Results for 1984 generally parallel and support results from the seed rain study and 1985 collections are currently being analyzed.

Seed bank results are summarized in Table 19 for four pipelines of various ages and three undisturbed sites in the Piceance Basin. The number of seeds per m^2 present varies from 57 in disturbed sagebrush vegetation near the Intensive Study Site to 749 in a three-year-old pipeline. Neither disturbed nor undisturbed sites had exclusively low or high seed densities; one disturbed and one undisturbed site had densities less than 100 while another disturbed-undisturbed pair had the two highest seed densities.

Dicots substantially outnumbered monocots (grasses) on all sites. Monocots attained their highest seed density in undisturbed vegetation. This was true even though the two youngest pipelines supported many seeded grasses.

Often the discrepancies in total propagules present among sites were related to of the abundance of only one or two species. For example, large numbers of Lappula redowskii and Polygonum aviculare occurred in the two youngest pipelines, and big sagebrush attained high density in one undisturbed site.

Table 19. Number of seeds per square meter in the soil bank of selected disturbed and undisturbed sites - Piceance Basin, 1984. The sites indicated by A-M correspond to the sites with the same designation in Figure 14.

	Field Succession Site and Age of Disturbance						
	A 1 yr	D 3 yrs	G 22 yrs	H 26 yrs	J Native	L Native	M Native
MONOCOTS							
Agropyron smithii		9.5			3.2	9.5	
Poa pratensis						3.2	
Unknown monocots	10.1	12.6		6.3	9.5	37.9	28.4
DICOTS							
Artemisia tridentata		3.2		110.6	158.0	3.2	22.1
Chrysothamnus nauseosus	2.5						3.2
Cirsium sp.		3.2					
Collensia parvifolia		6.3	3.2	3.2	12.6		
Erigeron eatoni	15.2		12.6	98.0	3.2		
Gutierrezia sarothrae		3.2	9.5				
Lappula redowskii		233.8					
Penstemon sp.		3.2					
Physaria actuifolia		3.2		6.3	60.0		
Pinus edulis							3.2
Polygonum aviculare	68.3	369.7			3.2		
Senecio multilobatus	7.6		3.2				
Taraxacum officinale	5.1	69.5			6.3		
Trifolium gymnocarpon					9.5		
Unknown dicots	27.8	31.6	28.4	47.4	60.0	37.9	47.4
TOTAL PLANTS	136.5	748.9	56.9	271.7	325.5	94.8	104.3

There were large numbers of ruderal seeds in the youngest pipelines, but few ruderals on old pipelines and undisturbed vegetation. Species represented by large numbers in the seed bank were growing on the site, but species growing on the site were not necessarily well represented in the seed bank. In addition, our observations indicated that species absent from a site but growing nearby are poorly represented in the seed bank. This even occurred with species that one would expect to be highly vagile, e.g., big sagebrush (small seeds) and pappus-bearing seeds.

One generalization, as with seed rain, is that there is much variation among sites in the seed stored in the soil as well as variation within a species in their ability to populate the soil of a particular site. For example, big sagebrush can attain high seed densities in undisturbed and disturbed sites where it dominates the vegetation (158 and 110 seeds per m^2 in sites J and H), yet may be poorly represented in the seed bank (3 seeds per m^2 in site L).

The seed bank of the Ecosystem Development Plot in the first season after construction was meager, with fumigated subplots having virtually no viable seeds. However, the non-fugmiated subplots also had a severe reduction in the numbers of propagules in the soil compared to undisturbed controls, most likely due to soil mixing during the plot construction.

Aboveground Net Primary Production

Effect of Disturbance

Table 20 shows the effect of disturbance on total NPP and NPP of the various plant groups on the Ecosystem Development Plot. By the end of the first growing season following disturbance, there was no significant difference in total NPP between disturbed and undisturbed communities. There were, however, a number of significant differences in NPP among plant groups. Disturbance resulted in significantly higher production by annuals and biennials, and significantly lower perennial herbaceous and perennial woody evergreen production. The disturbed sites showed greatest production by annuals and biennials, with the herbaceous perennial and woody classes showing progressively lower NPP. Apparently increased woodiness is accompanied by slower rates of establishment or growth. Production on the undisturbed sites showed a bimodal distribution, with perennial woody evergreen species and perennial herbaceous species having the greatest production.

Disturbed sites also had significantly greater production by nonmycorrhizal species, and significantly lower production by mycorrhizal perennials. Although the disturbed sites have lower mycorrhizal inoculum potential (see section on Microflora

Table 20. Effect of disturbance, fertilization, fumigation, and seeding on net primary production (NPP) in g m^{-2} of various plant groups on the Ecosystem Development Plot - Piceance Basin, 1985.

	Disturbance Effects		Fertilization Effects			
	D[1]	U	Control	N	N + P	P
Annual and biennials	107.57**	2.32	104.37	163.04	89.51	73.38
Perennial herbaceous species	1.36	23.04**	1.96	2.13	0.71	0.66
Perennial woody deciduous species	0.13	0.74	0.41	0.00	0.00	0.10
Perennial woody evergreen species	0.00	82.76***	0.00	0.00	0.00	0.00
Nonmycorrhizal species	98.81**	0.59	96.03	148.60	84.96	65.63
Mycorrhizal annuals	8.80	1.73	8.34	14.44	4.63	7.78
Mycorrhizal perennials	1.43	105.60***	2.34	2.12	0.54	0.71
Mycorrhizal perennial N-fixers	0.04	0.94	0.03	0.01	0.10	0.02
Stress tolerators (S)	0.00	4.13*	0.00	0.00	0.00	0.00
Competitors (C)	0.00	0.00	0.00	0.00	0.00	0.00
Ruderals (R)	14.79**	1.87	10.38	25.70	11.99	11.10
C-S	0.00	82.74***	0.00	0.00	0.00	0.00
C-R	93.05**	0.62	94.93	137.34	77.53	62.40
S-R	0.33	1.76	0.67	0.26	0.10	0.30
C-S-R	0.89	17.73**	0.75	1.87	0.61	0.35
TOTAL ABOVEGROUND NPP	109.07	108.86	106.74	165.16	90.22	74.14

	Fumigated Effects		Seeding and Transplanting Effects		
	F[2]	N	Control	Ruderal	Climax
Annual and biennials	192.08**	119.78	146.14 a	309.06 a	0.00 b
Perennial herbaceous species	1.25	2.61**	1.09	1.20	3.50
Perennial woody deciduous species	0.06	0.16	0.28	0.04	0.02
Perennial woody evergreen species	1.16	5.14	0.00 b	0.00 b	9.45 a
Nonmycorrhizal species	191.84***	110.70	141.83 a	299.55 a	0.00 b
Mycorrhizal annuals	0.14	9.08**	4.31 ab	9.51 a	0.00 b
Mycorrhizal perennials	2.48	7.82**	1.36 b	1.12 b	12.97 a
Mycorrhizal perennial N-fixers	0.00	0.09*	0.02	0.12	0.00
Stress tolerators (S)	0.00	0.00	0.00	0.00	0.00
Competitors (C)	0.00	0.00	0.00	0.00	0.00
Ruderals (R)	1.02	10.28	6.52 ab	10.41 a	0.00 b
C-S	1.24	5.37	0.00 b	0.00 b	9.93 a
C-R	191.51**	110.07	140.12 a	299.66 a	0.00 b
S-R	0.08	0.28	0.42	0.05	0.08
C-S-R	0.70	1.70*	0.47 b	0.18 b	2.96 a
TOTAL ABOVEGROUND NPP	194.56**	127.69	147.52 ab	310.31 a	12.97 b

[1]U = Undisturbed; D = Disturbed
[2]F = Fumigated; N = Nonfumigated

* Significantly different ($P < 0.10$)
** Significantly different ($P < 0.05$)
*** Significantly different ($P < 0.01$)

a or b Within a functional group, values followed by the same letter are not significantly different ($P < 0.05$)

Structure and Function), it is premature to conclude that lower production by mycorrhizal species is a direct result of reduced mycorrhizal inoculum. Nonmycorrhizal species may simply have faster or more efficient dispersal mechanisms which result in greater plant densities, or under the resource abundant conditions present on the disturbed sites they may have faster growth rates than mycorrhizal species with or without mycorrhizal associations. These possibilities must be eliminated before we can conclude that reduced mycorrhizal inoculum on disturbed sites is limiting production by mycorrhizal species.

The analysis using plant life history strategies (Grime 1979) showed that disturbance had significant effects on plants with particular strategies. Disturbance significantly increased production by ruderal and C-R strategists, but significantly reduced production by stress tolerators, C-S, and C-S-R strategists. Figure 12 shows the relative production by plants belonging to various plant strategies for the recently disturbed sites and the undisturbed big sagebrush community. Disturbance effectively reduced the number of strategies present, and only allowed survival of species having strategies with ruderal characteristics. Presumably, successional processes in the future will result in an increase in strategy diversity, and a general shift away from species having ruderal strategies and toward species with more stress tolerator components.

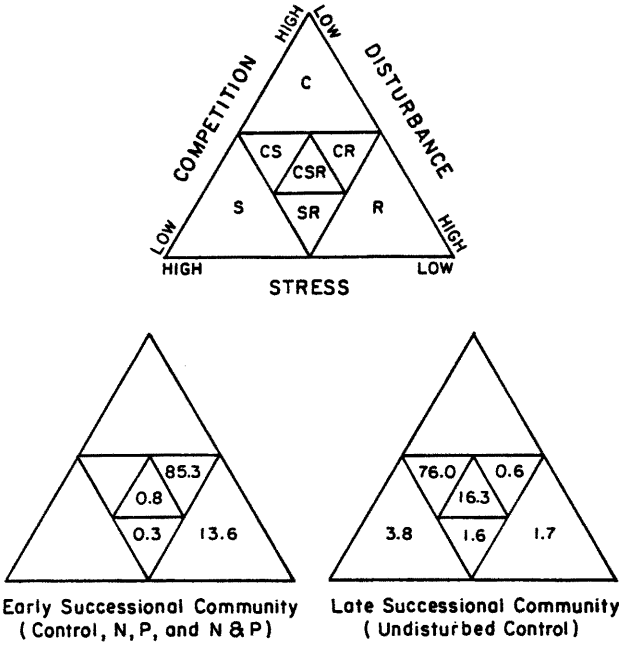

Figure 12. Relative aboveground production (%) by various plant strategies in early and late successional communities - Piceance Basin, 1985. Strategy definitions and triangular ordination are according to Grime (1979).

During the first growing season, fertilization treatments had no significant effects on either total NPP or NPP by specific plant groups. Apparently the amount of N and P on the disturbed sites was sufficient without fertilization to allow maximum production. In the future as plant establishment increases and nutrient resources become less abundant due to plant uptake, the plant community may show an increasingly greater response to fertilization.

Table 20 shows the effect of fumigation on the various plant groups. Fumigation resulted in significantly higher production by annuals and biennials but significantly lower production by perennial herbaceous species. Although perennial woody species also showed slightly lower production on fumigated sites, these differences were not significant.

Fumigation resulted in significantly higher production by nonmycorrhizal species and significantly lower production by all three groups of mycorrhizal species. It appears that this supports the hypothesis that establishment and production by mycorrhizal species on disturbed sites is dependent on the presence of mycorrhizal inoculum (since fumigation drastically reduced mycorrhizal inoculum potential). Unfortunately, fumigation also destroyed much of the vascular plant propagule bank and thus adversely effected propagule supply. Table 21 lists the plant species whose presence was most affected by fumigation. These results were obtained from species richness data and show plant species that were present on two or more blocks in the nonfumigated treatment but were never present in the fumigated treatment. Although there is only one nonmycorrhizal species on the list (Chenopodium berlandierei), there are many putatively facultatively mycorrhizal species which may have been able to establish without the presence of mycorrhizal inocula. It is interesting to note that almost a third of these species regenerate each year from belowground plant parts (bulbs or rhizomes). This leads us to suspect that the primary effect of fumigation was to eliminate plant species that were highly dependent for regeneration on plant propagules remaining in the soil.

These results suggest that fumigation significantly affected only two plant strategies. C-R strategists showed increased production while C-S-R strategists showed reduced production with fumigation.

Effect of Seeding, Transplanting, and Weeding

The purpose of these treatments was to rapidly establish early and late successional vascular plant communities on disturbed sites and to determine their effect on rates of microbial succession. The seeding, transplanting, and weeding was fairly effective in establishing the desired communities with significant differences between ruderal and climax treatments in NPP for most of the functional forms being evident (Table 20). In almost all cases where the differences between ruderal and climax treatments were significant, the control treatments were intermediate.

Table 21. Plant species present on more than one block in unfumigated treatments but never present in fumigated treatments (unless seeded) - Piceance Basin, 1985.

	Annual or Perennial
Agropyron dasystachyum	P
Allium textile	P
Astragalus convallerius	P
Chaenactis douglassi	A
Chenopodium berlandieri	A
Crepis accuminata	P
Crepis occidentalis	P
Haplopapous nuttalii	P
Ipomopsis congesta	P
Koeleria cristata	P
Linum lewisii	P
Mentzelia nuda	P
Phlox muscoides	P
Senecio multilobatus	P
Sphaeralcea coccinea	P
Zygadenus venenosus	P

Total aboveground NPP was significantly lower on the climax treatment than on the ruderal treatment. This is because the species seeded on the climax treatment had much slower rates of establishment and growth. Climax treatments had significantly lower annual and biennial production than ruderal treatments but significantly higher production by perennial woody evergreen species (almost exclusively big sagebrush) than either ruderal or control treatments. Climax seeding treatments had significantly lower production by nonmycorrhizal species or mycorrhizal annuals than ruderal treatments but significantly higher production by mycorrhizal perennials than either ruderal or control treatments. Climax seeding treatments also had significantly lower production by ruderals or C-R strategists than ruderal seeding treatments but significantly higher production by C-S and C-S-R strategists than either ruderal or control treatments. Figure 13 shows the distribution of strategies for the ruderal and climax treatments. When Figure 13 is compared to Figure 12 it can be seen that the climax treatment is more similar in strategy distribution to the undisturbed control than to either the control or ruderal treatments.

Belowground Root Standing Crop

The undisturbed control and ruderal treatments had significantly higher root biomass than the disturbed control, while the climax treatment was intermediate (Table 22). Because of the low sampling intensity used (eight 10 cm diameter cores were collected per treatment), these results should be considered tentative. Plant densities on disturbed control subplots were quite low and thus spatial distribution of root biomass was probably very heterogeneous. Under these conditions, the low sampling intensity may have resulted in an underestimation of root standing crop on the control treatment.

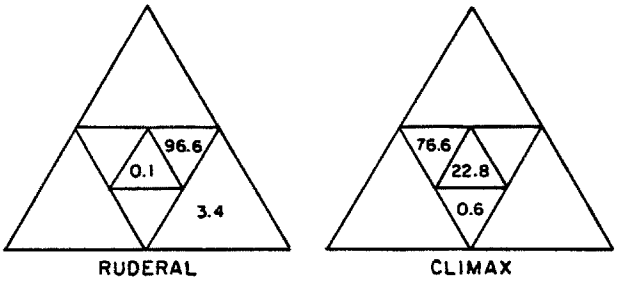

Figure 13. Relative aboveground production (%) by various plant strategies in ruderal and climax treatments - Piceance Basin, 1985. Key to triangle positions as in Figure 3.

Table 22. Belowground root standing crop - Piceance Basin, 1985. Values followed by the same letter are not significantly different ($P \leq 0.05$)

	$g\ m^{-2}$
Undisturbed control	188 a
Ruderal seeded subplots	185 a
Climax seeded subplots	120 ab
Control (non-seeded)	96 b

Testing the Facilitation Model

Table 23 lists the perennial species found in greater than trace amounts in the undisturbed big sagebrush community. Next to each species is the total number of plants that were established on the weeded subplots during 1985. Only six of the 30 species present in the undisturbed community failed to establish on the weeded subplots during the first growing season. Of those six species, four became established on other nonweeded subplots. The only species that completely failed to establish on the disturbed sites in 1985 were Juniperus osteosperma and Chrysothamnus depressus. Together, these two species comprised less than 3% of the total aboveground biomass of the predisturbance community. As a result, this preliminary set of data does not support the facilitation model of Connell and Slatyer (1977).

Table 23. Number of individuals of perennial plant species that became established on weeded subplots (2000 m^2 total) during the first growing season - Piceance Basin, 1985.

Scientific Name	# Plants
SHRUBS AND TREES	
Artemisia tridentata tridentata	2
Juniperus osteosperma	-
Chrysothamnus depressus	-
Gutierrizia sarothrae	10
Chrysothamnus viscidiflorus	11
Ceratoides lanata	+
Opuntia polycantha	+
GRASSES AND SEDGES	
Koeleria cristata	25
Agropyron dasystachium	3
Agropyron smithii	423
Stipa comata	212
Poa secunda	19
Sitanion hystrix	14
Poa fendleriana	+
Oryzopsis hymenoides	342
Agropyron inerme	+
Carex sp.	80
Agropyron desertorum	7
FORBS	
Phlox muscoides	9
Cryptantha flavoculata	59
Erigeron engelmannii	48
Sphaeralcea coccinea	696
Machaeranthera sp.	18
Trifolium gymnocarpon	44
Astragalus purshii	2
Hedysarum boreale	16
Senecio multilobatus	21
Phlox longifolia	1
Penstemon fremonti	5
Ipomopsis aggregata	1

\+ Indicates plants did not become established on weeded treatments but did become established on other disturbed treatments during the first growing season.

\- No plants became established.

Life History Strategies

Grime (1979) predicts that different life history strategies attain importance in different stages of succession. In general, ruderals (R) dominate early in succession; competitors (C) and generalists (C-S-R) become important later; and stress tolerators (S) characterize late successional stages (Figure 3). To test this prediction, percent relative cover of species in each life history strategy was summed and plotted for communities of associated undisturbed vegetation (Figure 14), which can be taken to represent a successional sequence. Ruderals (R) do indeed attain greatest importance in the youngest pipeline communities with C-S-R species becoming important later, only to be superseded by C-S species in the older pipelines and undisturbed communities (Figure 14). The only apparent anomaly in these results is the bimodal distribution of the C-S species. However, the C-S peak over the three-year-old community is attributed to high cover of Agropyron cristata, a C-S species seeded to this site after pipeline construction.

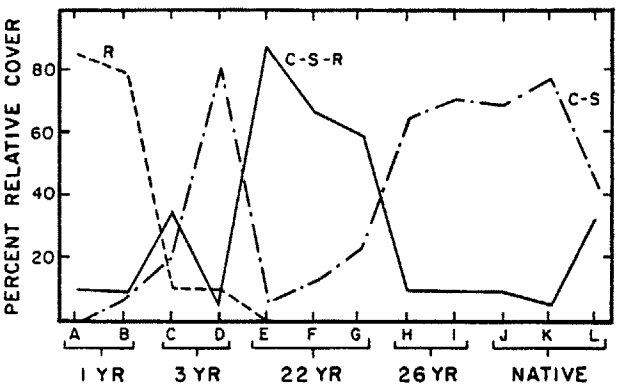

Figure 14. Percent relative cover of three life history strategies in communities developed on pipelines of different age and associated undisturbed vegetation - Piceance Basin, 1985. R = ruderal; C-S = competitive-stress tolerator; C-S-R = competitive-stress tolerator-ruderal.

The plant life history strategies not plotted in Figure 14 seldom exceed 20% relative cover but still are consistent with the predicted pattern. For example, the C and S-R species peak at about 23% cover in the 26-year-old communities while the C-R species have highest cover in the one- and three-year-old communities. Stress tolerators only occur on the oldest pipelines and the native communities.

Additional analyses also support Grime's prediction. Communities developing after other kinds of disturbances, as well as on other pipelines, were analyzed as above by computing the relative percent cover of each life history strategy. Relative cover values plotted in the triangular arrangement (Figure 15) of the life history strategies again reveal that younger communities tend to have higher values in the ruderal corner or central part of the triangle while older disturbed and native communities have higher values on the stress tolerator side of the triangle.

Notice, however, that there is some variation in the display of life history strategies among young communities. For example, the seven- and nine-year-old abandoned roads (Fig. 15 - e,f) have more ruderals than the five-year-old pipelines (Fig. 15 - c). Perhaps this is because the abandoned roads were not seeded while the pipelines were seeded with non-ruderal species.

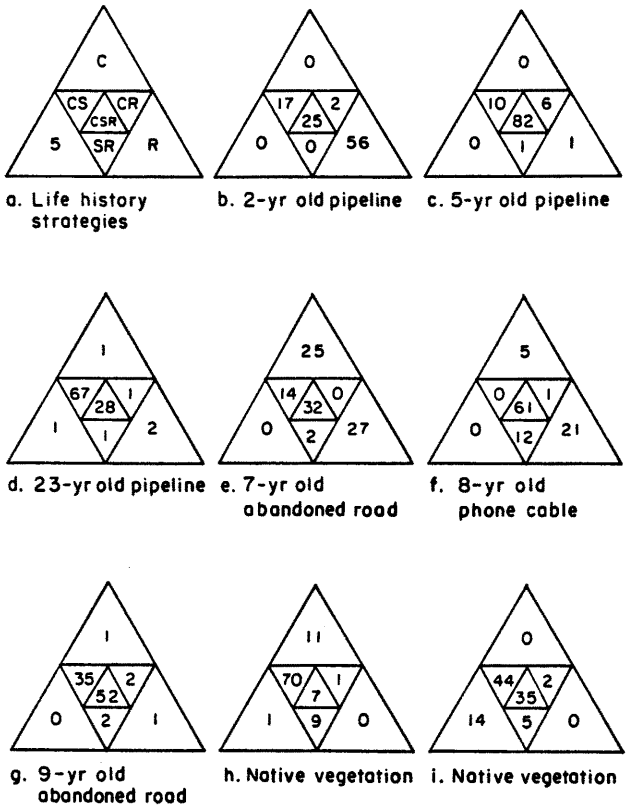

Figure 15. Relative percent cover of life history strategies in selected disturbed communities and undisturbed vegetation - Piceance Basin, 1985. R = ruderal; C = competitor; S = stress-tolerator.

Competition for Water and Allocation of Fixed Energy by Late Successional Species

Bluebunch Wheatgrass

Carbon allocation to different plant parts as affected by watering frequency is given in Table 24. Carbon allocation as a response to inter- and intraspecific competition and their interactions with water stress are shown in Figure 16 with significance differences in Figure 17.

Table 24. Carbon allocation (g/plant) to different plant parts of bluebunch wheatgrass under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Shoot	1.85	1.17	0.63
Root	1.24	0.73	0.36
Total Biomass	3.09	1.90	0.99

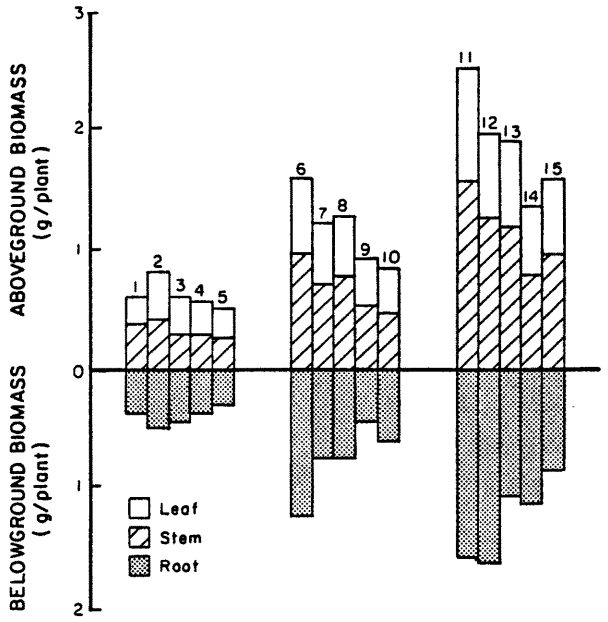

Figure 16. Above- and belowground biomass of the 15 treatment groups (see Table 2) of bluebunch wheatgrass. Significant differences between all possible pairs of means for the 15 treatment groups are shown in Figure 17.

Average biomass production decreased with increasing water stress (Table 24). Bluebunch wheatgrass plants in the wet and dry regimes produced significantly more root biomass when grown with a shrub than when grown with a grass (Fig. 17). Except for the wet regime, bluebunch wheatgrass grown with either shrub had no significant differences in biomass allocation to different compartments and their root:shoot ratios were different in the wet regime. There were no significant differences between biomass of bluebunch wheatgrass within a water regime when grown with either grass species. Niche response was derived from canonical analysis. Mean canonical points with 95% confidence limits for the biological data are shown in Figure 18.

Average soil moisture at the end of the drying cycle is shown in Table 25. Soil moisture in the bluebunch wheatgrass-winterfat combinations in the wet and dry regimes was significantly greater than with other combinations. In the moist regime, bluebunch wheatgrass-western wheatgrass combination had significantly less soil moisture than did other combinations. Mean stomatal conductance values are shown in Table 25. The stomatal conductance of bluebunch wheatgrass was not affected by co-species within a water regime except that in the wet regime, it was 25% more in bluebunch wheatgrass grown with winterfat from one of the plants in monoculture.

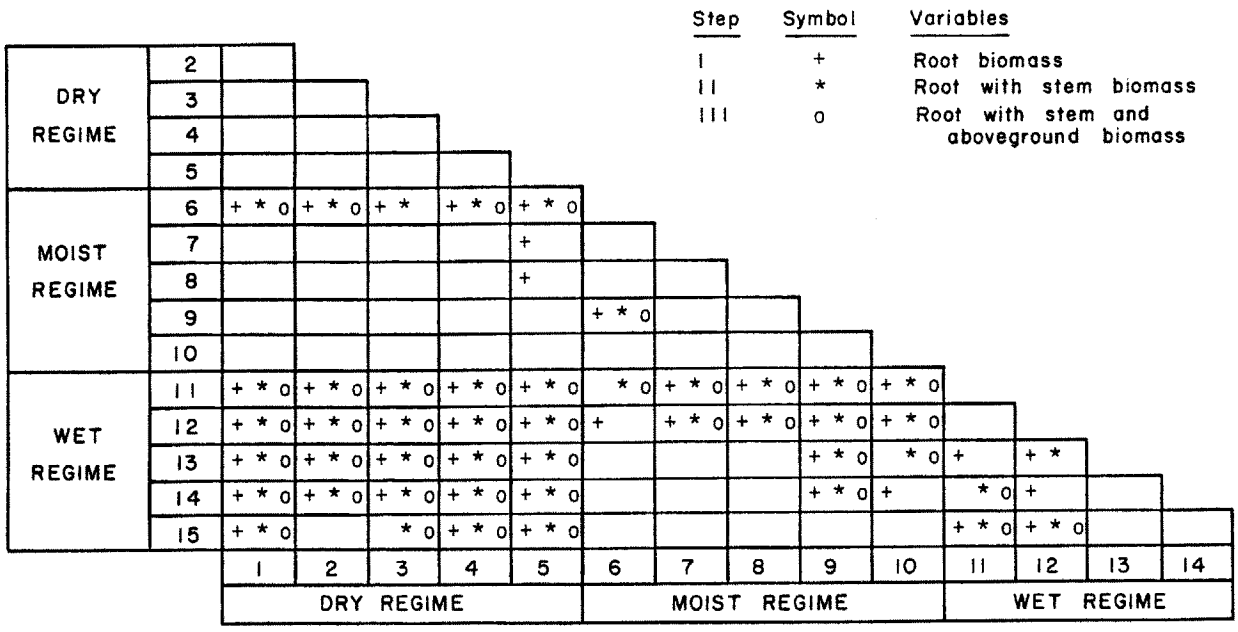

Figure 17. A matrix of biological variables which separate the 15 treatment groups (numerals) (see Table 2) of bluebunch wheatgrass in a stepwise discriminant analysis. In order to find which group is different from other groups, locate the intersecting row and column of interest. A blank box at the intersection of a row and column indicates that the two groups are not significantly different from each other ($P \leq 0.05$). If the box has one or more symbols, then the symbols indicate which variables are significant in separation between groups.

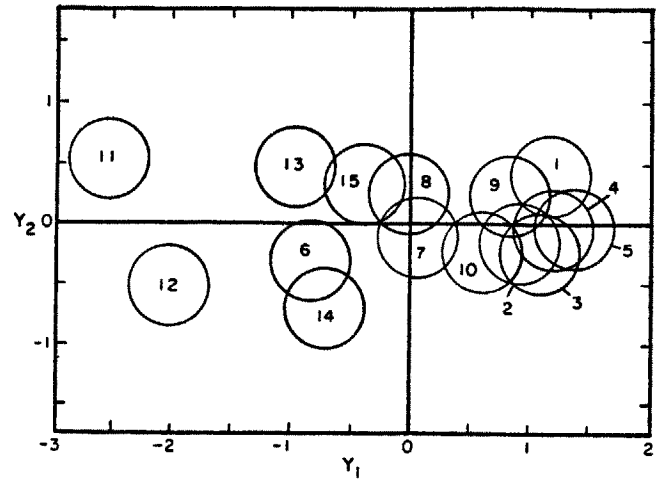

Figure 18. Biological 'niche response' of 15 treatment groups (see Table 2) of bluebunch wheatgrass shown as mean canonical points with 95% confidence limits. Overlap of circles along any one axis indicates no significant difference between those treatment groups along that gradient. Aboveground biomass and stem:root ratio correspond, respectively to the Y_1 and Y_2 axes of the biological niche response plane.

Table 25. Average soil moisture and stomatal conductance for bluebunch wheatgrass under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Soil moisture (%)	5.20	3.93	3.53
Stomatal Conductance (mmol m^{-2} s^{-1})	0.72	0.64	0.72

Western Wheatgrass

Carbon allocation to different plant parts as affected by watering frequency is given in Table 26. The data on carbon allocation as a response to inter- and intraspecific competition and their interactions with water stress are shown in Figure 19 and the statistical analyses are shown in Figure 20.

Regardless of combination, average biomass of different components decreased with increasing water stress (Table 26). Average biomass production was more when western wheatgrass was grown with either shrub than with a grass within the wet and dry regimes (Fig. 20). However, in the moist

Table 26. Carbon allocation (g/plant) to different plant components of western wheatgrass under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Shoot	1.10	0.73	0.52
Leaf	0.98	0.76	0.55
Root	1.87	0.97	0.57
Total Biomass	3.95	2.5	1.64

regime, the difference was only in root biomass. Within a water regime, there were no differences in the effects of combination with either shrub on biomass allocation of western wheatgrass. Similarly, there were no differences in carbon allocation due to combination with either grass. Intraspecific differences were significant only in the moist regime and were reflected by changes in stem:leaf ratio. Niche response analysis is shown in Figure 21.

Data on average soil moisture after the drying cycle is shown in Table 27. There were no significant differences in the soil moisture between different combinations within the dry and wet water regimes. However, in the moist regime, western wheatgrass plants grown with either shrub had higher moisture than other combinations.

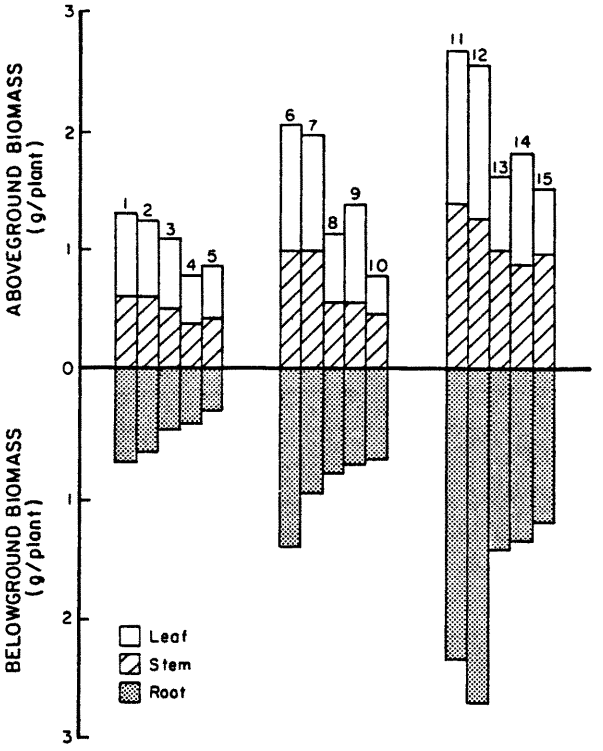

Figure 19. Above- and belowground biomass of the 15 treatment groups (see Table 2) of western wheatgrass. Significant differences between all possible pairs of means for the 15 treatment groups are shown in Figure 20.

Step	Symbol	Variables
I	+	Stem biomass
II	*	Stem with root biomass
III	o	Stem with root and leaf biomass

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
DRY REGIME	2														
	3														
	4														
	5														
MOIST REGIME	6	+ *	+ *	+ * o	+ * o	+ * o									
	7	+	+	+ * o	+ * o	+ * o									
	8						+ * o	+ * o							
	9						+ * o	+ * o							
	10						+ * o	+ * o		0					
WET REGIME	11	+ *	+ * o	+ * o	+ * o	* o	+ *	+ * o	+ * o	+ * o	+ * o				
	12	+ *	+ * o	+ * o	+ * o	* o	* o	* o	+ * o	+ * o	+ * o				
	13	+	+ * o	+ * o	+ * o	* o			+ * o	+ * o	+ * o	+ * o	* o		
	14			+ *	+ *	* o					+ *	+ * o	+ * o		
	15	+	+	+ *	+ *	* o			+ *	+ *	+ * o	+ * o	+ * o		
			DRY REGIME				MOIST REGIME					WET REGIME			

Figure 20. A matrix of biological variables which separate the 15 treatment groups (numerals) (see Table 2) of western wheatgrass in a stepwise discriminant analysis. In order to find which group is different from other groups, locate the intersecting row and column of interest. A blank box at the intersection of a row and column indicates that the two groups are not significantly different from each other ($P \leq 0.05$). If the box has one or more symbols, then the symbols indicate which variables are significant in separation between groups.

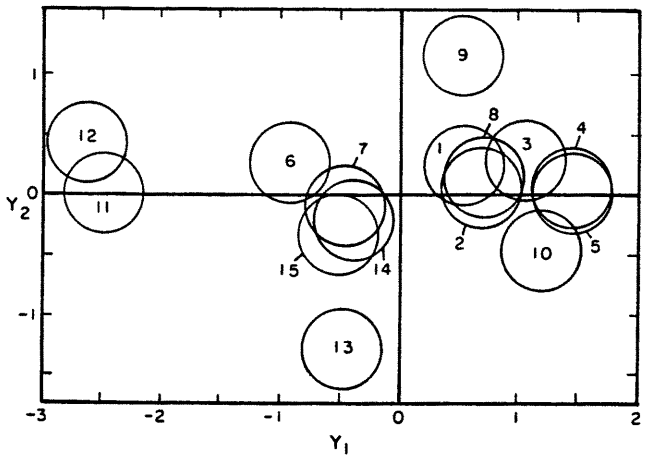

Figure 21. Biological 'niche response' of 15 treatment groups (see Table 2) of western wheatgrass shown as mean canonical points with 95% confidence limits. Overlap of circles along any one axis indicates no significant difference between those treatment groups along that gradient. Aboveground biomass and stem:root ratio correspond, respectively to the Y_1 and Y_2 axes of the biological niche response plane.

Table 27. Average soil moisture and transpiration for western wheatgrass under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Soil moisture (%)	5.2	3.3	3.1
Transpiration ($\mu g\ cm^{-2}\ s^{-1}$)	49	42	35

Average transpiration rates across all treatments are shown in Table 27. Inter- and intraspecific transpiration rates of western wheatgrass plants were significantly different in some combinations within a water regime.

Big Sagebrush

Carbon allocated to different plant parts as affected by watering is given in Table 28. Leaf and stem biomass were significant in separating treatment groups. Average shoot and root biomass production of the 15 treatment groups (see Table 2 for an explanation) is shown in Figure 22 with significant biological differences between 15 treatment groups are given in Figure 23.

Table 28. Carbon allocation (g/plant) to different plant parts of big sagebrush under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Shoot	0.28	0.20	0.20
Leaf	0.29	0.19	0.12
Root	0.13	0.11	0.10
Total Biomass	0.70	0.50	0.42

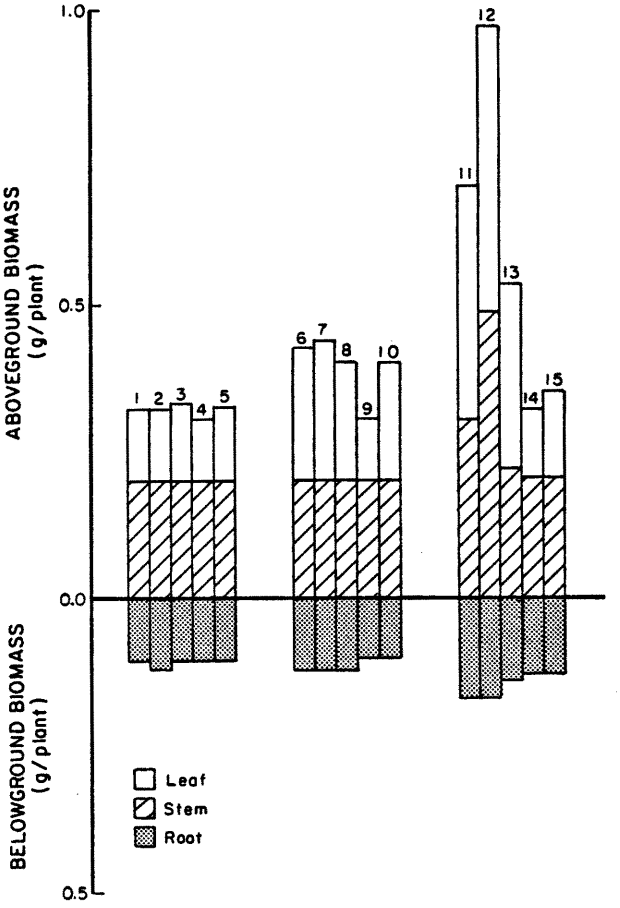

Figure 22. Above- and belowground biomass of the 15 treatment groups (see Table 2) of big sagebrush. Significant differences between all possible pairs of means for the 15 treatment groups are shown in Figure 23.

Regardless of the effect of combination, average biomass production decreased with increasing water stress (Table 28). Biomass of big sagebrush plants grown with either shrub in the wet regime was significantly more than biomass of plants grown with either grass (Fig. 23). There were strong intraspecific differences in allocation of carbon to different plant components in monoculture in the wet and moist regimes. One of

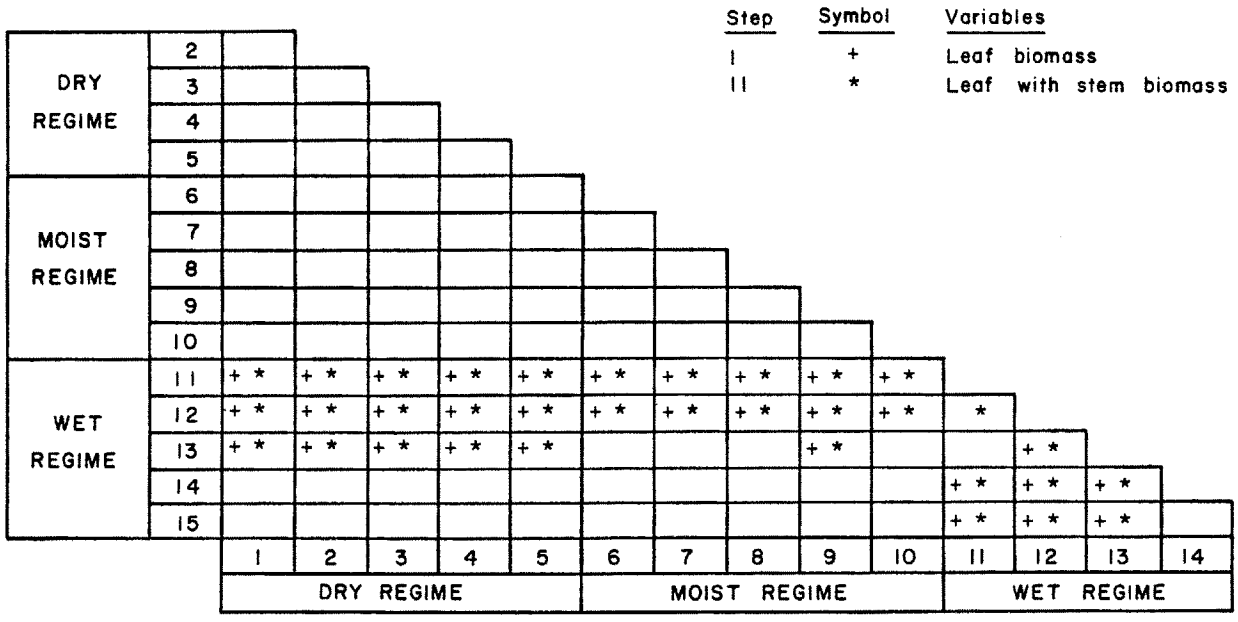

Figure 23. A matrix of biological variables which separate the 15 treatment groups (numerals) (see Table 2) of big sagebrush in a stepwise discriminant analysis. In order to find which group is different from other groups, locate the intersecting row and column of interest. A blank box at the intersection of a row and column indicates that the two groups are not significantly different from each other ($P < 0.05$). If the box has one or more symbols, then the symbols indicate which variables are significant in separation between groups.

the dominant individuals in monoculture had significantly more leaf biomass than big sagebrush plants grown with western wheatgrass. There were no significant differences in sagebrush biomass in other combinations in the moist regime and among all plants in the dry regime. Niche response analysis is shown in Figure 24.

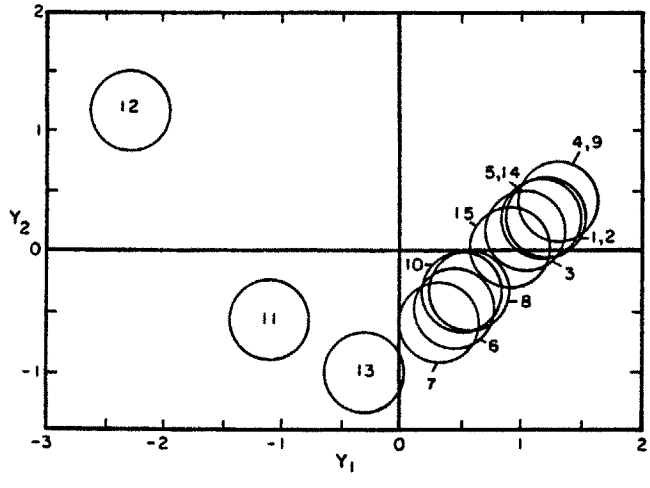

Figure 24. Biological 'niche response' of 15 treatment groups (see Table 2) of big sagebrush shown as mean canonical points with 95% confidence limits. Overlap of circles along any one axis indicates no significant difference between those treatment groups along that gradient. Aboveground biomass and stem:root ratio correspond, respectively to the Y_1 and Y_2 axes of the biological niche response plane.

Average soil moisture across all treatments is shown in Table 29. Soil moisture at the end of drying cycle in sagebrush combinations with either shrub was more than the combinations when big sagebrush was grown with either grass in the wet and dry regimes. In the moist regime, soil moisture of big sagebrush-winterfat combination was greater than other combinations. Data on average transpiration rates are shown in Table 29. Plants in pure culture had significant differences in transpiration and stomatal conductance only in the moist regime. Transpiration rate in big sagebrush plants grown with winterfat in the wet and moist regimes was greater than that for big sagebrush in other combinations. In the dry regime, in contrast, transpiration rate of big sagebrush plants grown with western wheatgrass was lower than big sagebrush in all other combinations.

Table 29. Average soil moisture, transpiration, and stomatal conductance for big sagebrush under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Soil moisture (%)	6.1	4.3	3.8
Transpiration ($\mu g\ cm^{-2}\ s^{-1}$)	130	87	66
Stomatal Conductance ($mmol\ m^{-2}\ s^{-1}$)	13.5	4.3	5.9

Winterfat

Carbon allocation to different plant parts as affected by watering frequency is given in Table 30. Average shoot and root biomass is shown in Figure 25 and the significant differences between treatments are shown in Figure 26.

Table 30. Carbon allocation (g/plant) to different plant components of winterfat under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Shoot	0.25	0.29	0.22
Leaf	0.16	0.11	0.11
Root	0.09	0.10	0.09
Total Biomass	0.50	0.50	0.42

Combinations of big sagebrush and bluebunch wheatgrass and western wheatgrass affected the leaf:stem ratio of winterfat in the wet and moist regimes (Fig. 25). Pure culture in the moist regime resulted in significant differences in the stem biomass of the two plants and in the dry regime affected leaf:stem ratio. In the dry regime, winterfat growing with big sagebrush produced significantly more biomass than winterfat plants grown with either grass. Biological niche responses are shown in Figure 27.

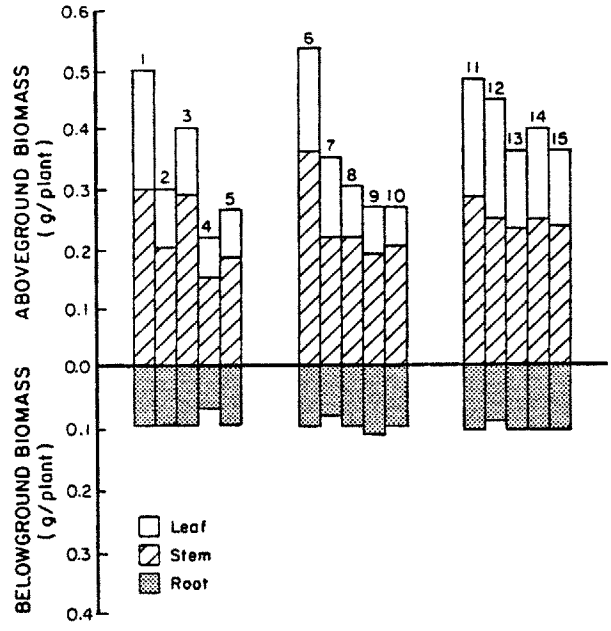

Figure 25. Above- and belowground biomass of the 15 treatment groups (see Table 2) of winterfat. Significant differences between all possible pairs of means for the 15 treatment groups are shown in Figure 26.

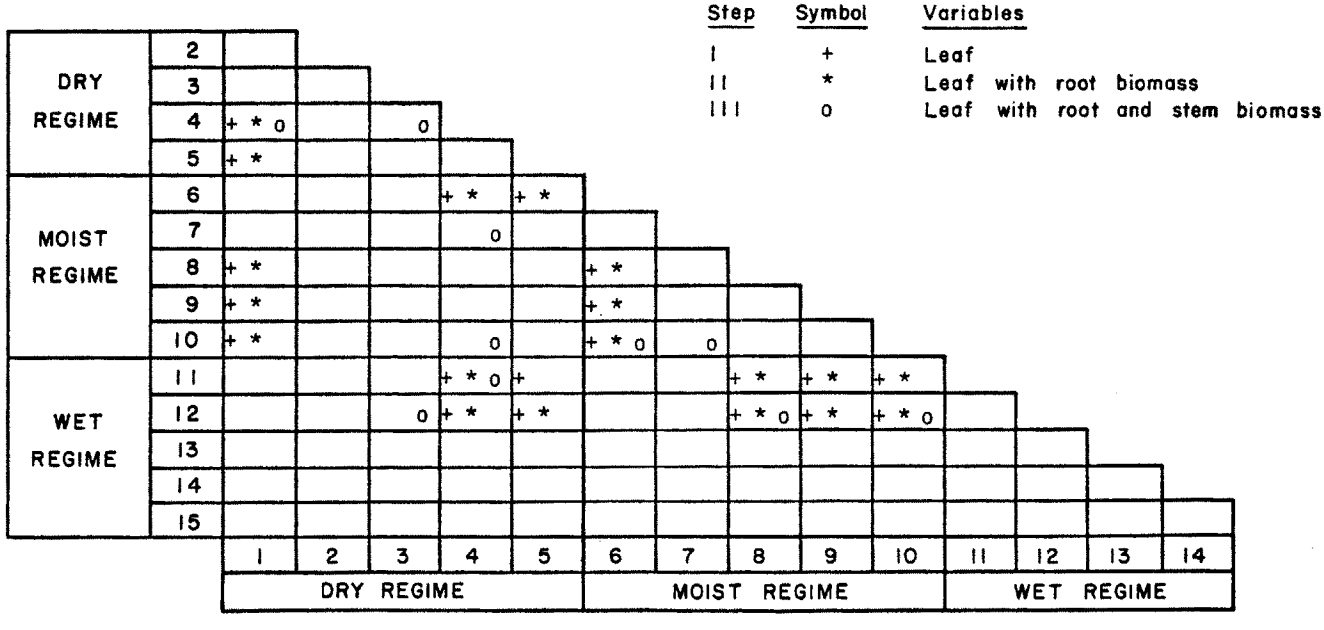

Figure 26. A matrix of biological variables which separate the 15 treatment groups (numerals) (see Table 2) of winterfat in a stepwise discriminant analysis. In order to find which group is different from other groups, locate the intersecting row and column of interest. A blank box at the intersection of a row and column indicates that the two groups are not significantly different from each other ($P < 0.05$). If the box has one or more symbols, then the symbols indicate which variables are significant in separation between groups.

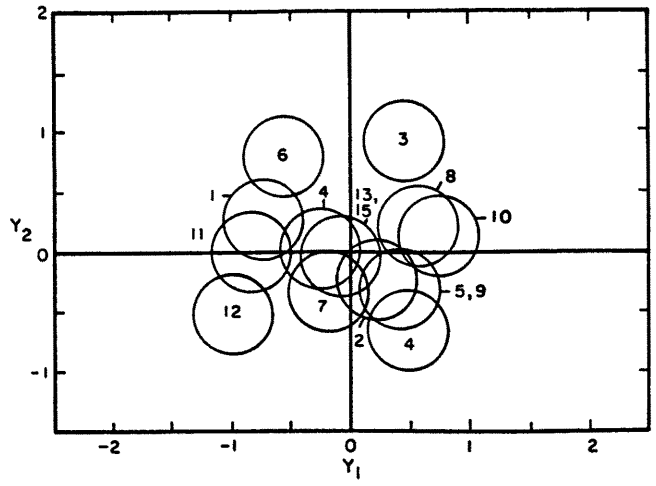

Figure 27. Biological 'niche response' of 15 treatment groups (see Table 2) of winterfat shown as mean canonical points with 95% confidence limits. Overlap of circles along any one axis indicates no significant difference between those treatment groups along that gradient. Aboveground biomass and stem:root ratio correspond, respectively to the Y_1 and Y_2 axes of the biological niche response plane.

Average soil moisture at the end of the drying cycle and average transpiration across all treatments are given in Table 31. There were significant differences in transpiration rate in all water regimes. There was no interspecific difference in transpiration in the wet regime. Winterfat plants in combination with either shrub had more soil moisture remaining than did winterfat combinations with grasses in the wet and moist regimes. Soil moisture remaining in the wet regime in winterfat-western wheatgrass combination was less than in the winterfat-bluebunch wheatgrass combination. In the dry regime, the winterfat-bluebunch wheatgrass combination had significantly less soil moisture remaining than in other combinations.

Table 31. Average soil moisture and transpiration for winterfat under three water regimes.

Plant Components	Water Regime		
	Wet	Moist	Dry
Soil moisture (%)	6.8	4.8	4.0
Transpiration ($\mu g\ cm^{-2}\ s^{-1}$)	66	41	49

RESPONSE OF SELECTED CLIMAX SPECIES AS AFFECTED BY INTRA- AND INTERSPECIFIC COMPETITION AND SOIL DISTURBANCE

Sampling Date

Stomatal conductance and transpiration were significantly affected by date of sampling or season from June 7 until October 3 when sampling ceased. For the three species, winterfat, bluebunch wheatgrass and western wheatgrass, stomatal conductance and transpiration were greater during spring when soil moisture was high and growth was rapid. As the season advanced loss of water from the plants decreased (as observed by lower rates of stomatal conductance), generally, until fall (October 3) when it was the lowest (Table 32).

Soil Disturbance

Loss of water, as observed from stomatal conductance, from the plants was consistently higher on the intensively disturbed soils for western wheatgrass during the entire season, June 7 to September 9, (Table 33). Bluebunch wheatgrass plants lost more water on the intensively disturbed sites during early growth (June 7 and June 27) as measured by stomatal conductance. Stomatal conductance was greater in bluebunch wheatgrass from the surface disturbed site than the intensively disturbed site on July 27 and October 3. The loss of water from winterfat was significantly greater on June 27 and July 9 on the intensively disturbed site but transpiration values showed significantly greater water loss from the shallowly disturbed soils on June 7 when moisture content of the soil had reached field capacity even at deeper depths than later in the season (Table 34). This would allow rapidly growing winterfat plants to obtain readily available water from deeper soil zones because of their more extensive root systems at deeper depths. Stomatal conductance was greater on the surface disturbed site than on the intensively disturbed site on October 3.

Intra- and Inter-specific Competition

Winterfat was more competitive when found in pure stands or in association with western wheatgrass on the June 7 and June 27 sample dates (Table 35). Stomatal conductance was significantly lower on winterfat found in combination with bluebunch wheatgrass than when found in pure stand pairs or in combination with western wheatgrass. Stomatal conductance was greatest on winterfat plants found in combination with western wheatgrass on September 9 (Table 35). Water loss was greater, however, carbon dioxide flux was also greater and growth late in the season was observed.

As shown in Table 36, bluebunch wheatgrass plants were more competitive with each other during early growth than when grown in combination with winterfat plant. Water loss as, measured by both a

Table 32. Stomatal conductance and transpiration of winterfat, bluebunch wheatgrass, and western wheatgrass in the Piceance Basin, Colorado, 1985.

Date	Winterfat		Bluebunch Wheatgrass		Western Wheatgrass	
	Stomatal Conductance*	Transpiration*	Stomatal Conductance*	Transpiration*	Stomatal Conductance*	Transpiration*
	- mmol m^{-2} s^{-1} -					
June 7	67.0a*	4.09a	59.0a	3.52a	156.7a	6.08a
June 27	20.5b	1.49c	21.2b	1.47b	43.9b	2.10b
July 9	23.3b	2.18b	15.5b	1.74b	37.1b	2.24b
July 27	23.6b	1.42c	22.5b	1.54b	47.6b	1.69c
August 15	10.9c	1.17c	12.4b	1.42b	18.5c	1.33c
September 9	12.3c	0.86d	17.9b	1.20b	29.2b	1.15c
October 3	9.0c	0.55e	10.1b	0.68c	13.4c	0.57d

* For each species, stomatal conductance and transpiration values followed by the same letter are not significantly different ($P \leq 0.05$).

Table 33. Stomatal conductance, transpiration of winterfat, bluebunch wheatgrass, and western wheatgrass on a shallowly disturbed and intensively disturbed soil in the Piceance Basin, Colorado, 1985.

Date	Stomatal Conductance*		Transpiration*	
	Shallow	Intense	Shallow	Intense
	- - - - - - mmol m^{-2} s^{-1} - - - - - -			
WINTERFAT				
June 7	69.9a	64.3a	4.88a	3.35b
June 27	14.7a	26.0b	1.50a	1.49a
July 9	20.1a	26.3b	2.03a	2.33a
July 27	25.9a	21.3a	1.20a	1.64a
August 15	10.2a	11.5a	1.13a	1.21a
September 9	11.6a	12.8a	0.69a	1.00b
October 3	13.4a	4.7a	0.64a	0.46a
BLUEBUNCH WHEATGRASS				
June 7	48.1a	69.0b	3.74a	3.32a
June 27	13.9a	28.9b	1.33a	1.60b
July 9	15.7a	15.2a	1.90a	1.61a
July 27	24.6a	20.6a	1.48a	1.59a
August 15	12.4a	12.3a	1.34a	1.51a
September 9	17.7a	18.0a	0.83a	1.49a
October 3	11.6a	8.5a	0.66a	0.69a
WESTERN WHEATGRASS				
June 7	133.2a	180.2b	6.02a	6.15a
June 27	30.8a	57.0b	2.06a	2.15a
July 9	32.6a	42.5b	2.00a	2.46b
July 27	43.3a	52.0b	1.32a	2.07b
August 15	15.6a	21.3b	1.16a	1.50b
September 9	22.1a	35.7b	0.66a	1.59b
October 3	12.5a	14.4b	0.46a	0.68a

* For shallow and intense disturbance, stomatal conductance and transpiration values followed by the same letter are not significantly different ($P \leq 0.05$).

stomatal conductance and transpiration, was less in bluebunch wheatgrass when growing with another bluebunch wheatgrass plant than when growing in association with a winterfat plant.

A western wheatgrass plant was considered more competitive when growing in association with a winterfat plant than when growing in association with another western wheatgrass plant during June 27 by both stomatal conductance and transpiration values and during July 9 by transpiration values (Table 37).

Species Combinations and Disturbance Interactions

Winterfat was significantly affected by a site-species combination interaction on June 27 as observed in stomatal conductance and transpiration (Table 38). Stomatal activity was significantly greater in pure stand pairs of winterfat found on the intensively disturbed site than any other winterfat plants. Water loss was more in these plants but carbon dioxide flux also was greater, accounting for increased carbon gains in terms of biomass. Stomatal conductance was higher on pure stand pairs and winterfat in combination with bluebunch wheatgrass on October 3 grown on the surface disturbed site (Table 38). The lowest stomatal conductance was observed on all winterfat plants from the intensively disturbed site. Water loss was greater on the surface disturbed site, however, this was expected because the soil was drier on the intensively disturbed site (Table 34).

Table 34. Percent soil moisture by weight and soil water potential (SWP) on surface disturbed and intensively disturbed soils, Piceance Basin, Colorado, 1985.

	Depth (cm)	Date						
		June 6	June 27	July 9	July 27	Aug 15	Sept 6	Oct 3
Surface Disturbed Site								
% Soil Water	0-20	20.7	8.1	5.5	10.3	7.1	5.1	9.0
SWP (-MPa)	0-20	0.1	7.4	56.6	2.1	14.8	76.0	4.2
% Soil Water	20-40	31.7	11.4	7.4	8.6	7.3	7.7	7.3
SWP (-MPa)	20-40	0.1	1.1	6.6	3.5	7.0	5.6	7.0
% Soil Water	40-60	29.9	12.9	8.1	8.4	7.2	6.6	
SWP (-MPa)	40-60	0.1	0.7	3/3	2.9	4.9	6.6	
Intensively Disturbed Site								
% Soil Water	0-20	17.9	8.4	8.7	11.7	7.2	6.1	8.4
SWP (-MPa)	0-20	0.1	2.9	2.5	0.7	5.6	11.3	2.9
% Soil Water	20-40	22.1	9.9	11.6	10.1	7.3	5.7	7.2
SWP (-MPa)	20-40	0.1	2.7	1.3	2.4	10.6	32.4	11.3
% Soil Water	40-60	25.2	12.8	11.7	11.8	6.4	7.4	
SWP (-MPa)	40-60	0.1	0.8	1.2	1.2	17.7	9.3	

Table 35. Stomatal conductance and transpiration of winterfat grown in combination with another winterfat plant (CELA), bluebunch wheatgrass (AGIN), and western wheatgrass (AGSM) in the Piceance Basin, Colorado, 1985.

Date	Stomatal Conductance*			Transpiration*		
	CELA	AGIN	AGSM	CELA	AGIN	AGSM
	- - - - - - mmol m^{-2} s^{-1} - - - - - -					
June 7	75.8a	54.9b	71.4a	4.41a	3.54b	4.38a
June 27	30.4a	14.4b	17.2b	1.67a	1.40b	1.40b
July 9	23.9a	23.0a	22.9a	2.45a	2.03a	2.06a
July 27	25.1a	21.0a	24.4a	1.41a	1.47a	1.38a
August 15	10.6a	11.9a	10.1a	1.14a	1.28a	1.09a
September 9	11.0b	11.2b	15.1a	0.93a	0.78a	0.89a
October 3	11.1a	8.1a	7.9a	0.70a	0.47b	0.47b

* For each species, stomatal conductance and transpiration values within the same date followed by the same letter are not significantly different ($P \leq 0.05$).

Table 36. Stomatal conductance and transpiration of bluebunch wheatgrass, grown in combination with winterfat (CELA) or another bluebunch wheatgrass (AGIN) in the Piceance Basin, Colorado, 1985.

Date	Stomatal Conductance*		Transpiration*	
	CELA	AGIN	CELA	AGIN
	- - - - - - mmol m^{-2} s^{-1} - - - - -			
June 7	72.4a	45.1b	3.74a	3.30b
June 27	16.8a	25.9b	1.39a	1.55a
July 9	16.8a	14.2a	1.65b	1.83a
July 27	23.6a	20.8a	1.59a	1.48a
August 15	12.3a	12.4a	1.35b	1.50a
September 9	16.7b	19.0a	1.21a	1.18a
October 3	10.4a	9.7a	0.63a	0.72a

* For each species, stomatal conductance and transpiration values within the same date followed by the same letter are not significantly different ($P \leq 0.05$).

Table 37. Stomatal conductance and transpiration of western wheatgrass, grown in combination with winterfat (CELA) or another western wheatgrass (AGSM) in the Piceance Basin, Colorado, 1985.

Date	Stomatal Conductance		Transpiration	
	CELA	AGSM	CELA	AGSM
	- - - - - mmol m^{-2} s^{-1} - - - - -			
June 7	143.1b	172.7a	5.72a	6.50a
June 27	35.1b	52.8a	1.96b	2.25a
July 9	37.6a	37.5a	1.92b	2.65a
July 27	52.6a	42.7b	1.75a	1.64a
August 15	19.4a	17.5a	1.32a	1.34a
September 9	26.2b	31.4a	1.06a	1.21a
October 3	13.6a	13.3a	0.62a	0.51a

* For each species, stomatal conductance and transpiration values within the same date followed by the same letter are not significantly different ($P \leq 0.05$).

Rooting Patterns

Winterfat

The level of soil disturbance significantly affected maximum rooting depth, depth of root zone concentration, and area of root zone concentration in winterfat. Individual plants grown on the control plot with no disturbance had an average deepest rooting depth of 127 cm. The greatest depth of winterfat roots on the intensively disturbed site and shallowly disturbed site was 79 cm and 61 cm, respectively (Figs. 28 and 29). The corresponding average depth of root zone concentration was 39 cm, 24 cm, and 21 cm for winterfat on the control plot, intensively disturbed site, and shallowly disturbed site, respectively.

We hypothesized that the intensive disturbance of the soil would allow for more soil moisture deep in the soil profile, which would in turn permit deeper root penetration. Soil moisture was greater at the 40-60 cm depth on the intensively disturbed site through the end of July, and then the shallowly disturbed site had more available water deeper in the soil (Table 34).

Table 38. Stomatal conductance (mmol m^{-2} s^{-1}) transpiration (mmol m^{-2} s^{-1}) and stem xylem potential (-MPA) of winterfat in soil disturbance competition interaction for winterfat in pure stand pairs (CELA/CELA), winterfat associated with bluebunch wheatgrass (CELA/AGIN), and winterfat associated with western wheatgrass (CELA/AGSM).

Date	Shallow Disturbance			Intense Disturbance		
	CELA/CELA	CELA/AGIN	CELA/AGSM	CELA/CELA	CELA/AGIN	CELA/AGSM
			STOMATAL CONDUCTANCE*			
June 7	79.5a	52.2a	78.1a	72.2a	57.2a	64.7a
June 27	14.2b	13.9b	16.1b	46.6a	14.9b	18.3b
July 9	22.2a	17.1a	20.3a	25.5a	27.9a	25.6a
July 27	29.0a	22.1a	25.5a	20.7a	20.0a	23.2a
August 15	10.8a	11.4a	8.5a	10.4a	12.5a	11.7a
September 9	12.5a	9.5a	13.3a	9.2a	12.4a	16.8a
October 3	17.5a	13.0a	9.6b	4.7c	3.2c	6.1c
			TRANSPIRATION*			
June 7	5.45a	3.94b	5.25a	3.37a	3.20a	3.51a
June 27	1.28a	1.68a	1.53a	2.07a	1.16b	1.28b
July 9	2.14a	2.16a	1.81a	2.77a	1.92b	2.31a
July 27	1.22a	1.34a	1.07a	1.64a	1.59a	1.69a
August 15	1.27a	1.28a	0.85b	1.01b	1.27a	1.34a
September 9	0.86a	0.63a	0.57a	1.01a	0.89a	1.18a
October 3	0.83a	0.60a	0.48b	0.57b	0.33c	0.46b
			STEM XYLEM POTENTIAL*			
July 9	2.8a	2.9a	2.3b	2.7a	2.8a	3.5b
July 27	2.5a	2.5a	2.4a	2.4a	2.4a	2.3a
August 15	3.9a	4.0a	3.7a	3.7a	3.7a	3.8a
September 9	3.6a	4.0a	3.6a	4.4a	4.2a	3.5a
October 3	4.0a	4.2a	5.3a	4.6a	4.3a	4.7a

* Significance is shown at $P \leq 0.05$ when letters differ among combinations of plant species within soil disturbance sites and dates.

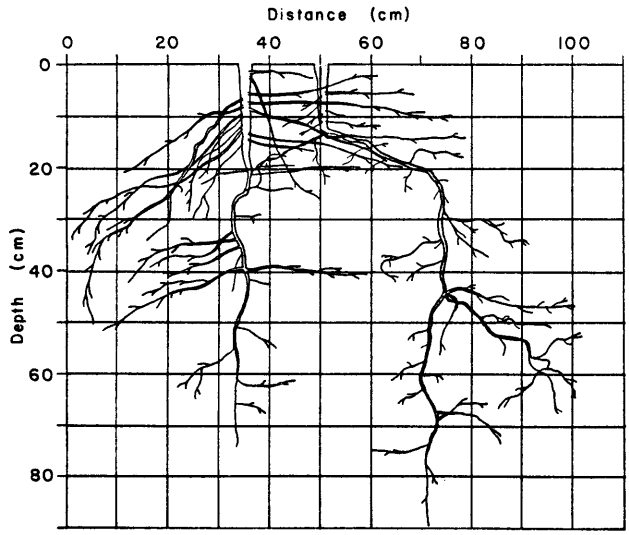

Figure 28. Root systems of winterfat in combination with winterfat from the Intensively Disturbed site, Piceance Basin, 1985.

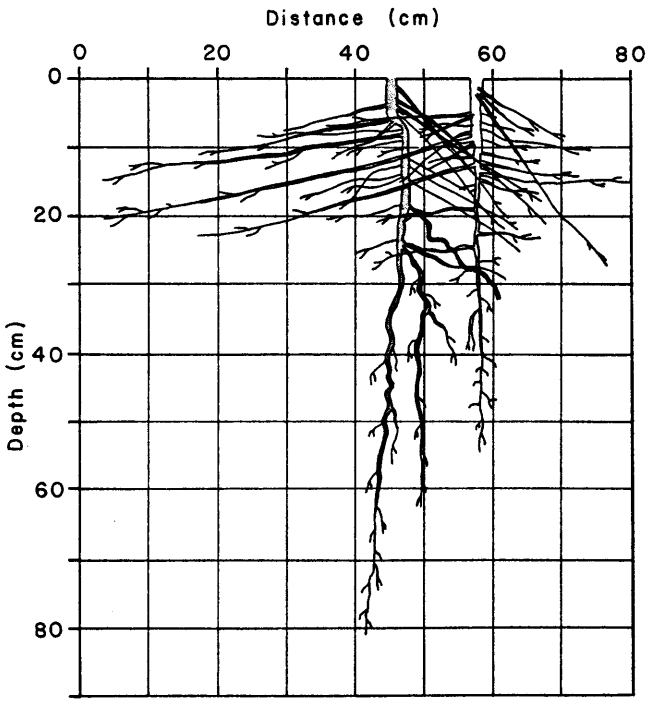

Figure 29. Root systems of winterfat in combination with winterfat from the Surface Disturbed Site, Piceance Basin, 1985.

Area of root concentration also was significantly different for levels of soil disturbance. The average area was 1328, 513, and 727 cm^2 for winterfat found on the control plot, intensively disturbed site, and surface disturbed site, respectively. Winterfat on the surface disturbed site had a greater area of root concentration, while greater depth of root penetration occurred in plants on the intensively disturbed site. All levels of soil disturbance showed significantly lower rooting depth and area of root concentration for winterfat than the plants from the control plot.

There were no significant differences in the maximum lateral spread of winterfat roots, number of axillary roots or the diameter of the zone of root concentration due to soil disturbance.

The species of plants grown in combination with winterfat significantly affected the rooting characteristics of winterfat (Figs. 30-33). Maximum rooting depth of winterfat was 13% greater for winterfat plants grown in association with another winterfat (Figs. 28 and 29) compared to plants grown in association with grasses. Maximum rooting depth for winterfat was 78, 69, and 65 cm for winterfat grown in combination with winterfat, bluebunch wheatgrass and western wheatgrass, respectively. Maximum lateral spread of roots was also significantly affected ($P \leq 0.01$) by species combination. Maximum lateral spread of winterfat roots were 45, 29, and 28 cm for winterfat grown in combination with winterfat, bluebunch wheatgrass, and western wheatgrass, respectively. The area of winterfat root concentration was 747, 660, and 470 cm^2 for winterfat grown in combination with winterfat, western wheatgrass, and bluebunch wheatgrass, respectively.

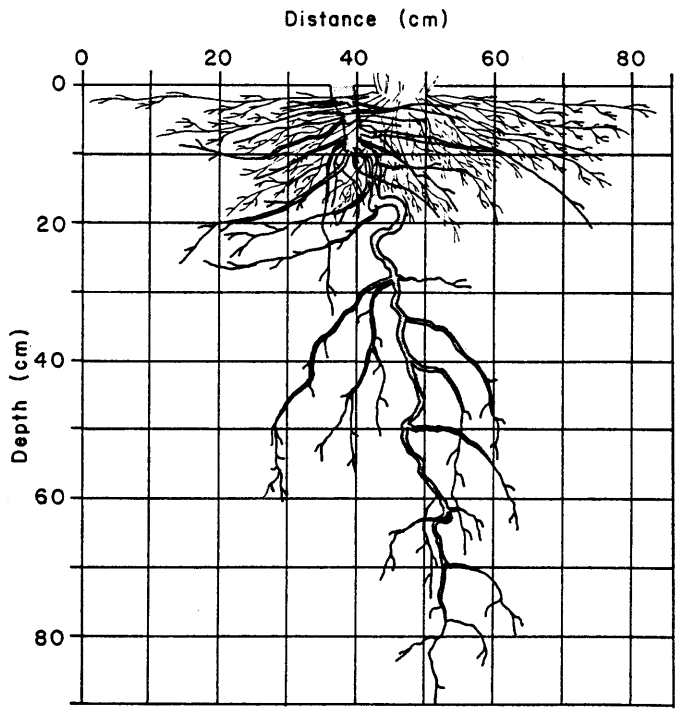

Figure 30. Root systems of winterfat in combination with bluebunch wheatgrass from the Intensively Disturbed site, Piceance Basin, 1985.

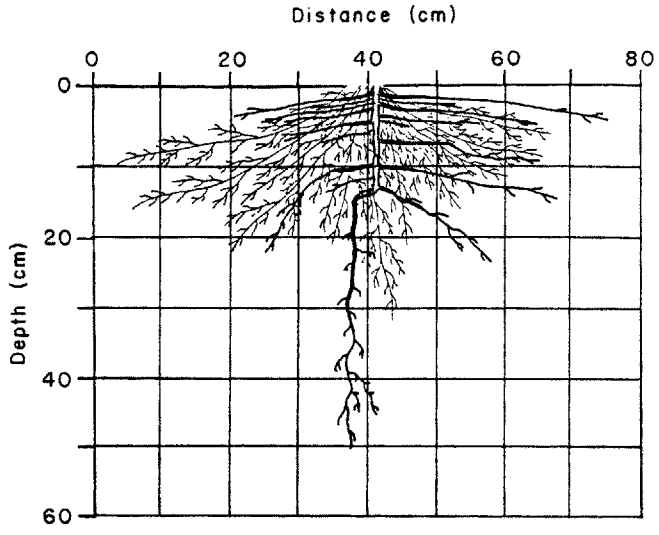

Figure 31. Root systems of winterfat in combination with bluebunch wheatgrass from the Surface Disturbed Site, Piceance Basin, 1985.

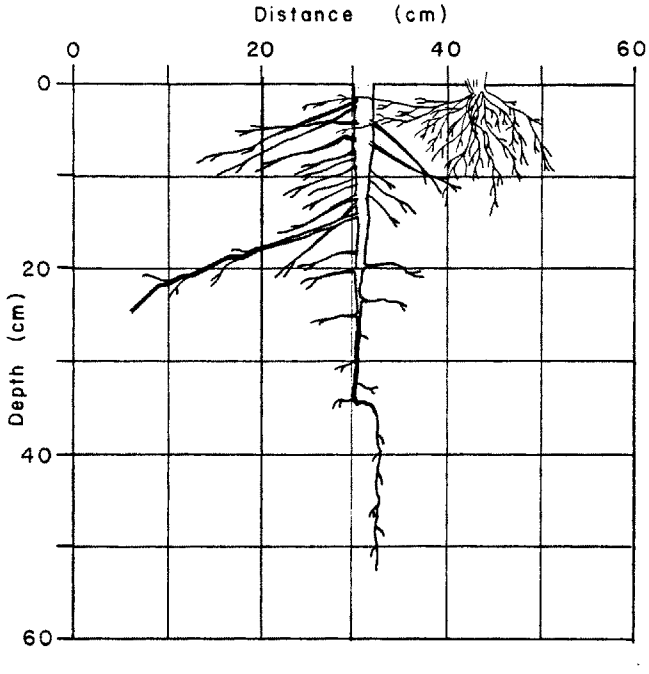

Figure 33. Root systems of winterfat in combination with western wheatgrass from the Surface Disturbed Site, Piceance Basin, 1985.

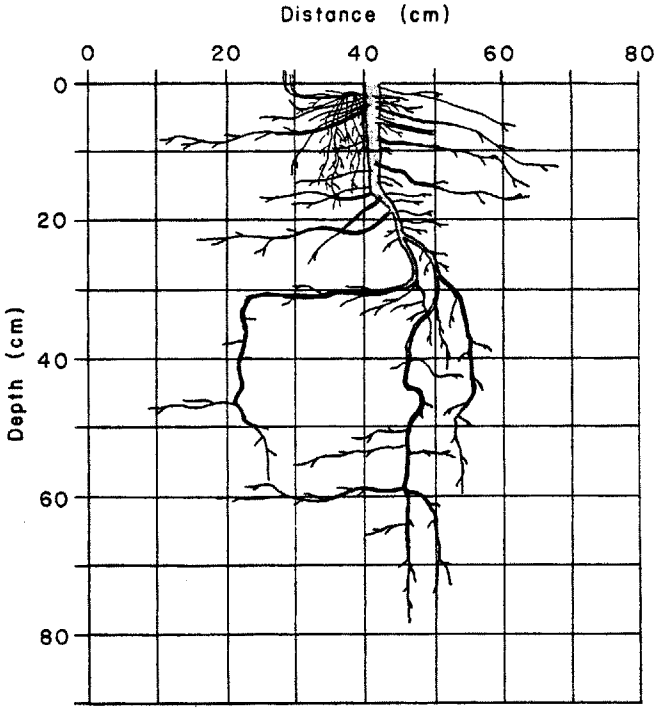

Figure 32. Root systems of winterfat in combination with western wheatgrass from the Intensively Disturbed site, Piceance Basin, 1985.

Bluebunch Wheatgrass

There were no significant differences in rooting depth of bluebunch wheatgrass on the surface disturbed or intensively disturbed sites, 39 and 37 cm, respectively. (Figs. 34 and 35). There was no significant difference in the maximum lateral spread or root concentration for bluebunch wheatgrass.

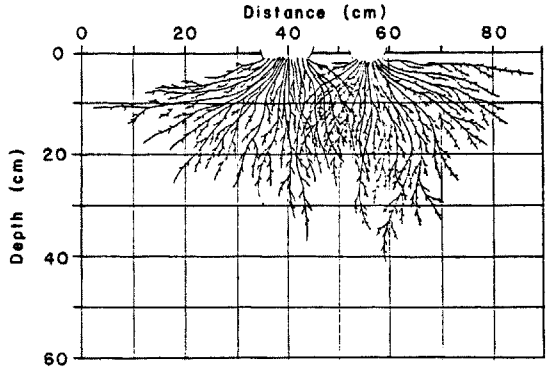

Figure 34. Root systems of bluebunch wheatgrass in combination with bluebunch wheatgrass from the Intensively Disturbed site, Piceance Basin, 1985.

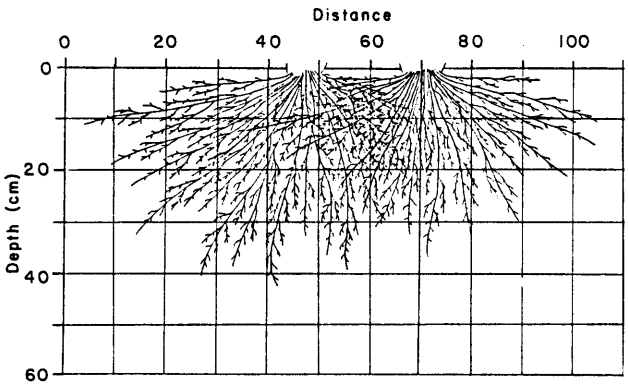

Figure 35. Root systems of bluebunch wheatgrass in combination with bluebunch wheatgrass from the Surface Disturbed Site, Piceance Basin, 1985.

Maximum rooting depth of bluebunch wheatgrass was significantly greater ($P \leq 0.01$) when bluebunch wheatgrass was grown in a pure stand pair (Figs. 34 and 35) compared to plants growing in association with other species. Maximum rooting depth was 41 cm for bluebunch wheatgrass in pure stand pairs and 30 cm for bluebunch wheatgrass in combination with winterfat (Figs. 30 and 31). The area of root concentration was also 58% greater ($P \leq 0.01$) for pairs of bluebunch wheatgrass than bluebunch wheatgrass found in combination with winterfat.

Western Wheatgrass

No significant differences were observed in maximum rooting depth, maximum lateral spread of roots or area of root concentration in western wheatgrass due to site disturbance (Fig. 36). Depth of the zone of root concentration was the only root characteristic to be affected by soil disturbance for western wheatgrass. The depth of root concentration for western wheatgrass in the intensively disturbed site was 37% greater than from the surface disturbed site; 15 and 11 cm, respectively.

No significant differences were observed in maximum rooting depth, maximum lateral spread of roots or area of root concentration due to species combination with western wheatgrass (Figs. 32 and 33).

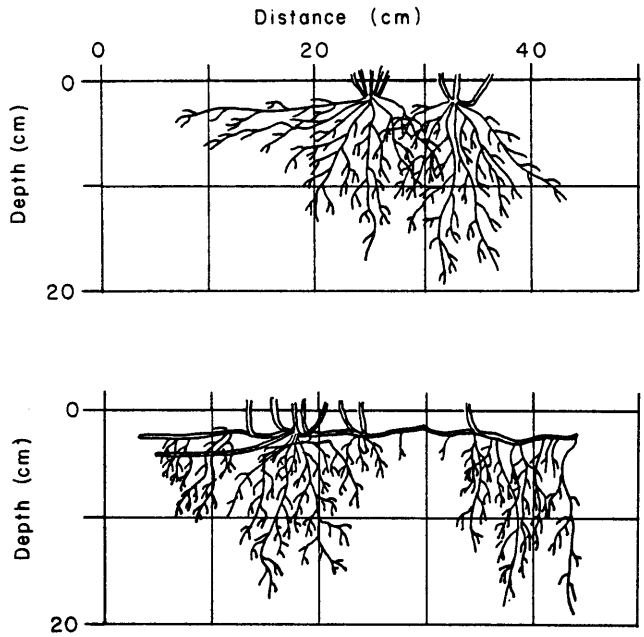

Figure 36. Root systems of western wheatgrass in combination with winterfat from the Intensively Disturbed site, Piceance Basin, 1985.

RECARBONATION OF RETORTED OIL SHALE AND PLANT UPTAKE OF TOXIC ELEMENTS

The trace element solubility data for Lurgi retorted shale before and after recarbonation are given in Table 39. The results show that exposing Lurgi retorted shale to pressurized $CO_2(g)$ and moisture lowered pH from 11.6 to 8.6. Further, these data suggest that lowering pH decreased the concentrations of Mo, Cr, Sr, Ba, and F in solution. However, little, if any change in concentrations of Fe, Mn, Zn, B, Se, Cd, Cu, and As was observed.

The mean dry matter yields of tall wheatgrass grown in different treatments are given in Table 40. However, seeds did not germinate in Lurgi retorted shale. Possible reasons are high alkalinity and salinity. The data in Table 40 show that dry matter yields of tall wheatgrass grown on recarbonated Lurgi shale with soil cover were increased compared to Lurgi retorted shale with soil cover or control. But the increase was not statistically significant ($P \leq 0.01$).

Table 39. Solubility of trace elements in Lurgi retorted shale before and after recarbonation.

Recarbonation Status	pH	EC	Fe	Mn	Zn	Cd	Cu	Mo	Cr	Sr	B	Ba	As	Se	F
		dSm^{-1}	- - - - - - - - - - - - - - - -					(- log mol L^{-1})			- - - - - - - - - - - - - - - -				
Before recarbonation	11.6	16.0	6.74	BD	BD	BD	6.32	3.65	4.47	3.82	4.77	6.05	7.27	6.11	3.23
After recarbonation	8.6	13.0	5.54	5.59	5.73	6.57	6.32	3.77	5.40	4.66	4.07	6.44	5.17	5.20	4.28

BD = below the detection limit (<0.01 ppm).
All the measurements were made in duplicate.

Table 40. Mean dry matter yields of tall wheatgrass as affected by different treatments.

	Mean dry matter* yield (g/pot)
Soil Control	0.83
Lurgi retorted shale	†
Lurgi retorted shale with soil cover	0.82
Recarbonated Lurgi shale with soil cover	1.10

† Seeds did not germinate
* NS - not significant at 0.05 level.

The mean trace element concentrations in tall wheatgrass grown in different treatments are given in Table 41. These results suggest that plants did not accumulate significant levels of As, Se, Cd, Ti, Cr, Ni, and Cu in recarbonated Lurgi shale with soil cover or Lurgi retorted shale with soil cover compared to the control. The mean uptake of B for plants grown in the control, Lurgi retorted shale with soil cover, and recarbonated Lurgi shale with soil cover were 8.8, 13.0, and 8.2, respectively. These values are below the toxic level. Further, data in Table 41 show that B uptake by plants was significantly decreased by the recarbonation of Lurgi shale.

Manganese uptake by plants, grown in recarbonated Lurgi shale with soil cover was increased significantly over the control and the Lurgi retorted shale with soil cover. This suggests that decreasing the pH of retorted shale Lurgi shale by recarbonation increases the solubility of Mn and possibly its availability to plants. Strontium uptake by plants grown in control or Lurgi retorted shale with soil cover was 3 to 4 times higher than in the plants grown in recarbonated Lurgi shale with soil cover. A similar trend was observed for Ba. Fluorine uptake by tall wheatgrass was not affected by the recarbonation of Lurgi shale. The mean F concentrations in plants grown in control, Lurgi retorted shale with soil cover, and recarbonated Lurgi shale with soil cover were 3.1, 1.5, and 1.6, respectively. These values are well below the toxic limit.

Even though the solubility of Mo decreased upon recarbonation (Table 39), plants accumulated significantly higher concentrations of Mo in recarbonated Lurgi shale compared to unrecarbonated Lurgi shale. The mean Mo concentrations ranged from 1.8 to 31.3 ppm in tall wheatgrass grown in different treatments, with the highest Mo concentration resulting from the recarbonation of Lurgi shale followed by the unrecarbonated Lurgi shale. These results were consistent with those of Schwab et al. (1983) and Smith (1984). The results in Table 41 suggest that plants grown in recarbonated as well as unrecarbonated treatments had higher concentrations of Mo and low Cu:Mo ratios compared to the control treatment. Thus, plants grown in recarbonated or unrecarbonated shales may be toxic to animals.

Table 41. Mean trace element concentration (ppm) in tall wheatgrass subject to different treatments.

Treatment	As	Ba	B	Cd	Cr	F	Mn	Mo	Ni	Cu	Se	Sr	Ti	Cu/Mo
Soil Control	0.22a	35.5a	8.8a	0.32a	4.0a	3.1a	60.4a	1.8a	3.6a	8.0a	0.17a	21.8a	5.5a	4.50
Lurgi retorted shale†	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lurgi retorted shale with soil cover	0.23a	15.5b	13.0b	0.32a	2.3a	1.5b	82.0b	14.2b	2.5a	10.0a	0.40a	23.4a	7.3a	0.70
Recarbonated Lurgi shale with soil cover	0.16a	3.2c	8.2a	0.22a	1.5a	1.6b	138.0c	31.3c	2.7a	9.4a	0.48a	8.0b	5.5a	0.30

Concentrations followed by a different letter in columns are significantly different ($P < 0.01$ and 0.05 level).

† Seeds did not germinate.

DISCUSSION

RESOURCE ABUNDANCE

In general, disturbance on the Ecosystem Development Plot increased resource abundance. Although P showed little change as a result of disturbance, NO_3^- concentration and water potential were significantly higher on disturbed sites than on undisturbed sites. Increased resource abundance on disturbed sites apparently is caused by reduced resource uptake, or in the case of mineral nutrients, by increased mineralization. Soil moisture data confirm that plant communities growing on the disturbed sites use considerably less soil water than communities on the undisturbed sites. Analyses of plant N and P data are not yet complete so the amount of nutrient uptake in the two communities unfortunately can not be compared. Although laboratory analyses showed that potentially mineralizable N was no higher on disturbed sites than on undisturbed sites, actual rates of N mineralization were probably greater on disturbed sites because of greater soil moisture.

It is interesting to note that although water consumption was considerably higher on undisturbed sites than on disturbed sites of the Ecosystem Development Plot, aboveground NPP was almost exactly the same. Ruderal seeded treatments had aboveground NPP that was almost three times that in undisturbed treatments, but soil moisture consumption was considerably lower. These results show, at least for the aboveground biomass, that early successional communities had higher water-use efficiencies than late successional communities. Although late successional communities had lower water-use efficiencies, they appear able to extract and use moisture over a broader range of soil water potentials. It may be that because early successional species are unable to extract soil moisture at low water potentials, they have evolved high water-use efficiencies. Above- and belowground NPP and water consumption need to be monitored more closely before conclusions can be drawn, however, these results raise interesting questions regarding water-use relationships among early and late successional species.

MICROFLORA STRUCTURE AND FUNCTION

Measurements of belowground processes in relation to disturbance, fumigation, and fertilization indicate that major changes in these microbial communities still exist. Organic matter measurements do not appear to be particularly sensitive to these treatments, as observed in earlier studies (Klein et al. 1985), however, several other parameters that have been monitored have shown more sensitivity to these short-term responses. Mineralizable nitrogen, a measure of N in microbial biomass, was lower with weeding, suggesting retarded microbial community development without organic carbon accretion by the plant community.

Enzymatic responses to these treatments also were evident. Acetylene reduction and phosphatase both were decreased (acetylene reduction significantly) by fertilizer presence. Fumigation of disturbed soils showed continued effects, with decreases in phosphatase, glucose-amended dehydrogenase and especially nitrogen fixation and nitrification still evident. These results indicate that fumigation still has distinct effects on the critical N cycling processes, as an indication of broader effects on the belowground microbial community which can influence ecosystem development.

The rhizosphere development studies were limited by the plant materials available on the test plots. Despite these constraints, it was possible to compare early (cheatgrass) and late (western wheatgrass) successional plants in relation to fertilization. Generally, cheatgrass had a higher microbial population, however, the mean levels were not consistently different, based on statistical analyses. Fungal diversity was higher, especially with fertilizer, in the rhizosphere than in the nonrhizosphere environment of early and late successional plants evaluated in this study. In terms of enzymatic activity, cheatgrass apparently had higher dehydrogenase, nitrogenase, urease, and phosphatase compared to western wheatgrass. These preliminary results, however, should be interpreted carefully because the comparisons involve an annual vs. a perennial species. Studies that will be conducted in the future will involve comparisons between perennial species.

Little attention has been paid by biologists to the ecology of the soil microflora and its activities during plant succession. In attempts that have been made (Biondini et al. 1985; Klein et al. 1985), little information has been provided concerning the relationship of the rhizosphere microflora to the competitive dynamics of plant species during the initial stages of succession. Presumably a dominant species may influence its rhizosphere microflora in two ways: first, by the diversion of fixed carbon toward the maintenance of rhizosphere populations, and second, by the degree of root biomass development that determines the number of colonization sites available for microbial community development. Physiological properties may influence the development of the plant rhizosphere microlfora. For example, C_4 plants

generally have a rapid rate of photosynthesis and growth, and are thought to translocate more of their photosynthate to the roots and exude more of their carbohydrates to the surrounding rhizosphere than do C_3 plants (Salsbury and Ross 1970). Western wheatgrass and cheatgrass are C_3 plants, but as mentioned above, one is a perennial while while the other is an annual.

The greater number of adventitious roots in cheatgrass, in contrast to western wheatgrass roots, probably results in greater length per unit weight and a greater root surface area for colonization by microorganisms. Of the parameters tested in the control treatment, microorganisms such as bacteria, Streptomyces, ammonium oxidizers, and fungal propagules were higher in the rhizosphere of cheatgrass compared to western wheatgrass. Also, most enzyme activities followed this same general pattern. Most rhizosphere populations of cheatgrass increased with fertilization over those in the rhizosphere of western wheatgrass and fertilization was related to general increases in the rhizosphere populations when compared to non-fertilized plants. In general, the growth of plants was influenced by fertilizer presence, thereby exerting a distinct influence on the microbial composition of the root environment.

The analyses of bacterial community functional characteristics in the rhizosphere of these same plants also suggested that major functional and structural characteristics of the microbial community had occurred. The use of the API procedures, although suggesting that these changes had taken place, were carried out using unit characters with limited relevance to the functional characteristics of the microbial community in this particular environment. Based on these experiences, our future work will combine a greater degree of environmental relevance in terms of unit character selection with more simplified technical procedures.

Saprobic soil fungi often are regarded as "opportunistic decomposers." Such a descriptive term denotes the saprobic fungal part of the entire microbial community that is separate from the other microflora and microfaunal members of the community with which they coexist (Gochenaur 1981). Gochenaur has listed several alterations in the soil microbial component that are assumed to be associated with disturbance of the higher plant community. Our results support several of her suggested responses as presented below.

Gochenaur suggested that microbial community organization will not be altered following disturbance of the higher plant community. Our data showed a high degree of similarity in major fungal taxa among the three different treatments, viz. undisturbed, disturbed, and fumigated. This similarity was reflected in the relatively high Sorensen Index values.

Microbial community structure, however, will be modified by disturbance (Gochenauer 1981). We found significant changes in the dominant species that occupy the disturbed and fumigated sites as contrasted with the undisturbed site. However, there did not appear to be a decline in the mucoraceous taxa with disturbance; indeed, Mortierella increased with disturbance and fumigation when contrasted with the relative density found in the undisturbed plots. There was an increase in melanized (dematiaceous) fungi; the most important melanized dominants were Penicillium d, Phoma, Cladosporium c, and Sterile a. Although not strictly "melanized", Penicillium d produces black sclerotia on normally used media and on G25 the hyphae are melanized and the colonies are black.

As nutrient diversity is reduced after the initial disturbance, fewer taxa will be supported resulting in decreased diversity (Gochenaur 1981). Our data supports this idea in that among the dominant forms present (relative density in excess of 1%), there appears to be a reduction in the number of taxa with disturbance. In the undisturbed habitat there are 29 taxa in excess of 1%, whereas in the disturbed area there are only 26 taxa, and in the fumigated plots only 24 major taxa were detected.

Gochenaur suggests that the microbial community that develops after disturbance is transitory and composed of "pioneers" that will exist only as long as the conditions remain constant. We found several important "pioneer" species, viz., Penicillium d, Phoma, and Cladosporium that assume dominance on the disturbed and fumigated plots in 1984. These same taxa remain dominants in 1985. Data for 1985 indicate that sufficient time for replacement of these pioneers has not yet occurred.

As data for 1985 are complied we will be better able to determine if there are significant changes in the population after one year and if relatively minor differences among subplots, e.g. fertilization treatments, contribute to significant changes in the population of opportunistic decomposer fungi.

Our work on mycorrhizal inoculum potential (MIP) in 1985 was in full agreement with our previous findings that disturbance of semiarid soils significantly reduces the MIP of the soil (Reeves et al. 1979; Moorman and Reeves 1979; Doerr et al. 1984) and the findings of other investigators of semiarid environments (Miller 1979; Allen and Allen 1980; Loree and Williams 1984).

The apparent consistent and continued decline of MIP values in the second year on the Ecosystem Development Plot disagrees with the findings of reasonably rapid (within 8 months) recovery of the mycorrhizal population in certain soils of England (Warner 1983). However, reports of slow recovery of the VA mycorrhizal population are common in many soils (Gerdemann and Trappe 1974; Mosse et al. 1982) and support our findings.

Because mycorrhiza-dependent plants cannot succeed without their fungal associate(s) and "...the sensitivity of such associations can have important implications to ecosystem resistance to gross stresses and to the recovery therefrom..." (Parkinson 1979), the role of these fungi in the recovery of semiarid ecosytems becomes relevant to programs for restoring disturbed lands.

Based on our study of the change of the mycorrhizal population in soils with disturbance and fumigation, we will be able to correlate the relative success of various native plant species with different levels of mycorrhizal fungi. We

anticipate being able to determine the "relative field mycorrhizal dependency" (Plenchette et al. 1983a and 1983b) of plants, and correlate these findings with our hypotheses regarding the interplay of VA mycorrhizal fungi, secondary succession, plant life history strategies, and resource competition on semiarid soils (Reeves 1985).

Under natural conditions, vesicular-arbuscular mycorrhizal (VAM) fungi are ubiquitous in soils (Gerdemann 1968, 1970; Smith 1974), they form mycorrhizae with most plant species (Gerdemann 1968, 1975), they show little host specificity (Mosse 1973; Smith 1980), and they are involved in nutrient uptake by plants (Mosse 1957, 1973; Cooper 1984).

Several researchers have suggested that plants exhibit different degrees of mycorrhizal dependency (Stahl 1900; Janos 1980; Allen 1984; Allen and Allen 1984; Reeves 1985); and that plant composition of communities may be partially directed by the presence or absence of mycorrhizal fungi (Reeves et al. 1979; Miller 1979; Janos 1980, 1985). Mycorrhizal dependency ranges from species that are effectively non-mycotrophic (M-) to those that are facultatively mycotrophic (M±) to those that are obligately mycotrophic (M+). Limited experimental evidence indicates that, under competitive conditions, facultatively mycotrophic species may show increased shoot biomass when mycorrhizal as compared to conditions where the same species is non-mycorrhizal (Allen and Allen 1984); thus the mycorrhizal interactions appear to influence plant community composition by affecting competition among plants (Crush 1974; Fitter 1977; Hall 1978; Janos 1981, 1985; Allen and Allen 1984).

The magnitude of the VAM effect on plant growth depends on the nutritional status of the soil (Abbott and Robson 1984). It is not possible to define the nutritional status of a soil relative to potential plant growth either from chemical measurements on soil or from absolute levels of nutrients applied since the amount of nutrient required for maximum growth of a species varies greatly with the soil type (Barrow 1975; Abbott and Robson 1984). Therefore response curves for both mycorrhizal and non-mycorrhizal examples of the same species at various applied nutrient levels are essential to assay the mycorrhizal effect (Abbott and Robson 1984).

Our working hypothesis is that early successional species will show less mycorrhizal dependency than do late successional species. Assuming that P competition is closely tied to the mycorrhizal status of a species, we suggest that: (1) Late successional species will exhibit greater mycorrhizal dependency than early successional species because they use the mycorrhizal fungi to increase P uptake; (2) Mycorrhizal dependency in late successional species can be partially obviated by the addition of P to the growth medium; and (3) early successional species will exhibit less growth response to added P than late successional species.

These predictions are consistent with the concept that nutrient availability is initially high after disturbance and that nutrient availability decreases with secondary succession (Odum 1969) because the nutrients become immobilized in plant materials. During this successional time sequence there is a shift in dominance of non-rhizosphere to rhizosphere organisms and late successional species typically show obligate mycorrhizal dependency (Reeves et al. 1979; Reeves 1985; Janos 1980, 1985) because the proportion of nutrients cycled within the rhizosphere increases in proportion to nutrients cycled by non-rhizosphere microorganisms.

We have examined the effect of mycorrhizae and added P on growth several semiarid species (Kiel and Reeves 1986) and assembled the literature on these effects on several other semiarid species (Allen 1984; Lindsey 1984) as presented below:

Bromus tectorum, a R species (Appendix Table 3) is mycorrhizal in contrast to most other ruderal species, but shows no mycorrhizal dependency (Allen 1984).

Sitanion hystrix, a C-R species (Appendix Table 3) shows no significant growth enhancement with added P or mycorrhizal fungi (Kiel and Reeves 1986).

Agropyron smithii, a C-S-R species (Appendix Table 3) shows limited growth enhancement with mycorrhizal fungi (Allen 1984; Kiel and Reeves 1986).

Artemisia tridentata, a C-S species (Appendix Table 3) shows significant growth enhancement with mycorrhizal fungi and increased P uptake (Kiel and Reeves 1986).

Chrysothamnus nauseosus, a C-S-R species (Appendix Table 3) shows significant growth enhancement with mycorrhizal fungi (Lindsey 1984).

Juniperus osteosperma, a S species (Appendix Table 3) shows a high degree of mycorrhizal dependency when grown in semiarid soils (unpublished data).

Although this is a very limited sample of the major species present on semiarid soils, the data support our concept of increasing dependency of later successional species for mycorrhizal fungi and the correlation of this increased dependency and plant growth strategy.

VASCULAR PLANT COMMUNITY STRUCTURE AND RESOURCE USE

Studies of seed rain and seed bank on disturbed and undisturbed sites indicates that the seed bank is more important than short term dispersal to the supply of seeds on a site. Seed rain on sites is highly variable and typically composed of a few species (often annuals) already growing on the site or adjacent to the site. Important species in the native vegetation (e.g., big sagebrush and perennial grasses) often do not appear in the supply of seeds dispersed to a site in the course of a growing season, but accumulate in the seed bank through periodic if not sporadic dispersal events.

We presume that infrequent dispersal and storage in the soil seed bank as well as vegetative reproduction accounts for the presence and regeneration of many species in the communities studied. These presumptions have implications for the establishment of communities on disturbed sites in which the seed bank is destroyed. With no soil reserve (or seeding treatment), only a few species (by ability or accident) will initially inhabit the site; and the complement of species may well differ from site to site.

During the first growing season on the Ecosystem Development Plot, propagule supply apparently was the primary factor controlling the structure of the early successional vascular plant community. Plant species most strongly represented in the propagule bank and seed rain were the most abundant plant species on the disturbed sites. In addition, modification of propagule supplies (by seeding climax and ruderal species) had major effects on plant community structure.

Resource competition did not appear to be important in determining the structure of the early successional vascular plant community. The results showing that N or P fertilization had no significant influence on plant community structure indicate that neither N or P were limiting on the disturbed nonseeded sites. The soil moisture data, which showed that soil water potentials rarely dropped below -0.4 MPa in depths <15 cm, indicate that soil moisture was not limiting plant growth. In addition, plant densities were low enough (2.5 plants/m^2) so that strong competition interactions would not be expected.

The primary effect of disturbance on the plant community was to eliminate or severely reduce production by species with stress tolerant strategies, perennials and especially woody perennials, and to increase production by species having ruderal tendencies. The increase in resource abundance caused by disturbance would be expected to favor plant species with high growth rates such as ruderals (R) and competitive ruderals (C-R), while not substantially helping those species adapted to high stress environments. As resources become rarer due to increased plant establishment, growth, and resource use, plants adpated to stress should increase in abundance.

During the first growing season, the weeding study has demonstrated that the facilitation model of Connell and Slatyer (1977) does not adequately explain the processes occurring during secondary succession in the disturbed big sagebrush communities of this area. It does not appear that additional modification of the environment is a prerequisite for establishment of most of the late successional species studied.

The competition study involving bluebunch wheatgrass, western wheatgrass, big sagebrush, and winterfat indicated that these species were capable of survival in a given community subjected to a wide range of water stress. The ability of these species to survive together depends on their different specializations. For example, allocation of more fixed energy to stems, roots, or changes in root:shoot ratio, stem:leaf ratio, and ability to control loss of water all were evidence of species specialization. Bluebunch wheatgrass and western wheatgrass had a faster rate of plant growth and a more extensive root system compared to big sagebrush and winterfat. Therefore, these grasses had a competitive advantage over the two shrubs in the establishment phase. Grasses use most of the available soil moisture and produced more biomass than did the shrubs, however, when two grasses were grown together, they compete for the available water resource. Consequently, their biomass production was less than when a grass was grown with a shrub.

Biomass production of all four species decreased with an increase in moisture stress due to reduced frequency of watering, pre-emptive water consumption by grasses (when grown with shrubs) or higher demand for soil moisture when two grasses were grown together. The pattern of water use for some species also changed under competition indicating that competition may result in lower water use efficiency.

The results of this study make it possible to better understand the expected structure of a community reseeded with the four species used. A mixture of these species, if used for restoring drastically disturbed ecosystems, would be capable of coexistence. However, in order of importance in the community, the two grasses would be dominant, followed by two shrubs. This would be so because grasses grow faster and preempt available soil moisture. Of the two shrubs, big sagebrush would have an advantage over winterfat because of its ability to better use available water.

We have hypothesized that water use and biomass partitioning into different plant parts were responses of primary producers to competition and soil disturbance. Winterfat, bluebunch wheatgrass, and western wheatgrass were used to test for effects of soil disturbance and the presence of associated plants on biomass production.

The photosynthetic activity, water relations, and growth and development of winterfat were affected by soil disturbance. Aboveground and belowground biomass were greatest on plants from native, undisturbed communities when compared to disturbed sites. Above- and belowground biomass always were greater on intensively disturbed sites than on surface disturbed sites. The proportion of biomass allocated to aboveground biomass on undisturbed sites was greater than that portion allocated to the belowground component. This suggested that water relations are important in the long-term allocation of carbon in these plants. Plants were able to tap limited resources, such as moisture or nutrients, by allocating a greater proportion of their biomass to belowground structures.

Above- and belowground biomass of winterfat was significantly less when the plants were associated with another plant that had an extensive root system. The greatest amount of above- and belowground biomass was observed on plants with no near neighbors or when winterfat was associated with western wheatgrass. Winterfat was able to use limited moisture from deep in the intensively disturbed site while grasses suffered from water stress. This also was seen in results of stomatal conductance and transpiration. Winterfat was observed to be a better competitor with grasses on intensively disturbed sites as indicated by the amounts of carbon fixed and stomatal conductance.

Physiological responses of winterfat showed similar trends to observed biomass allocation. Stomatal conductance of winterfat remained greater for a longer period into the growing season on the intensively disturbed site. This was because there was more water deep in the soil profile of the intensively disturbed site. In addition, the greatest rooting depth of winterfat was 30% more on the intensively disturbed site than on the surface disturbed site.

Bluebunch wheatgrass had the most leaf biomass early in the season when spring rains and snow melt provided abundant water. Bluebunch wheatgrass was the most responsive to dry soil, it rolled its leaves during the heat of the day in the dry season. Carbon was allocated to green stems that were more efficient structures for conserving water.

Stomatal conductance of bluebunch wheatgrass was greater on the intensively disturbed site early in the season. However, bluebunch wheatgrass plants on the surface disturbed site had significantly greater stomatal conductance late in the season. Available soil moisture was greater on the intensively disturbed site early in the season, and greater on the surface disturbed site late in the season. Stomatal conductance of bluebunch wheatgrass also was significantly greater on plants grown in combination with winterfat than when grown with another bluebunch wheatgrass plant. This suggested that bluebunch wheatgrass is more responsive to intraspecific competition; it is better able to obtain moisture when a shrub, such as winterfat, is present than when another bluebunch wheatgrass is present.

Western wheatgrass had the largest leaf area per leaf of the three species studied. Some green leaf area was maintained throughout the growing season, and the plant controlled the amount of leaf area subject to transpiration stress by rolling up its leaves during the heat of the day. Large soluble carbon reserves may have served to protect western wheatgrass during moisture stress. The largest percentage of western wheatgrass roots were in shallow soil (0-20 cm). Root biomass was greatest on the surface disturbed site during spring when moisture was plentiful. However, when competition for moisture became more intense, root biomass of western wheatgrass increased on the intensively disturbed site.

Western wheatgrass photosynthetic rates and transpiration were consistently greater on the intensively disturbed site throughout the growing season. Stomatal conductance was also greater for western wheatgrass plants grown in pure stands than when grown in combination with winterfat early in the season.

RECARBONATION OF RETORTED OIL SHALE AND PLANT UPTAKE OF TRACE ELEMENTS

The experimental results of this study showed that exposing Lurgi retorted shale to pressurized $CO_2(g)$ and moisture lowered pH from 11.6 to 8.6. Further, these results suggest that lowering the pH of retorted shales decreased the concentrations of soluble Ba, Cr, F, Mo, and Sr in solution. The data obtained from the greenhouse experiment show that tall wheatgrass grown in recarbonated Lurgi shale with soil cover accumulated significantly lower concentrations of B, Ba, and Sr compared to unrecarbonated Lurgi shale with soil cover. Uptake As, Cr, F, Ni, and Se by plants was below the toxic level in all the treatments. However, Mo uptake appeared to be increased in plants grown on recarbonated and unrecarbonated Lurgi shale with soil cover treatments were below the recommended level of 2:1, suggesting that molybdenosis could be a problem for animals using plants grown on retorted shales.

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APPENDIX

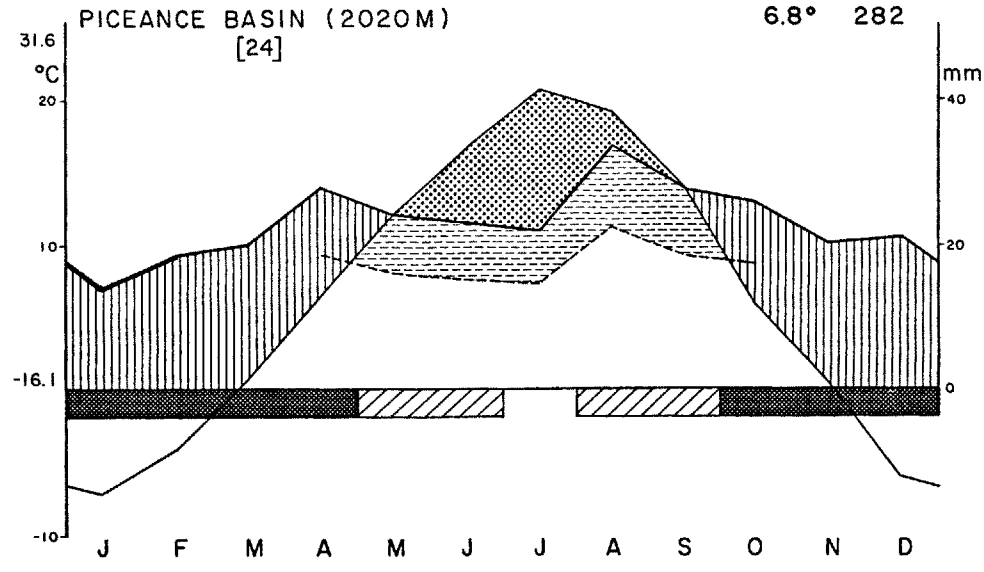

Figure 1. Ecological climate diagram for the Piceance Basin. The thick line represents mean monthly precipitation; the thin line represents mean monthly temperature. When drawn at these scales, the temperature curve approximates a potential evapotranspiration curve. The vertical lines represent humid periods, dashed lines represent dry periods, and the dotted area represents the duration and intensity of the drought period. The black bar at the base of the graph represents the cold period (months that have at least one minimum daily temperature below 0°C). The diagonally shaded bar represents the cool season (months in which an absolute minimum below 0°C). The diagonally shaded bar represents the cool season (months in which an absolute minimum below 0°C has been recorded). For further explanation see Walter (1979). All data derived from averages of Rangely and Little Hills weather station data for the period 1951-1974.

Table 1. Species composition of the predisturbance plant community.

Scientific Name	Aboveground Herbaceous Biomass (g/m^2)	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
Gutierrizia 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 macrantha	6.3	4.8	0.73	0.66	12.7	11.8	100
Agropyron dasystachium	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 hirsuta	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 convallarius	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	16.08	1.70	04.5	26.8	

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

Table 2. YAMAC LOAM - Fine-loamy, mixed, Borollic Camborthid

Parent Material: Eolian material

A1 0-1 cm. Pink (7.5 YR 7/3) loam, brown (7.5 YR 5/4) moist; moderate thick platy structure; slightly hard, very friable, slightly stocky, and slightly plastic; common very fine vesicular pores; strongly effervescent, mildly alkaline (pH 7.6); abrupt smooth boundary.

A2 1-7 cm. Pink (7.5 YR 7/4) loam, dark brown (7.5 YR 3/4) moist; strong fine granular structure; slightly hard, friable, slightly sticky, and plastic; many very fine and fine roots; many very fine and few fine continuous pores; violently effervescent, mildly alkaline (pH 7.5); abrupt wavy boundary.

A3 7-14 cm. Pink (7.5 YR 7/4) loam, brown (7.5 YR 4/4) moist; moderate medium granular structure; slightly hard, friable, slightly sticky, and slightly plastic; common very fine and fine roots; common very fine and few fine continuous pores; violently effervescent, mildly alkaline (pH 7.7); clear wavy boundary.

AB 14-30 cm. Pink (7.5 YR 7/4) loam, brown (7.5 YR 5/4) moist; strong medium subangular blocky structure; hard, firm, sticky, and slightly plastic, common very fine and few fine roots; common very fine and few fine continuous pores; fine roots concentrated in empty Cicada burrows; common insect krotovinas; violently effervescent, moderately alkaline (pH 7.9); clear wavy boundary.

Bwk1 30-60 cm. Pink (7.5 YR 7/4) loam, brown (7.5 YR 5/4) moist; strong medium subangular blocky structure; hard, firm, sticky, and plastic; common very fine and few fine roots; common very fine continuous pores; fine roots limited to empty Cicada burrows; common insect krotovinas; violently effervescent with segregated lime coating ped surfaces and occurring as threads within pores, strongly alkaline (pH 8.7); gradual wavy boundary.

Bwk2 60-86 cm. Pink (7.5 YR 7/4) loam, brown (7.5 YR 5/4) moist; strong medium subangular blocky structure; hard, firm, sticky, and plastic; common very fine roots; common very fine continuous pores; fine roots limited to empty Cicada burrows; common insect krotovinas; violently effervescent with segregated lime coating ped surfaces and occurring as threads within pores, strongly alkaline (pH 8.6); gradual wavy boundary.

BCk 86-104 cm. Pink (7.5 YR 7/4) loam, brown (7.5 YR 5/4) moist; moderate medium subangular blocky structure; hard, friable, sticky, and plastic; common very fine roots; common very fine continuous pores; few insect krotovinas; violently effervescent with segregated lime occurring as threads within pores, strongly alkaline (pH 8.6); gradual wavy boundary.

Ck 104-160 cm. Pink (7.5 YR 7/4) loam, brown (7.5 YR 5/4) moist; weak medium subangular blocky structure; slightly hard, very friable, slightly sticky, and slightly plastic; few very fine roots; common very fine continuous pores; violently effervescent with segregated lime occurring as filaments within pores, strongly akaline (pH 8.6).

Table 3. Tentative classification of plant species important in the Piceance Basin into Grime's plant life history strategies with mycorrhizal status given.

Scientific Name	Common Name	Mycorrhizal Status
RUDERALS		
Alyssum alyssoides	Pale alyssum	M-
Amaranthus albus	Tumbleweed pigweed	M-
Amaranthus graecizans	Tumbleweed amaranth	M-
Bromus tectorum	Cheatgrass	M+
Collinsia parviflora	Littleflower collinsia	M+
Descurainia pinnata	Pinnate tansymustard	M-
Descurainia richardsonii	Richardson tansymustard	M-
Lappula redowskii	Bluebur stickseed	M+
Polygonum aviculare	Prostrate knotweed	M-
Sisymbrium altissimum	Tumbling hedgemustard	M-
Sisymbrium officinale	Common hedgemustard	M-
Schoenocrambe linifolium	Plainsmustard	M-
COMPETITIVE RUDERALS		
Atriplex argentea	Tumbling saltbush	M-
Atriplex rosea	Tumbling orach	M-
Chaenactis douglasii	Douglas dustymaiden	M+
Chenopodium album	Lambsquarter goosefoot	M-
Chenopodium berlandieri	Pitseed goosefoot	M-
Chenopodium leptophyllum	Narrowleaf goosefoot	M-
Cirsium vulgare	Bull thistle	M+
Eriogonum alatum	Wing wildbuckwheat	M-
Erysimum asperum	Plains wallflower	M-
Hedysarum boreale	Northern sweetvetch	M+
Ipomopsis aggregata	Scarlet gilia	M+
Kochia scoparia	Fireweed summer cypress	M-
Lactuca scariola	Prickly lettuce	M+
Linum lewisii	Lewis flax	M+
Machaeranthera canescens	Hoary aster	M+
Melilotus officinalis	Sweetclover	M+
Poa pratensis	Kentucky bluegrass	M+
Salsola iberica	Russian thistle	M+
Sitanion hystrix	Bottlebrush squirreltail	M+
Taraxacum officinale	Common dandelion	M+
Tragopogon dubius	Yellow salsify	M+
STRESS-TOLERANT RUDERALS		
Agoseris glauca	Pale agoseris	M+
Allium acuminatum	Tapertip onion	M+
Allium textile	Prairie onion	M+
Calochortus nuttallii	Sego mariposa lily	M+
Carex geyeri	Elk sedge	M-
Crepis sp.	Hawks beard	M+
Cryptantha flavoculata	Roughseed cryptantha	M+
Cryptantha serecia	Cryptantha	M+
Delphinium nelsonii	Nelson larkspur	M+
Erigeron eatonii	Eaton fleabane	M+
Erigeron engelmannii	Wild daisy	-
Euphorbia fendleri	Fendler spurge	M+

Table 3. (Continued).

Scientific Name	Common Name	Mycorrhizal Status
STRESS-TOLERANT RUDERALS (Continued)		
Lomatium spp.	Lomatium	M+
Oenothera caespitosa	Tufted evening primrose	-
Oenothera trichocalyx	Evening primrose	-
Phlox longifolia	Longleaf phlox	M+
Physaria acutifolia	Twinpod	M-
Poa secunda	Sandberg's bluegrass	M+
Sphaeralcea coccinea	Scarlet globemallow	M+
Trifolium gymnocarpon	Holyleaf clover	M+
Zigadenus venenosus	Meadow death camus	M+
COMPETITIVE AND STRESS-TOLERANT RUDERALS		
Agropyron dasystachum	Thickspike wheatgrass	M+
Agropyron intermedium	Intermediate wheatgrass	M+
Agropyron trichophorum	Pubescent wheatgrass	M+
Agropyron smithii	Western wheatgrass	M+
Artemisia frigida	Fringed sagewort	M+
Astragalus convallarius	Timber milkvetch	M+
Chyrosthamnus nauseosus	Rubber rabbitbrush	M+
Chyrosthamnus viscidiflorus	Green rabbitbrush	M+
Gutierrezia sarothrae	Broom snakeweed	M+
Haplopappus nuttallii	Nuttall goldenweed	M+
Ipomopsis congesta	Bull head gilia	M+
Koeleria cristata	Prairie junegrass	M+
Oryzopsis hymenoides	Indian ricegrass	M+
Senecio multilobatus	Lobeleaf groundsel	M+
Stipa comata	Needle-and-thread	M+
Tetradymia canescens	Gray horsebrush	M+
COMPETITORS		
Amelanchier utahensis	Utah serviceberry	M+
Balsamorrhiza sagittata	Arrowleaf balsamroot	M+
Bromus inermis	Smooth brome	M+
Cercocarpus montanus	Mountain mahogany	M+
Hymenopappus filifolius	Fineleaf hymenopappus	M+
Lupinus caudatus	Tailcup lupine	M+
Lupinus spp.	Lupine	M+
Purshia tridentata	Antelope bitterbrush	M+
STRESS-TOLERANT COMPETITORS		
Agropyron cristatum	Crested wheatgrass	M+
Agropyron inerme	Bluebunch wheatgrass	M+
Agropyron spicatum inerme	Beardless bluebunch wheatgrass	M+
Agropyron trachycaulum	Slender wheatgrass	M+
Artemisia tridentata	Big sagebrush	M+
Eriogonum lonchophyllum	Spearleaf wild buckwheat	M+
Hymenoxys acaulis	Stemless actinea	M+
Penstemon strictus	Rocky mountain penstemon	M+
Penstemon spp.	Pentsemon	M+

Table 3. (Continued).

Scientific Name	Common Name	Mycorrhizal Status
STRESS-TOLERANT COMPETITORS (Continued)		
Poa ampla	Big bluegrass	M+
Poa fendleriana	Mutton bluegrass	M+
Stipa lettermannii	Letterman needlegrass	M+
Symphoricarpos oreophilus	Mountain snowberry	M+
STRESS TOLERATORS		
Astragalus caespitosus	Cicer milkvetch	M+
Astragalus chamaeleuce	Cicada milkvetch	M+
Astragalus purshii	Pursh milkvetch	M+
Astragalus spatulatus	Spoonleaf milkvetch	M+
Comandra umbellata	Common bastard toadflax	-
Juniperus osteosperma	Utah juniper	M+
Lygodesmia juncea	Rush skeleton plant	M+
Opuntia polyacantha	Plains pricklypear	M+
Phlox muscoides	Cushion phlox	M+
Pinus edulis	Pinyon pine	M+
Townsendia incana	Common townsendia	M+