DOE/ER/60612--4

DE93 000384

NITROGEN AVAILABILITY AS A CONTROL MECHANISM OF SECONDARY SUCCESSION WITHIN A SEMIARID SHRUBLAND ECOSYSTEM

FINAL REPORT

for period October 1, 1990 - June 27, 1992

Edward F. Redente and Terry McLendon

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

25 September 1992

Prepared for
The U.S. Department of Energy
Agreement No. DE-FG02-87ER60612

ABSTRACT

Three experiments were conducted within a semiarid shrubland to test the role of nitrogen (N) availability as a control mechanism in secondary succession. Secondary succession patterns were documented for seven years and effects of increased and decreased N availability levels, fumigation, and competition by early-seral species were tested. Differential responses by seral species were determined and related to successional patterns.

Nitrogen availability was found to be a primary mechanism controlling the rate of succession. Relative growth rate was an important factor determining which species initially dominated and N availability became the primary control factor by the third year. As N availability increased, the rate of succession decreased. Conversely, as N availability was decreased, the rate of succession increased. The abundance of annuals was increased and abundance of perennials decreased by increased N availability. Tissue N concentration was related to lifeform and seral position, and these relationships were important in the transition from early- to mid-seral stages. Decomposer subsystem dynamics were correlated with seral community dynamics. The effect of fumigation was minimized by initially planting with late-seral species. A conceptual model of secondary succession is presented based on N availability, relative growth rate, lifeform, and decomposition dynamics.

TABLE OF CONTENTS

Page

INTRODUCTION

Nutrient Availability and Secondary Succession

Secondary succession is the process of community change following disturbance. The most obvious characteristic of this process is the change in species composition that takes place over time. Those species that dominate early in secondary succession are most commonly rapidly-growing annuals. Those species that dominate the site relatively late in the process, when rate of change in community composition is much slower, are commonly long-lived perennial species with relatively slow growth rates. In many ecosystems, these late-seral species are shrubs or trees which accumulate large amounts of nutrients within their perennial tissues, thereby creating a temporal nutrient sink (Vitousek and Reiners 1975, Lang and Forman 1978). Mid-seral species, commonly herbaceous perennials and short-lived shrubs, dominate seral communities between those of early-seral annuals and late-seral perennials.

Although this pattern is common to most ecosystems and has been recognized since the earliest period of ecology (Cowles 1899, Clements 1916), the mechanisms causing species replacement are still not clearly understood. Seral replacement of species A by species B results from 1) abiotic conditions changing such that they become intolerable for the continued success of species A but not for species B or 2) species B, through accumulation of sufficient biomass or by modification of environmental conditions, denies resources to species A and thereby reduces the ecological success of species A. In either case, changes in the availability of at least one required resource to at least one of the species is involved. The process may or may not involve competitive displacement (Grace 1987), but commonly there seems to be a correlation between species replacement and changes in resource availability (Van Hulst 1978, 1979, Tilman 1990).

Changes in nutrient availability have been observed to occur during secondary succession (Lamb 1980, Parrish and Bazzaz 1982, Smith and Rice 1983, Tilman 1984, Inouye et al. 1987) and these changes have been suggested to be a primary cause of secondary succession rather than simply a result of the successional process (Tilman 1982 and 1987, Inouye et al. 1987, Pastor et al. 1987). Nitrogen (N) is an important plant nutrient that becomes limiting to plant growth in a number of natural ecosystems (Fisher et al. 1988, Robertson et al. 1988, Gleeson and Tilman 1990). Available N has been found to decrease during early secondary succession in some ecosystems (Foster et al. 1980, Vitousek 1983, Dormaar et al. 1990) and the addition of N has been shown to be a major factor modifying successional dynamics in a number of ecosystems following disturbance (Parrish and Bazzaz 1982, Heil and Diemont 1983, Tilman 1984 and 1986, Carson and Barrett 1988, McLendon and Redente 1991 and 1992a).

Species replacement patterns characteristic of secondary succession have been attributed to changes in competitive relationships among species induced by changes in N availability (Raynal and Bazzaz 1975, Peterson and Bazzaz 1978, Tilman 1982, Miller and Werner 1987). Species with higher growth rates are favored over those with slower growth rates under conditions of high N availability (Berendse et al. 1987, Heil and Bruggink 1987, Aerts and Berendse 1988) and early-seral species characteristically have high growth rates (Bazzaz 1979). Therefore, early-seral species, predominantly annuals, may dominate sites by rapidly utilizing the available resource or causing other resources (e.g., light) to become limited to slower-growing species. These rapidly growing early-seral species might continue to dominate a site as long as they can maintain their high production levels. However, high available nutrient levels are required for these species to reach their growth potentials and if resources become too limited to meet these requirements, species with lower nutrient requirements should begin to have a competitive advantage (Grime 1979, Leps et al. 1982, McGraw and Chapin 1989).

Central to this explanation is the concept that secondary succession occurs, at least in part, because of competitive displacement of species (Grace 1987). If true, and if degree of competition increases as a specific resource (e.g., soil N) becomes more limited, the rate of replacement of early-seral species by mid-seral species should increase as the resource becomes more limited. Resource limitation dynamics may, therefore, explain, at least in part, the species replacement patterns that define succession.

If decreased N availability is correlated with secondary succession, there may be a relationship between the seral position of a species and the N concentration of its tissue (Tilman and Wedin 1991). For instance, early-seral species should be able to exploit higher levels of available N more effectively than late-seral species because of the more rapid growth rates of early-seral species (Berendse et al. 1987, Redente et al. 1992). There should also be a relationship between the tissue N concentration of a species and the seral stage in which it is growing, e.g., the tissue N concentration of an early-seral species growing in an early-seral stage should be higher than that of the same species growing in a late-seral stage. In addition, if late-seral species are more effective N competitors than early-seral species under low N availability conditions (Wedin and Tilman 1990, Redente et al. 1992), the difference in tissue N concentration under early- and late-seral stages should be less for late-seral species than for early-seral species.

Objectives Associated With Nutrient Availability and Succession

We believe that N availability is a primary mechanism controlling the rate and direction of secondary succession and that the species replacements that define succession are, at least in part, the result of differential responses by species to changes in N availability. Three steps necessary to the development of this hypothesis are 1) to show that patterns of seral replacements during secondary succession can be experimentally controlled by manipulating N availability, 2) to show that these species replacements are correlated with differential responses by plant species to changes in N availability, and 3) to show how such changes in N availability occur naturally during secondary succession.

The validity of the first step has been established for European mesic shrublands (Heil and Diemont 1983, Heil and Bruggink 1987, Aerts and Berendse 1988) and for old field communities in eastern North America (Parrish and Bazzaz 1982, Tilman 1984, Carson and Barrett 1988, Wilson and Tilman 1991). A primary objective of the research which is the subject of this report was to determine whether or not it was also valid for semiarid shrublands. Results from two of the experiments summarized in this report (McLendon and Redente 1991, 1992a) have established this validity by showing that an increase in available N slows the rate of secondary succession and a decrease in N availability increases the rate of secondary succession on a disturbed semiarid shrubland site. Three additional manuscripts, one in press (McLendon and Redente 1992b) and two in preparation (McLendon and Redente 1992c, Stevenson et al. 1992), address the related questions of 1) the validity of postulated relationships between tissue N concentration and seral position, 2) how changes in N availability occur naturally during secondary succession, and 3) how such changes in N availability function as a control mechanism through differential responses of plant species to N availability gradients. Work partially supported by this grant has also led to the development of a conceptual model of the roles of N availability, relative growth rate, and decomposition rate as control mechanisms in secondary succession in semiarid shrubland ecosystems (McLendon and Redente 1992b).

METHODS

Study Area

The study area was located in the Piceance Basin of northwest Colorado, approximately 70 km northwest of Rifle, Colorado, at an elevation of 2020 m. The climate is semiarid with mean annual precipitation of approximately 28 cm, half of which occurs as snowfall. Soils are Yamac loams (fine-loamy mixed, Borollic Camborthids) and the pre-disturbance plant community was a big sagebrush (Artemisia tridentata) shrubland with a predominantly perennial-grass understory composed primarily of Agropyron dasystachyum, Agropyron smithii, Koeleria pyramidata, Cryzopsis hymenoides, and Stipa comata.

A disturbance was created within each of four blocks within the sagebrush community in the summer of 1984, each block serving as a replication. Within each block, the existing vegetation and top 5 cm of topsoil were removed by scraping with a bulldozer and the next 35 cm of soil was mixed with a motor-grader. This disturbance was used to simulate anthropic disturbances associated with energy development and commonly found throughout the Colorado Plateau. The disturbance led to a 90% reduction in soil seed bank (Carpenter et al. 1990). After soil disturbance, ten experimental treatment plots (500 m^2 each) were established in each of the four blocks. The ten plots per replication were used to conduct three experiments: 1) N and P Experiment (4 plots per replication), 2) Sucrose Experiment (1 plot per replication), and 3) Fumigation Experiment (5 plots per replication). A fifth experimental treatment plot (500 m^2) was established in an undisturbed portion of the sagebrush community adjacent to each of the four disturbed blocks and was used as an undisturbed control.

N and P Experiment

The purposes of the N and P Experiment were to determine the patterns of secondary succession within a semiarid shrubland ecosystem and the effects of increased nitrogen (N) and phosphorus (P) availabilities on these patterns. There were five treatments, each replicated within each of the four blocks:

Treatment 1:	Control (disturbed but not fertilized, i.e., natural nutrient availabilities following disturbance);
Treatment 2:	Phosphorus (disturbed and fertilized with triple super phosphate at a P level of 100 kg/ha/yr, i.e., elevated P availability but unelevated N availability);
Treatment 3:	Nitrogen (disturbed and fertilized with ammonium nitrate at a N level of 100 kg/ha/yr, i.e., elevated N availability but unelevated P availability);
Treatment 4:	Nitrogen + Phosphorus (disturbed and fertilized with ammonium nitrate at a N level of 100 kg/ha/yr and with triple super phosphate at a P level of 100 kg/ha/yr, i.e., elevated N availability and elevated P availability); and
Treatment 5:	Undisturbed (undisturbed and unfertilized sagebrush community).

Fertilizer applications were hand-broadcast annually in three equal increments (spring, early summer, and late summer) except for 1984 when the entire annual amount was added in October.

The vegetation was sampled annually beginning in 1985. At each of two sampling dates (early- and late-summer), 10 quadrats (each 0.5 m^2) were randomly located within each of the 20 plots. Treatment 5 (undisturbed) plots were not sampled in 1988-90. If a quadrat location overlapped a previously sampled location, that quadrat was randomly relocated. Current-year aboveground biomass was harvested to ground level by species, oven-dried (48 C), and weighed. For shrubs, only the current-year's leaves and twigs were harvested. Samples from the 10 quadrats were composited for each plot. The two sampling dates were considered adequate to estimate annual aboveground net primary production since plant growth at the study site occurs in two pulses during the growing season (Lauenroth et al. 1987, McLendon and Redente 1991). Cool-season species primarily grow from late April to late June and warm-season species from late May through August. The total annual aboveground production for each species was taken to be the larger of the values of the two sampling dates. Harvested material, by species and by plot, from 1987-91 was analyzed for tissue N concentration by the micro-Kjeldahl process (Bremner 1965). Five soil samples (0-20 cm depth) were collected from each plot in August 1991. The samples were randomly selected from 5 of the 10 quadrat locations used in the August vegetation sampling. The five samples were composited by plot into a single sample and all samples were collected within 18 hours. The samples were kept on ice until delivered to the laboratory and were analyzed for NO_3-N, NH_4-N, total phosphorus, and total organic matter.

Univariate (paired t-tests) and multivariate (stepwise discriminant analysis) techniques were used to analyze the data. Effect of year was tested by testing the significance of differences in aboveground production and relative biomass annual means of each lifeform and of each major species between years by use of paired t-tests. All two-way combinations of years were tested with separate analyses used for each treatment. Paired t-tests, rather than analysis of variance and a mean separation test, were used because there were significant year-to-year differences between replications for some variables after the third seral year (i.e., succession was progressing more rapidly within some blocks than within others, although the patterns and response to treatments were the same). Pairing by replication is a useful method of eliminating among-pair variation (Li 1964, Snedecor and Cochran 1967). However, use of paired t-tests to test combinations of pairs (in our case, years) may increase the probability of Type I error (John 1971). Under such conditions, multivariate analyses should be used to verify the conclusions reached by the univariate analyses (Stroup and Stubbendieck 1983, Gurevitch and Chester 1986). We did so by use of discriminant analysis. Significance of differences between annual means within treatments for species richness and for tissue N concentration were tested in a similar manner.

Stepwise discriminant analysis (Lachenbruch 1975) was used to multivariately test differences among treatment-year groups (Matthews 1979, McLendon and Dahl 1983). Two discriminant analyses were used. The first included the control, phosphorus, and undisturbed plots. This analysis multivariately tested the conclusions reached by using paired t-tests on time series data and established the seral pattern on control plots. The second discriminant analysis included the nitrogen and nitrogen + phosphorus plots with the control, phosphorus, and undisturbed plots to test the effect on N addition on seral dynamics.

Sucrose Experiment

Results from the N and P Experiment established that increased N availability slows the rate of secondary succession within the semiarid shrubland ecosystem we studied. The purpose of the Sucrose Experiment was to determine if the reverse is also true, i.e., will a decrease in N availability increase the rate of secondary succession? In this experiment, we used the concept of N immobilization by decomposers to test the effect of an induced N availability gradient on the replacement of plant species during early stages of secondary succession. We added sucrose as a rapidly utilizable energy source for the purpose of decreasing available soil N by increasing decomposer biomass (Lamb 1980, Hunt et al. 1988). We then compared species composition dynamics on plots receiving sucrose (low available N) to those receiving supplemental N (high available N) and to control plots receiving no amendments (intermediate available N).

One unfertilized 500-m^2 plot within each of the four blocks that were disturbed in 1984 was weeded by hand for two years following disturbance. In November 1987, these plots were seeded with a mixture of species characteristic of both early- and late-seral stages at the site to minimize the effect of migration as a possible factor in the early seral dynamics of the plots. Each plot was subdivided into three equal-sized (160 m^2) subplots and each subplot received one of three treatments:

Treatment 1:	Control (disturbed, weeded, and seeded, but with no additions, i.e., intermediate N availability);
Treatment 2:	Nitrogen (disturbed, weeded, seeded, and fertilized with ammonium nitrate at 100 kg N/ha/yr, i.e., high N availability); and
Treatment 3:	Sucrose (disturbed, weeded, seeded, and sucrose added at a rate of 1600 kg C/ha/yr, i.e., low N availability).

The N and sucrose were hand broadcast annually, the N in three equal increments (spring, early summer, and late summer) and the sucrose at eight equal increments (spring to late summer). The sucrose was applied more frequently to allow for a more uniform microbial uptake.

Sampling began in 1988 and was conducted at two dates (early- and late-summer) annually for three years. At each sampling date, 20 quadrats (0.25 m^2) were randomly located within each of the 12 subplots. Within each quadrat, canopy cover was estimated by species and number of plants was recorded by species. Canopy cover was converted to relative canopy cover for statistical analysis to minimize variation due to annual fluctuations in precipitation and to possible annual variations between blocks. The data were analyzed by use of Student's t-tests (Snedecor and Cochran 1967) for each species, each life-form group (shrubs, perennial grasses, perennial forbs, annual grasses, and annual forbs), and for species richness by treatment for each year and overall.

In September 1990, each subplot was divided into quarters and samples of five major species representative of different seral positions at the site were collected from each quarter. In the event that a given species was not present within a quarter, another sample was collected from one of the remaining quarters. Approximately 5 g of aboveground material was collected (clipped to ground level) for each species within each quarter from one individual, or from several individuals if there was insufficient material available from a single plant. All samples within a quarter were collected from locations as near to each other as possible to minimize microtopographical variation. In addition, one soil sample (1-20 cm composite) was taken from the center of each quarter. All samples were dried and analyzed for total N content by the micro-Kjeldahl process. The species sampled included two annual forbs (Kochia scoparia and Salsola iberica), one perennial forb (Aster canescens), one perennial grass (Agropyron smithii), and one shrub (Chrysothamnus nauseosus). The five species formed the seral gradient:

Salsola > Kochia > Aster > Agropyron > Chrysothamnus

based on temporal position of dominance or subdominance characteristic of each species (McLendon and Redente 1991, 1992a).

Fumigation Experiment

The N and P Experiment and the Sucrose Experiment established the potential of N availability as a control mechanism in secondary succession within semiarid shrubland ecosystems. However, for N availability to be established as an actual control mechanism in natural systems, the method whereby N availability changes during naturally occurring secondary succession must also be determined.

We believe that this method resides in the dynamics of the decomposer subsystem and its coupling to the seral plant communities. The purpose of the Fumigation Experiment was to determine if radical changes in the decomposer subsystem immediately following disturbance would have a significant effect on subsequent successional dynamics. If so, this would begin to link seral dynamics within the decomposer subsystem to those of the plant communities.

Three unfertilized 500-m^2 plots within each of the four blocks were separated from adjacent plots by placing plywood (2 cm thick) strips 50 cm into the ground around their perimeters. In September 1984, these plots were covered with plastic tarps and fumigated by injecting approximately 3 kg of methyl bromide under the tarps at 5 m intervals, resulting in an application of 45 kg of methyl bromide per plot. The tarps were left for 24 hours to allow for an adequate reduction of microbial populations.

This experiment consisted of seven treatments, each applied to one 500-m^2 plot within each of the four blocks:

Treatment 1:	Undisturbed control (undisturbed, not fumigated nor seeded);
Treatment 2:	Fumigated control (disturbed, fumigated, but not seeded);
Treatment 3:	Fumigated climax (disturbed, fumigated, and seeded to a mixture of late-seral species);
Treatment 4:	Fumigated ruderal (disturbed, fumigated, and seeded to a mixture of early-seral species);
Treatment 5:	Non-fumigated control (disturbed, not fumigated nor seeded);
Treatment 6:	Non-fumigated climax (disturbed but not fumigated, seeded to the same mixture of late-seral species as Treatment 3); and

Treatment 7: Non-fumigated ruderal (disturbed but not fumigated, seeded to the same mixture of early-seral species as Treatment 4.

In October 1984, big sagebrush seedlings were transplanted into the fumigated climax and the non-fumigated climax plots at a density of approximately 0.3 seedlings per m^2. In November 1984, the seeded treatment plots were broadcast with their appropriate seed mixtures (Redente and Cook 1986) and the plots were lightly hand-raked to cover the seed.

Succession was allowed to progress on each of these plots for 7 years. The vegetation was sampled at two dates (June and August) during the summer of 1991 by the same methodology as in the N and P Experiment. At each date, one soil core (5-10 cm depth) was collected from the center of each clipped quadrat. Two composite samples per plot were created by randomly combining five of the soil cores into each composite sample. Soil samples were placed on ice immediately after sampling and transported to the laboratory. Each composite sample was thoroughly mixed and then separated into two parts. One portion was analyzed for organic matter content, total N and KCl-extractable NH_4-N (kjeldahl method), mineralizable N, NO_3-N and P (DPTA-extractable), soil moisture, EC, and pH. The second portion was used to analyze for vesicular-arbuscular mycorrhizal fungi infection levels using a corn-bioassay method (Moorman and Reeves 1979).

Decomposition rates were measured within each plot by the weight-loss method. Two litter bags made from 1.4 mm mesh fiberglass screen were filled with 3 g of plant material and placed at ground surface in each plot in July 1991. The plant material within all bags was taken from a composite sample consisting of equal amounts of the three most abundant species from each of the four non-fumigated control and the four undisturbed control plots sampled in June 1991. Prior to placement within the bags the plant material was analyzed for lignin, ash, and total N contents. The bags were collected in July 1992, reweighed, and the material within each bag analyzed for lignin and total N. All plant material was ashed to determine ash-free weights.

Significance of differences in plant community composition among the treatments was tested by use of stepwise discriminant analysis. Differences in treatment means for each plant, soil, and decomposer subsystem variable were tested by use of analysis of variance and paired t-tests and possible significant relationships between variables were tested by correlation analysis.

RESULTS

N and P Experiment

Both univariate and multivariate analyses indicated that there were no significant ($P < 0.05$) overall differences in species composition or production values between control and phosphorus or between nitrogen and nitrogen + phosphorus plots. Therefore, control and phosphorus plots were pooled into a single treatment and nitrogen and nitrogen + phosphorus plots were pooled into a second treatment. Throughout the remainder of this report, unless overwise stated, the term control, in reference to the N and P Experiment, will be applied to the pooled group consisting of the four control and the four phosphorus plots and the nitrogen treatment designation will be applied to the pooled group consisting of the four nitrogen plus the four nitrogen + phosphorus plots.

During the first seven years following disturbance, secondary succession on control plots proceeded through four seral communities that differed enough from each other to be easily recognizable and to be separated statistically (Table 1). However, with the exception of the second-year Salsola-dominated seral community, annual differences between seral communities were relatively indistinct and consisted of gradual year-to-year transitions in species composition rather than sudden shifts from one year to the next (Table 2, Fig. 1). Annual forbs dominate the site for the first two years following disturbance and are followed by the annual grass Bromus tectorum the third year. Control plots are dominated by a transitional seral community for the next three years (third seral community, Table 1) where mid-seral shrubs, primarily Chrysothamnus nauseosus, and mid-seral perennial grasses become increasingly important and the importance of annuals decreases. Perennials become site-dominant by the seventh year following disturbance and this seral community is dominated by perennial grasses with a strong mid-seral shrub subdominance.

Maximum aboveground production occurred the second-year following disturbance (Table 3), the result of large production by annual forbs, primarily Salsola iberica. Production by annual forbs decreased dramatically after the second year and overall production became relatively stable by the fourth year. Annual aboveground production by perennial grasses approximately doubled each year for the first four years and then increased by approximately 50% annually thereafter. Aboveground production by shrubs also increased through the seventh year and seventh-year shrub production on control plots was approximately one-third that of the undisturbed community. However, shrub production on disturbed plots was primarily from the mid-seral shrubs _Chrysothamnus nauseosus_ and _Gutierrezia sarothrae_ rather from the late-seral shrub _Artemisia tridentata_ which produced most of the production within the undisturbed community.

Mean species richness increased with succession through the fifth year then declined to approximately the level of the undisturbed community (Table 3). Annual recruitment of new species decreased steadily from the first year and the undisturbed community did not contain any species that were not present within at least some of the control plots by the seventh year. Thirty-eight plant species were encountered on control plots during the seven years in sufficient quantities to determine seral indices for the species. Of these, 19 were early-seral species, 11 were mid-seral, and 8 were late-seral (Table 4). Annuals predominated as early-seral species and perennial grasses and shrubs as mid- and late-seral species. All annuals were early-seral species and early-seral species were predominately (84%) forbs.

Tissue N concentration was affected by species, lifeform, and seral year (Table 5, Fig. 2). Grasses had lower tissue N concentrations than shrubs and forbs and tissue N concentration varied more among species within the forb lifeform than within the shrub or grass lifeforms. In general, annual forbs had higher tissue N concentrations than did perennial forbs. Tissue N concentration of most species was affected by secondary succession but this effect was influenced by lifeform and relative seral position of the species. Tissue N concentration of shrubs and perennial grasses decreased along the seral gradient (1987 to undisturbed, Table 5). Tissue N concentration also decreased in forbs, but the pattern was not uniform, perhaps the result of the diverse ecological, morphological, and physiological characteristics within this lifeform. Mid- and late-seral species within each lifeform exhibited a pattern of decreasing values over the seral gradient but the pattern was weak or non-existent in early-seral species (Fig. 3). Tissue N concentrations were lowest for all lifeforms and all relative seral positions within lifeforms on the undisturbed plots.

The first-year seral community incorporated approximately 1450 mg N/m^2 within aboveground plant biomass (Table 6). This amount more than tripled during the second year and then gradually decreased during the next three years. From the fourth seral year, N incorporation on the control plots was relatively constant and approximated that of the undisturbed community. Mean tissue N concentration remained virtually constant within the undisturbed community and surprisingly stable within the undisturbed seral communities after the first year (Table 6) despite a wide variation in source of incorporation and tissue N concentration of the species involved (Table 5).

The addition of N significantly altered seral dynamics. Plots receiving additional N remained dominated by annuals through the seventh year (Figs. 4 and 5). Plots receiving additional N supported seral communities within greater amounts of annual forbs and total annual production than those on control plots and lesser amounts of shrubs, perennial grasses, and perennial forbs. Annual grass production (Bromus tectorum) was not significantly affected by N addition but species richness was reduced after the second year. Tissue N concentrations were higher on plots receiving additional N than on control plots for most species and for all lifeforms, although the degree of increase on N plots over values on control plots (i.e., luxury consumption) varied by species, lifeform, and relative seral position. Luxury consumption was greatest by perennial grasses and least by shrubs and legumes (Table 7). Addition of N resulted in an increased N incorporation in aboveground tissue, over that on control plots, of 216% the second seral year, decreasing to 165% over control by the seventh year. Three species, all annuals, accounted for 86% of N incorporation on N plots. Salsola iberica dominated the N incorporation on N plots during the first two years (69%) and Kochia scoparia and Bromus tectorum dominated thereafter (58%).

Sucrose Experiment

Plots receiving sucrose supported seral communities that were more species rich, had more perennial forbs and annual grasses, and had less annual forbs than those receiving the N treatment (Table 8). Sucrose plots also consistently had higher amounts of shrubs and perennial grasses than N and control plots (Fig. 6). Aboveground tissue N concentrations at the end of the study displayed a pattern consistent with the seral pattern of the species (Fig. 7). The N concentrations of both early-seral forbs (Salsola iberica and Kochia scoparia) differed significantly among all treatments, increasing from the low (sucrose) to the high (N) treatments. The two mid-seral herbaceous species (Aster canescens and Agropyron smithii) displayed patterns similar to each other but different from the early-seral response pattern. Nitrogen concentration increased in the mid-seral species between sucrose and N treatments, but not between sucrose and control treatments and their N concentrations increased much less between sucrose and N treatments than with the early-seral species. Nitrogen concentration in the species occurring last in the seral gradient, Chrysothamnus nauseosus, was not influenced by treatment and, of the five major species, had the highest N concentration under the low-available N (i.e., sucrose) treatment.

Fumigation Experiment

Fumigation had a significant effect on seral development seven years after disturbance and fumigation, but this effect was modified by seeding regime. The multivariate statistical analysis indicated that the fumigated control (unseeded) plots had significantly less seral development (i.e., less similar to the undisturbed community) than non-fumigated control plots (Tables 9, 10). However, seral communities on fumigated-ruderal plots (i.e., those disturbed in 1984 and seeded to early-seral species) were not significantly different from those on non-fumigated ruderal plots and seral communities on non-fumigated ruderal plots were not significantly different from those on non-fumigated control plots. Seral communities on all four of these treatments were significantly different from those on plots seeded to late-seral species and from the undisturbed community. Fumigation had no significant effect after seven years on plots seeded to late-seral species.

Fumigation decreased the relative biomass of perennial grasses and perennial forbs, increased that of annual grasses, and had no significant effect on the relative biomass of shrubs and annual forbs (Table 11) or total aboveground production (Table 12). Overall, fumigation had no significant effect on relative biomass of late-seral species but increased the abundance of mid-seral species and decreased the abundance of early-seral species (Table 11). Of the 12 major species tested, fumigation decreased the abundance of two (Gutierrezia sarothrae and Oryzopsis hymenoides) and increased the abundance of two (Koeleria pyramidata and Kochia scoparia). Fumigation also decreased species richness and the rate of decomposition (Table 12). Organic matter content and pH were higher on non-fumigated plots than on plots that were fumigated and electrical conductivity was lower (Table 12). Although the means of these three soil variables were statistically different between treatments, the differences were small and may not be important ecologically.

There was a significant seeding effect on relative biomass of all lifeforms except biennial forbs (Table 11). Seeding to late-seral species increased the abundance of shrubs and perennial grasses and decreased the abundance of perennial forbs and annual grasses over the respective values on control plots. Perennial grasses were also more abundant and annual grasses and annual forbs less abundant on plots seeded to late-seral species than on those seeded to early-seral species. Plots seeded to early-seral species also had less perennial forbs and less annual grasses than control plots. Late-seral species were more abundant and early-seral species were less abundant on late-seral seeded plots than on either control or early-seral seeded plots (Table 11). Four species, all part of the original seeding mixture, were most abundant on plots seeded to late-seral species and two species, also within the respective seeding mixture, were most abundant on the early-seral plots (Table 11). Two species, Bromus tectorum and Oryzopsis hymenoides, were most abundant on control plots and the mid-seral shrub Chrysothamnus nauseosus was equally abundant on control and early-seral seeded plots in spite of the fact that it had been seeded on the later. Total aboveground production was highest on control plots and species richness was lowest on plots seeded to late-seral species (Table 12).

Decomposition was slowest on control plots and was not significantly different between plots seeded to late-seral species and plots seeded to early-seral species (Table 12). Control plots had the lowest organic matter contents, lowest NH_4-N concentrations, and highest NO_3-N concentrations of the three seeding treatments and P concentrations were lowest on plots seeded to late-seral species (Table 12).

DISCUSSION

Effect of N availability on secondary succession in a semiarid shrubland

Results of the N and P Experiment and the Sucrose Experiment establish the fact that the rate of secondary succession within the disturbed semiarid shrubland that we studied can be effectively controlled by manipulating available soil N. Increased N availability decreases the rate of secondary succession and decreased N availability increases the rate. Under conditions of natural secondary succession following anthropic mechanical disturbance (the control plots of the N and P and the Sucrose Experiments, i.e., disturbed but without further manipulation of N availability), a mixed shrub-perennial grass seral community dominated the site within seven years of disturbance. Annual forb communities dominated for only two years and an annual grass community for one year. Throughout the seven years, shrubs and perennial grasses increased in abundance gradually but continually and most mid- and late-seral species were present from the earliest seral stages. Species richness increased through the third year and then declined slightly to the level of the undisturbed community.

Increased N availability, experimentally induced by the annual application of 100 kg N/ha, effectively stopped succession. Plots receiving supplemental N remained dominated by an annual forb seral community seven years after disturbance and five years after the annual forb communities on control plots were replaced. Most of the major mid-and late-seral species on control plots were present on these N plots, but their relative abundance was low and they were unable to increase significantly and species richness was reduced. In contrast, succession was more rapid than on control plots on plots where N availability was experimentally reduced below control levels by annual applications of sucrose.

Differential responses of plant species to changes in N availability

Succession is most often defined in terms of changes in species composition over time. For species composition to change, there must be some differential response of the individual species to changing conditions, whatever the cause of the change in conditions. The factor of interest that changed in our experimental systems was N availability and we have shown that these changes in N availability induced changes in species composition that correspond to patterns corresponding to naturally occurring seral communities within the region. However, for species composition to change there must be at least one mechanism operating that induces differential responses among the seral species. And for this to be relevant to our research, this mechanism must be directly related to N availability.

Our data suggest that this mechanism can be defined in terms of three factors: 1) relative growth rate, 2) the resultant N requirement for tissue production, and 3) relative competitive ability to secure this required N. The initial seral community at our site is dominated by annual forbs (76% relative biomass, Table 1), of which Salsola iberica is most important. These species have rapid growth rates (Redente et al. 1992), producing large amounts of biomass within a single growing season (over 400 g/m^2 the second seral year, Table 3). These species also have relatively high N concentrations within their tissues (Table 5). Under conditions of relatively high N availability, these species are effective accumulators of N and are able to secure the levels of N necessary to produce the large quantities of aboveground biomass that result in their dominance of the site. They apparently dominate the site by securing large amounts of a number of resources (e.g., space, light, moisture, N) and thereby denying these resources to slower-growing species such as shrubs and perennial grasses. As long as belowground resources are sufficient, competitive advantage should rest with those species that have rapid growth rates and are able to allocate maximum amounts of resources to aboveground tissue (Iwasa and Roughgarden 1984, Ingestad and Agren 1991). Without their rapid rates of growth, annual forbs probably could not secure these resources against perennials. Any resource limiting the growth of the annuals could present a barrier to their continued dominance since without large biomass production they cannot secure the other resources (Grime 1973, Shipley and Peters 1990). Nitrogen apparently becomes the first resource that limits high biomass production by annuals since the addition of N allows annual forbs to continue their dominance. Wilson and Tilman (1991) found that as N availability decreased, competition for aboveground resources decreased and competition for belowground resources intensified.

As N availability decreases at our site during secondary succession (discussed under the next heading), production by annual forbs becomes more limited and other resources become more available to species with lower N requirements for tissue production. Overall, grasses require 30-40% less N than annual forbs for biomass production (Table 7). Therefore, as N availability decreases, grasses have an increased competitive advantage over annual forbs because grasses are able to produce more biomass per unit of available N and their increased biomass production allows them to secure more of other potentially limited resources. The grass Bromus tectorum replaced the annual forbs as the third-year dominant (Table 1) and this annual grass had the lowest average N requirement of all species sampled except for the succulent Opuntia polyacantha (Table 5). In addition, grasses are able to tolerate decreasing available N levels better than other species (rate of change between 1987 tissue N concentration and 1991 concentration, Table 5) and, therefore, become increasingly tolerant of decreasing available N levels. Therefore, N availability is the trigger that causes the shift from dominance by rapidly-growing and resource-exploitive annual forbs to slower growing (Redente et al. 1992) grasses which exploit resources less rapidly than annual forbs but which maintain their control over these resources for longer periods of time (i.e., perennial growth habit).

Not only do mid-seral perennial grasses have lower tissue N requirements than early-seral annual forbs but the perennials also have increased ability to secure limited soil resources such as moisture and N. Two primary reasons perennials have this advantage in resource acquisition are 1) their perennial growth habit which allows for access to a greater resource volume-space and a longer resource tenure than possible with an annual growth habit and 2) greater mutualistic coupling relationships with the decomposer subsystem. The annuals that dominate early in secondary succession in our system have high shoot:root ratios (Redente et al. 1992) and are non-mycorrhizal (Doerr et al. 1984). Both of these characteristics are useful immediately following disturbance because belowground resources are relatively abundant, but become detrimental as competition for belowground resources intensifies. The mid-seral perennial species have greater root:shoot ratios than the annuals (Redente et al. 1992) and they are mycorrhizal (Doerr et al. 1984). The perennial and more extensive root systems of the mid-seral species allow them to exploit greater soil volume, thereby accessing supplies of soil N unavailable to annuals and, in turn, having an increasingly important effect on soil N availability (Wedin and Tilman 1990). The mycorrhizal linkages allow for transfer of nutrients among root systems and greater saturation of the entire rooting zone (Francis et al. 1986, Hetrick et al. 1989). The net effect of such linkages may be to increase the "directing" of belowground resources to the host plants, thus increasing their competitive advantage over non-mycorrhizal species.

Decrease in N availability during secondary succession

Our research has established that experimentally induced changes in N availability have significant effects on successional dynamics within a semiarid shrubland ecosystem and that species characteristic of different seral positions within this succession respond differently to these changes in N availability. Both of these points were necessary to establish the role of N availability as a control mechanism in secondary succession. However, a third point must also be established, i.e., how do the necessary changes in N availability occur naturally following a disturbance? Specifically, 1) what causes N availability to increase immediately following disturbance and 2) what causes it to decline as succession proceeds?

Available soil N was not measured annually during this study. However, soil samples were taken from each plot within the N and P Experiment in 1991 and analyzed for concentrations of NO_3-N, NH_4-N, total N, and organic matter. Control plots had higher NO_3-N levels than did adjacent undisturbed plots (Fig. 8). Assuming that soil N levels were statistically equal between the undisturbed plots and the control plots prior to disturbance, the increased soil N on control plots in 1991 had to come from somewhere. The most probable sources would be the decomposition and mineralization of the belowground biomass of the late-seral community and the mineralization of a portion of the soil organic matter following disturbance. Control plot soils contained less organic matter than undisturbed soils seven years after disturbance (Fig. 8) and the N content of this mineralized organic matter was probably added to the available N pool. In addition, we have estimated that the decomposition and mineralization of belowground plant material during the first two years following disturbance may have released approximately 2.8 $g/N/m^2$ into the upper 30 cm of the soil profile on the disturbed sites (McLendon and Redente 1992b). These two sources of N, plus surplus first-year atmospheric inputs, should have been sufficient to significantly raise the available N levels within the upper profiles of the disturbed plots, perhaps by approximately 6.2 g N/m^2 within the top 30 cm of the profile (McLendon and Redente 1992b). This answers the question as to how available N levels initially increase following disturbance.

These high levels of available N allow annuals to produce large amounts of aboveground biomass and dominate the site. However, these high production levels should rapidly reduce the available soil N pool within their rooting zone because the rate of incorporation exceeds the rate of decomposition and mineralization (e.g., Foster et al. 1980). Aboveground primary production on control plots in 1986 was 404 g/m^2 which incorporated 5.7 g N/m^2 in aboveground plant tissue (Table 6) with perhaps an additional 0.9 g N/m^2 in belowground biomass (McLendon and Redente 1992b). These two values sum to 6.6 g/m^2, which exceeds the estimated available soil N pool of 6.2 g N/m^2 in the upper 30 cm of the soil profile (McLendon and Redente 1992b). Therefore, the Salsola-dominated second-year seral community probably depleted the available N pool to a depth of 30-35 cm.

Vitousek (1983) reported that only 13% of N within ragweed (Ambrosia artemisiifolia) litter in a mesic oldfield community was returned to the soil within five months. Pastor et al. (1987) found that after the first month, N in little bluestem (Schizachyrium scoparium) litter in Minnesota was immobilized for at least 18 months. Decomposition of, and N release from, Salsola litter at our site is probably slower than ragweed or little bluestem litter in those studies because of the semiarid climate at our site and because most Salsola litter is not deposited at the soil surface but remains well above the surface for 1-3 years. Decomposition rate increases as contact with the soil is increased (Holland and Coleman 1987). Therefore, little of the large quantity of N incorporated within the Salsola litter the second seral year probably was returned to the soil by the beginning of the third growing season. The result would have been a significant N deficiency in the upper 30-35 cm of the soil profile, the zone in which most annuals are dependent upon (at least as seedlings) for their N supply. This could explain why annual forbs, with their high N requirement, did not dominate control plots the third year. In support of this hypothesis, annual forbs did dominate those plots the third year that received additional N.

Control plots were dominated the third year by the annual grass Bromus tectorum. The ability of Bromus tectorum to begin growth early in the growing season gives it a competitive advantage over most associated species (Eckert and Evans 1963, Harris 1967) and at our site would have allowed it to preemptively utilize whatever small amounts of N may have become available through decomposition or from precipitation. The high N-use efficiency of this species (Table 5) would have given it a strong competitive advantage over the associated annual forbs and its rapid growth rate would have given it at least temporary advantage over associated young perennials in preemptive utilization of N and soil moisture (Link et al. 1990).

Total aboveground annual production on control plots continued to decrease the fourth seral year and then stabilized at approximately the level of the undisturbed community (Table 3). The fourth year was the first year that annuals produced less than 50% of the total annual aboveground production on control plots (Table 1) and perennials produced over 60% of total annual aboveground production on control plots from the fifth year. The low tissue N concentrations of perennial grasses (Table 5) should give them competitive advantage over annual forbs under conditions of low N availability and once established, perennial grasses have advantage over Bromus tectorum, in part, because their perennial and more extensive root systems give them a competitive advantage belowground (Bookman and Mack 1982). We believe that by the time decomposition and mineralization returned significant amounts of the N incorporated in the second- (Salsola) and third-year (Bromus) litter (perhaps by the fifth seral year) perennials had become sufficiently established to effectively exploit these N resources, as well as moisture and other soil resources, as they became available.

Therefore, we suggest that incorporation of large amounts of available N in the biomass produced by annuals and a subsequent slow rate of decomposition and mineralization caused a decrease in available soil N early in secondary succession. Differences in growth rate, tissue N concentration, and growth habit then resulted in changes in competitive advantage among species as N availability decreases. We believe that these dynamics are the primary causes of the replacement of annuals by perennials during early secondary succession.

Nitrogen is a major resource required for the production of plant biomass and the rate of secondary succession is significantly influenced by its availability. In the semiarid system we studied, the rate of species replacement is inversely related to the availability of soil N. The decomposer subsystem is a primary component in the supply of available soil N. The application of sucrose carbon decreased available soil NO_3-N levels (Fig. 7). Similar results have been reported in laboratory systems utilizing glucose (Lamb 1980) and starch (Robertson 1982) and have been attributed to greater N use by heterotrophic microorganisms which have increased competitive advantage as C:N ratios increase. A similar reduction in available soil N levels apparently occurs during early secondary succession as large amounts of litter are quickly added to the system. Under such conditions, decomposition rate would be important in the successional process for at least two reasons: 1) the replenishment of available soil N through mineralization and 2) the reduction of available soil N through immobilization. The rate of species replacement during secondary succession may be slowed by an increase in mineralization and accelerated by increased immobilization.

Fumigation had a significant initial effect on the decomposer subsystem (Redente and Cook 1986). Overall activity levels of the decomposers were significantly reduced nine months after fumigation, the composition of saprobic fungi was altered, and mycorrhizal inoculum potential (MIP) values were greatly reduced (from 8.0 to 0.6 on fumigated control plots before and after fumigation, respectively). MIP levels on fumigated control plots declined further during the nine months following fumigation (0.3 in the summer of 1985).

Seven years after fumigation, the decomposer subsystem continued to show a negative effect. The rate of decomposition was 20% slower on fumigated plots than on non-fumigated plots (Table 12), indicating a lower activity level on fumigated plots and suggesting that successional redevelopment following disturbance also takes place within the decomposer subsystem. The effect of fumigation was minimized on plots seeded to late-seral species (Table 9), also suggesting a linkage between the seral plant community and redevelopment of the decomposer subsystem. Plots seeded to late-seral species were the most successionally advanced (Tables 9 and 11) and had lower soil NO_3-N concentrations than the less successionally advanced control plots (Table 12).

Conceptual Model

Based on this research and of related research at other sites, we have developed a conceptual model of the role of N availability as a mechanism controlling the rate of secondary succession (Fig. 9). The available soil N pool is initially high following most disturbances in most ecosystems. This allows annual forbs to dominate early seral stages because of their rapid growth rates which allow them to accumulate large quantities of resources. Although perennial seedlings may also be present in these early seral communities, the accumulation of soil resources and the domination of access to aboveground resources by rapidly growing annuals effectively denies most of these resources to the perennials, thereby limiting their growth early in succession. However, annuals can not deny all resources to perennials. Therefore, perennials do increase in biomass and relative importance over time. As they do, they eventually dominate the site, but the rate is slow as long as available N remains high.

Relatively high levels of available N are required to support the high biomass production that allows annuals to dominate the site. Annuals are effective accumulators under conditions of high available N, in part because of rapid growth rates, thus annuals possess a significant competitive advantage over slower-growing perennials. As available N decreases, annuals do not have sufficient N available to sustain the rapid and abundant production of biomass required for them to dominate the site. Since perennials have lower N requirements per unit biomass than annuals, conditions of lower available soil N affects them less. As a result, growth rates of perennials are nearer their optimum, resulting in increased competitive advantage to perennials. Similar relationships involving growth rate, lifeform, N availability, and seral position also exist within perennial species characteristic of mid- and late-seral stages (Fig. 9).

However, for N limitation to be a possible control mechanism in secondary succession, there must be a naturally occurring process that could cause such limitations. We believe that there are at least five.

1) Incorporation of N within biomass produced by annuals.
   Annuals produce large amounts of biomass in relatively short periods even in semiarid zones. Annual-dominated early-seral communities on control plots within our system produced as much as 300 g/m^2 aboveground biomass within 60 days. Annual N incorporation within this tissue exceeded 6 g/m^2 on some plots.

2) Slow rate of decomposition early in secondary succession.
   At least two factors slow decomposition. First, annuals typically have high shoot:root ratios; therefore, most of their production becomes aboveground litter, which has a slower decomposition rate than belowground litter. Second, as available soil N levels decrease because of incorporation into the biomass of annuals, less N is available for decomposers and immobilization exceeds mineralization. Because of these two factors, mineralization of N during early secondary succession may lag 2-3 years behind incorporation.

3) Incorporation of N into perennial structures.
   As perennials increase in abundance, a smaller proportion of the N incorporated by the seral community returns to the decomposer subsystem via litter in a given year.

4) Decrease in litter quality.
   As succession proceeds, litter produced by the seral community decreases in quality because mid- and late-seral species have higher C:N ratios and are higher in structural materials such as lignin, cellulose, and

hemicellulose than early-seral species. This decrease in litter quality slows decomposition and delays mineralization of N contained in the litter (Buyanovsky et al. 1987).

5) <u>Competitive advantage of perennials as soil N becomes limited</u>.

Perennials become increasingly more competitive for limited soil N because of four characteristics: a) greater structural development (e.g., more extensive root systems), b) lower N requirements per unit biomass, c) greater ability to supply a portion of their N requirements from internal sources, and d) increased directing of soil N to perennials because of increased mutualistic coupling relationships between perennials and the decomposer subsystem.

CONCLUSIONS

Our research indicates that the transition from annual-dominated to perennial-dominated communities during early secondary succession is controlled, at least in the semiarid system we have studied, by N availability. An increase in N availability slows the rate of seral change, allowing annuals to dominate longer, and a decrease in N availability increases the rate of change, allowing perennials to dominate sooner. Annuals dominate primarily because they have more rapid growth rates than perennials and are, therefore, able to more quickly accumulate available soil nutrients and moisture and perhaps also reduce perennial growth through shading. Such a high-level of production requires high-levels of available N but it also reduces the available soil N pool by incorporation in aboveground tissue. Decomposition of this aboveground litter is much slower than production, and, therefore, mineralization is slow and immobilization increases for several years. During this time, perennials increase in importance and dominate the site since they are better able to tolerate these low-N availability levels because of their lower N requirements and their greater structural development (e.g, greater root:shoot ratios, rooting depth, and mycorrhizal fungi infection). Perennials have lower N requirements than most annual forbs because of lower tissue N concentrations (especially grasses) and perennial storage between years.

LITERATURE CITED

Aets, R. and F. Berendse. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. Vegetatio 76:63-69.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10:351-371.

Berendse, F., H. Oudhof, and J. Bol. 1987. A comparative study on nutrient cycling in wet heathland ecosystems. I. Litter production and nutrient loss from the plant. Oecologia 74:174-184.

Bookman, P.A. and R.N. Mack. 1982. Root interaction between Bromus tectorum and Poa pratensis: a three-dimensional analysis. Ecology 63:640-646.

Bremner, J.M. 1965. Nitrogen availability indexes. In: C.A. Black (ed.) Methods of Soil Analysis. Part 2. Agronomy 9:1324-1345. American Society of Agronomy. Madison, Wisconsin.

Buyanovsky, G.A., C.L. Kucera, and G.H. Wagner. 1987. Comparative analyses of carbon dynamics in native and cultivated ecosystems. Ecology 68:2023-2031.

Carpenter, A.T., J.C. Moore, E.F. Redente, and J.M. Stark. 1990. Plant community dynamics in relation to nutrient addition following a major disturbance. Plant and Soil 126:91-100.

Carson, W.P. and G.W. Barrett. 1988. Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. Ecology 69:984-994.

Clements, F.C. 1916. Plant Succession. Carnegie Institute of Washington Publication 242. Washington, D.C.

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:95-117, 167-202, 281-308, 361-391.

Doerr, T.B., E.F. Redente, and F.B. Reeves. 1984. Effects of soil disturbance on plant succession and levels of mycorrhizal fungi in a sagebrush-grassland community. Journal of Range Management 37:135-139.

Dormaar, J.F., S. Smoliak, and W.D. Wilms. 1990. Soil chemical properties during succession from abandoned cropland to native range. Journal of Range Management 43:260-265.

Eckert, R.E., Jr. and R.A. Evans. 1963. Responses of downy brome and crested wheatgrass to nitrogen and phosphorus in nutrient solution. Weeds 11:170-174.

Fisher, F.M., J.C. Zak, G.L. Cunningham, and W.G. Whitford. 1988. Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. Journal of Range Management 41:387-391.

Foster, M.M., P.M. Vitousek, and P.A. Randolph. 1980. The effects of ragweed (<u>Ambrosia</u> <u>artemisiifolia</u> L.) on nutrient cycling in a 1st-yr old-field. American Midland Naturalist 103:106-113.

Francis, R., R.D. Finlay, and D.J. Read. 1986. Vesicular-arbuscular mycorrhiza in natural vegetation systems. IV. Transfer of nutrients in inter- and intra-specific combinations of host plants. New Phytologist 102:103-111.

Gleeson, S.K. and D. Tilman. 1990. Allocation and the transient dynamics of succession on poor soils. Ecology 71:1144-1155.

Grace, J.B. 1987. The impact of preemption on the zonation of two Typha species along lakeshores. Ecological Monographs 57:283-303.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344-347.

Gurevitch, J. and S.T. Chester, Jr. 1986. Analysis of repeated measures experiments. Ecology 67:251-255.

Harris, G.A. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. Ecological Monographs 37:89-111.

Heil, G.W. and M. Bruggink. 1987. Competition for nutrients between Calluna vulgaris (L.) Hull and Molinia caerulea (L.) Moench. Oecologia 73:105-107.

Heil, G.W. and W.H. Diemont. 1983. Raised nutrient levels change heathland into grassland. Vegetatio 53:113-120.

Hetrick, B.A.D., G.W.T. Wilson, and C.E. Owensby. 1989. Influence of mycorrhizal fungi and fertilization on big bluestem seedling biomass. Journal of Range Management 42:213-216.

Holland, E.A. and D.C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68:425-433.

Hunt, H.W., E.R. Ingham, D.C. Coleman, E.T. Elliott, and C.P.P. Read. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69:1009-1016.

Ingestad, T. and G.I. Agren. 1991. The influence of plant nutrition on biomass allocation. Ecological Applications 1:168-174.

Inouye, R.S., N.J. Huntly, D. Tilman, J.R. Tester, M. Stillwell, and K.C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. Ecology 68:12-26.

Iwasa, Y. and J. Roughgarden. 1984. Shoot/root balance of plants: optimal growth of a system with many vegetative organs. Theoretical Population Biology 25:78-105.

John, P.W.M. 1971. Statistical Design and Analysis of Experiments. MacMillan, New York.

Lachenbruch, P.A. 1975. Discriminant Analysis. Hafner, New York.

Lamb, D. 1980. Soil nitrogen mineralization in a secondary rainforest succession. Oecologia 47:257-263.

Lang, G.E. and R.T.T. Forman. 1978. Detrital dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. Ecology 59:580-595.

Lauenroth, W.K., H.W. Hunt, D.M. Swift, and J.S. Singh. 1987. Estimating aboveground net primary production in grasslands: a simulation approach. Ecological Modelling 33:297-314.

Leps, J., J. Osbornova-Kasinova, and M. Rejmanek. 1982. Community stability, complexity and species life history strategies. Vegetatio 50:53-63.

Li, J.C.R. 1964. Statistical Inference. Vol I. Edwards Brothers. Ann Arbor, Michigan.

Link, S.O., G.W. Gee, and J.L. Downs. 1990. The effect of water stress on phenological and ecophysiological characteristics of cheatgrass and Sandberg's bluegrass. Journal of Range Management 43:506-513.

Matthews, J.A. 1979. A study of the variability of some successional and climax plant assemblage-types using multiple discriminant analysis. Journal of Ecology 67:255-271.

McGraw, J.B. and F.S. Chapin, III. 1989. Competitive ability and adaptation to fertile and infertile soils in two _Eriophorum_ species. Ecology 70:736-749.

McLendon, T. and B.E. Dahl. 1983. A method for mapping vegetation utilizing multivariate statistical techniques. Journal of Range Management 36:457-462.

McLendon, T. and E.F. Redente. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. Ecology 72:2016-2024.

McLendon, T. and E.F. Redente. 1992a. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia (In press).

McLendon, T. and E.F. Redente. 1992b. Role of nitrogen availability in the transition from annual-dominated to perennial-dominated seral communities. Proceedings of a Symposium on the Ecology, Management and Restoration of Intermountain Annual Rangelands. Intermountain Research Station. United States Forest Service. Logan, Utah.

McLendon, T. and E.F. Redente. 1992c. Aboveground production, species composition, and nitrogen content dynamics during seven years of secondary succession in a semiarid shrubland ecosystem. Ecological Monographs (In preparation for submission).

Miller, T.E. and P.A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. Ecology 68:1201-1210.

Moorman, T.B. and F.B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semiarid West. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany 66:14-18.

Parrish, J.A.D. and F.A. Bazzaz. 1982. Responses of plants from three successional communities on a nutrient gradient. Journal of Ecology 70:233-248.

Pastor, J., M.A. Stillwell, and D. Tilman. 1987. Little bluestem litter dynamics in Minnesota old fields. Oecologia 72:327-330.

Peterson, D.L. and F.A. Bazzaz. 1978. Life cycle characteristics of <u>Aster pilosis</u> in early successional habitats. Ecology 58:1005-1013.

Raynal, D.J. and F.A. Bazzaz. 1975. Interference of winter annuals with <u>Ambrosia artemisiifolia</u> in early successional fields. Ecology 56:35-49.

Redente, E.F., J.E. Friedlander, and T. McLendon. 1992. Response of early and late semiarid seral species to nitrogen and phosphorus gradients. Plant and Soil 140:127-135.

Redente, E.F. and C.W. Cook (eds.). 1986. Structural and functional changes in early successional stages of a semiarid ecosystem. Research Report. Dept. Range Science. Colorado State Univ. Fort Collins, Colorado. DOE DE-AC02-76EV04018.

Robertson, G.P. 1982. Factors regulating nitrification in primary and secondary succession. Ecology 63:1561-1573.

Robertson, G.P., M.A. Huston, F.C. Evans, and J.M. Tiedjie. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69:1517-1524.

Shipley, B. and R.H. Peters. 1990. A test of the Tilman model of plant strategies: relative growth rate and biomass partitioning. The American Naturalist 136:139-153.

Smith, J.L. and E.L. Rice. 1983. Differences in nitrate reductase activity between species of different stages of old field succession. Oecologia 57:43-48.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical Methods. Sixth Edition. The Iowa State University Pres, Ames.

Stevenson, B.A., E.F. Redente, and T. McLendon. 1992. Relationship between decomposer subsystem redevelopment and secondary succession patterns following disturbance of a semiarid shrubland (In preparation).

Stroup, W.W. and J. Stubbendieck. 1983. Multivariate statistical methods to determine changes in botanical composition. Journal of Range Management 36:208-212.

Tilman, D. 1982. Resource Competition and Community Structure. Monographs in Population Biology 17. Princeton Univ. Press, Princeton, N.J.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecology 65:1445-1453.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology 67:555-563.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189-214.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Tilman, D. and D.A. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72:685-700.

Van Hulst, R. 1978. On the dynamics of vegetation: patterns of environmental and vegetational change. Vegetatio 38:65-75.

Van Hulst, R. 1979. On the dynamics of vegetation: succession in model communities. Vegetatio 39:85-96.

Vitousek, P. 1983. Nitrogen turnover in a ragweed-dominated 1st-year old field in southern Indiana. American Midland Naturalist 110:46-53.

Vitousek, P.M. and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25:376-381.

Wedin, D.A. and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84:433-441.

Wilson, S.D. and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72:1050-1065.

Table 1. Mean species composition (% relative biomass of major species) within each of the five seral communities separated by discriminant analysis as occurring on control plots during the first seven years of secondary succession in a disturbed semiarid shrubland ecosystem in northwest Colorado.

Plant species	Seral Community First (1-2 yr)	Second (3 yr)	Third (4-6 yr)	Fourth (7-? yr)	Undisturbed (>75 yrs ?)
Artemisia tridentata	t	1	1	1	63
Chrysothamnus nauseosus	2	5	14	12	1
Total shrubs	2	8	19	21	75
Agropyron smithii	1	2	11	10	2
Koeleria pyramidata	t	t	t	1	6
Oryzopsis hymenoides	t	2	8	12	1
Stipa comata	1	1	5	10	5
Total perennial grasses	2	7	29	36	18
Aster canescens	1	1	3	3	t
Phlox bryoides	0	0	t	t	4
Sphaeralcea coccinea	1	1	1	2	t
Total perennial forbs	2	2	7	7	8
Melilotus officinalis	2	2	9	t	t
Total biennial forbs	2	2	9	t	t
Bromus tectorum	15	64	22	24	1
Total annual grasses	15	64	22	24	1
Chenopodium berlandieri	20	t	t	t	0
Kochia scoparia	3	4	4	7	t
Salsola iberica	42	8	3	4	t
Sisymbrium altissimum	6	4	t	0	t
Total annual forbs	76	17	13	12	1

t indicates a trace (< 0.5 %) amount.

Table 2. F-ratios between year-group means from the discriminant analysis of the aboveground production values of 10 major species from control plots. Significant F-values are 4.74 ($P < 0.05$) and 3.30 ($P < 0.10$) for Groups 1985-1991 and 2.67 ($P < 0.05$) and 2.14 ($P < 0.10$) for Undisturbed (Unds).

Group	1985	1986	1987	1988	1989	1990	1991
1986	7.62						
1987	3.44	4.03					
1988	0.50	7.60	2.33				
1989	1.43	8.45	2.95	0.37			
1990	2.03	9.58	3.93	0.74	0.13		
1991	4.67	9.91	4.21	2.34	1.14	0.85	
Unds	16.58	37.62	26.19	18.35	20.89	21.78	27.72

Table 3. Annual aboveground production (g/m^2) by lifeform and species richness on control plots following disturbance in 1984. Annual growth-year precipitation (mm) is for the period from 1 September of the prior year through 31 August of the designated year.

	1985	1986	1987	1988	1989	1990	1991	Unds
Shrubs	1	12	17	6	24	33	36	95
Perennial grasses	2	8	14	24	30	40	63	23
Perennial forbs	3	7	6	5	12	8	12	8
Biennial forbs	1	13	5	32	t	t	t	0
Annual grasses	11	71	142	38	23	12	42	t
Annual forbs	73	294	39	16	15	11	22	1
Total aboveground	92	404	222	121	103	104	175	127
Number of species	12	14	19	18	19	18	17	17
Precipitation	268	311	302	234	275	159	246	

t indicates a trace (< 0.5 g/m^2) amount.

Table 4. Seral index means for the 38 plant species encountered on control plots during 7 years of secondary succession within a disturbed sagebrush ecosystem. Low index values indicate early seral position. Late-seral species are those with maximum aboveground production values in the undisturbed sagebrush community.

Species	Seral index	Lifeform
Late-seral		
Artemisia tridentata	5.4	perennial shrub
Erigeron engelmanni	6.3	perennial forb
Koeleria pyramidata	5.4	perennial grass
Opuntia polyacantha	3.6	perennial succulent
Phlox bryoides	7.0	perennial forb
Poa secunda	4.6	perennial grass
Sarcobatus vermiculatus	4.3	perennial shrub
Senecio multilobatus	5.1	perennial forb
Mid-seral		
Agropyron desertorum	7.0	perennial grass
Gutierrezia sarothrae	6.6	perennial shrub
Oryzopsis hymenoides	6.5	perennial grass
Chrysothamnus nauseosus	6.1	perennial shrub
Agropyron smithii	6.0	perennial grass
Linum lewisii	6.0	perennial forb
Stipa comata	5.9	perennial grass
Aster canescens	5.7	perennial forb
Tragopogon dubius	5.5	biennial forb
Taraxacum officinale	5.3	perennial forb
Sisymbrium linifolium	5.0	perennial forb
Early-seral		
Kochia scoparia	4.6	annual forb
Sphaeralcea coccinea	4.5	perennial forb
Hedysarum borale	4.3	perennial forb
Lepidium perforatum	4.3	annual forb
Sitanion hystrix	4.0	perennial grass
Melilotus officinalis	4.0	biennial forb
Cryptantha flavoculata	4.0	perennial forb
Agropyron dasystachyum	3.8	perennial grass
Penstemon fremonti	3.5	perennial forb
Descurainia sophia	3.5	annual forb
Descurainia pinnata	3.3	annual forb
Astragalus diversifolius	3.3	perennial forb
Trifolium gymnocarpon	3.1	perennial forb
Lactuca scariola	3.0	annual forb
Bromus tectorum	2.9	annual grass
Sisymbrium altissimum	2.4	annual forb
Lappula redowskii	2.2	annual forb
Salsola iberica	2.0	annual forb
Chenopodium berlandieri	1.0	annual forb

Table 5. Mean N concentration (%) of aboveground tissue of major plant species from control plots during 5 years of secondary succession within a disturbed sagebrush ecosystem and from the adjacent undisturbed sagebrush community (Unds).

Species	Overall	1987	1988	1989	1990	1991	Unds
Shrubs							
Artemisia tridentata	1.82	1.82	1.93	1.81	1.69	1.71	1.39
Chrysothamnus nauseosus	1.77	2.31	1.71	1.67	1.74	1.47	1.51
Gutierrezia sarothrae	1.75	1.96	1.88	1.99	1.61	1.73	1.53
Opuntia polyacantha	0.84	na	na	na	0.84	na	0.46
Grasses							
Agropyron dasystachyum	1.29	1.15	na	0.74	1.34	1.52	1.03
Agropyron desertorum	1.13	na	na	1.34	1.36	1.06	0.77
Agropyron smithii	1.19	1.52	1.31	1.35	1.08	1.03	1.02
Bromus tectorum	1.11	1.71	1.11	0.93	1.11	1.23	1.09
Koeleria pyramidata	1.31	na	na	1.45	1.43	1.14	1.04
Oryzopsis hymenoides	1.23	1.40	1.36	1.25	1.23	1.03	1.08
Sitanion hystrix	1.31	1.16	1.64	1.58	1.53	0.95	0.88
Stipa comata	1.21	1.47	1.38	1.28	1.24	1.01	0.99
Legumes							
Astragalus diversifolius	2.20	2.22	2.49	2.17	2.16	2.10	1.59
Hedysarum borale	1.90	2.06	2.93	1.81	1.17	1.48	2.30
Melilotus officinalis	2.38	3.24	1.96	3.00	1.89	2.77	na
Trifolium gymnocarpon	1.94	na	1.80	1.72	1.89	2.30	2.38
Perennial forbs (non-legumes)							
Aster canescens	1.80	1.94	1.83	1.72	1.71	1.72	1.50
Cryptantha flavoculata	2.04	2.53	2.10	2.00	1.93	1.72	1.57
Erigeron engelmanni	1.61	na	1.99	1.60	1.52	1.48	1.47
Linum lewisii	1.94	3.87	2.18	1.90	1.41	1.50	na
Phlox bryoides	1.35	na	na	na	na	1.35	0.85
Senecio multilobatus	1.38	na	1.44	1.42	1.55	1.28	1.31
Sisymbrium linifolium	2.02	2.80	2.04	1.98	1.83	1.88	1.02
Sphaeralcea coccinea	2.19	2.57	2.06	2.29	2.09	2.57	1.55
Taraxacum officinale	2.22	na	2.18	1.65	2.39	2.34	na
Tragopogon dubius	1.81	2.88	2.05	2.13	2.42	1.39	na
Annual forbs							
Chenopodium berlandieri	2.16	na	1.58	1.85	na	2.22	na
Descurainia pinnata	2.40	na	2.16	2.24	2.91	na	na
Descurainia sophia	1.87	2.26	1.13	2.12	1.62	1.99	na
Kochia scoparia	1.67	1.52	1.26	1.86	1.66	1.99	1.01
Lactuca scariola	2.05	2.13	1.87	1.62	2.41	na	na
Lappula redowskii	1.29	na	1.13	1.31	1.56	1.31	na
Salsola iberica	1.81	1.49	1.58	1.80	2.20	1.82	na
Sisymbrium altissimum	1.84	1.25	2.01	na	na	na	na

Table 6. Annual incorporation of N (mg/m^2) within aboveground plant tissue within an undisturbed sagebrush community and on control plots in a disturbed sagebrush ecosystem.

	1985	1986	1987	1988	1989	1990	1991	Mean
Undisturbed community								
Shrubs	1799	765	1457	na	na	na	1379	1350
Perennial grasses	490	177	289	na	na	na	222	295
Perennial forbs	337	74	102	na	na	na	113	157
Biennial forbs	0	0	0	na	na	na	0	0
Annual grasses	41	6	31	na	na	na	0	20
Annual forbs	2	3	2	na	na	na	0	2
Total	2669	1025	1881	na	na	na	1715	1824
Mean tissue N (%)	1.32	1.36	1.37	na	na	na	1.34	1.35
Disturbed community								
Shrubs	23	279	276	109	331	525	508	
Perennial grasses	39	112	213	365	356	441	665	
Perennial forbs	69	147	120	105	213	146	221	
Biennial forbs	31	340	246	634	6	13	13	
Annual grasses	131	955	1886	426	242	132	508	
Annual forbs	1156	3891	506	245	313	212	278	
Total	1449	5724	3247	1884	1461	1469	2193	
Mean tissue N (%)	1.60	1.44	1.46	1.54	1.47	1.43	1.24	

Table 7. Comparison of aboveground tissue N concentration (%), by lifeform, between species occurring on nitrogen (N) plots and on control (C) plots. Values are 5-year means (1987-1991).

Lifeform	Nitrogen	Control	N/C
Shrubs	2.21	1.78	1.24
Perennial grasses	1.84	1.24	1.48
Annual grasses	1.51	1.11	1.36
Legumes	2.58	2.16	1.19
Non-leguminous perennial forbs	2.74	1.95	1.41
Non-leguminous annual forbs	2.56	1.86	1.38

Table 8. Relative canopy cover (%) of major species and lifeform groups and species richness values on nitrogen, control, and sucrose plots. Values are overall means from 4 plots per treatment averaged over 3 years. Confidence intervals of the means are at the P < 0.05 level.

Variable	Nitrogen	Control	Sucrose
Chrysothamnus nauseosus	0.3 ± 0.9	1.1 ± 0.8	3.2 ± 3.4
Agropyron smithii	0.5 ± 0.5	1.2 ± 1.5	2.3 ± 2.6
Aster canescens	0.1 ± 0.1	0.7 ± 1.1	1.7 ± 1.1
Melilotus officinalis	0.6 ± 0.7	1.2 ± 1.4	3.1 ± 2.6
Sphaeralcea coccinea	0.7 ± 0.6	1.5 ± 1.0	1.0 ± 0.6
Kochia scoparia	66.4 ± 20.7	52.1 ± 16.9	33.2 ± 17.1
Salsola iberica	25.6 ± 20.3	25.9 ± 18.6	34.8 ± 21.6
Shrubs	0.5 ± 0.5	1.3 ± 1.0	3.4 ± 3.4
Perennial grasses	0.7 ± 0.6	1.4 ± 1.5	2.5 ± 2.7
Perennial forbs	2.0 ± 1.1	4.0 ± 2.4	7.8 ± 2.3
Annual grasses	4.0 ± 3.9	13.6 ± 6.4	17.5 ± 8.8
Annual forbs	92.9 ± 4.3	79.7 ± 5.5	68.8 ± 12.4
Number of species	9.4 ± 2.0	11.8 ± 1.5	13.9 ± 1.8

Table 9. Mahalanobis-D^2 values between treatment group means from the discriminant analysis of the fumigation experiment relative biomass data. Asterisks (*) designate significantly different groups ($P < 0.05$). Treatment groups are UnCo = undisturbed control, NFCo = non-fumigated control, FmCo = fumigated control, NFCl = non-fumigated climax, FmCl = fumigated climax, NFRd = non-fumigated ruderal, and FmRd = fumigated ruderal.

Group	NFCl	FmCl	NFCo	FmCo	NFRd	FmRd
UnCo	46.3*	25.9	221.0*	455.2*	360.8*	484.8*
NFCl		9.2	97.6*	269.2*	202.1*	294.9*
FmCl			158.1*	345.0*	277.6*	376.8*
NFCo				75.2*	26.9	79.8*
FmCo					17.0	1.6
NFRd						16.6

Table 10. Species composition (% relative biomass basis) of the seral communities on plots of the seven treatments of the fumigation experiment. Values are 1991 means (4 replications each). Within-row means followed by the same letter are not significantly different ($P < 0.05$). Treatment abbreviations are: UnCo = undisturbed control, NFCl = non-fumigated climax, FmCl = fumigated climax, NFCo = non-fumigated control, FmCo = fumigated control, NFRd = non-fumigated ruderal, and FmRd = fumigated ruderal. An asterisk (*) following a species indicates that it was seeded in the NFCl and FmCl plots in 1984 and a (x) indicates that it was seeded in the NFRd and FmRd plots.

Variable	UnCo	NFCl	FmCl	NFCo	FmCo	NFRd	FmRd
Shrubs							
<u>Artemisia</u> <u>tridentata</u> *	69a	31c	45b	1d	3d	1d	td
<u>Chrysothamnus</u> <u>nauseosus</u> x	3a	1a	1a	12a	17a	22a	14a
<u>Gutierrezia</u> <u>sarothrae</u> x	2bc	4bc	tc	7bc	1bc	24a	15ab
Perennial grasses							
<u>Agropyron</u> <u>desertorum</u>	ta	3a	0a	3a	ta	6a	0a
<u>Agropyron</u> <u>smithii</u> *	3b	18a	15a	7ab	1b	3b	0b
<u>Agropyron</u> <u>spicatum</u> *	0b	17a	13ab	tb	2ab	0b	0b
<u>Koeleria</u> <u>pyramidata</u> *	6ab	6abc	9a	2bc	1bc	tbc	0c
<u>Oryzopsis</u> <u>hymenoides</u> *	1b	4b	3b	14a	0b	5b	1b
<u>Sitanion</u> <u>hystrix</u> x	1b	0b	0b	tb	2b	8ab	17a
<u>Stipa</u> <u>comata</u> *	7a	13a	9a	12a	1a	2a	2a
Annual grass							
<u>Bromus</u> <u>tectorum</u> x	ta	ta	2a	22b	46c	11ab	21b
Annual forbs							
<u>Kochia</u> <u>scoparia</u> x	0a	0a	1a	2a	21a	7a	23a
<u>Salsola</u> <u>iberica</u> x	0b	1b	tb	6a	1b	2ab	1ab
Total shrubs	74a	36b	46ab	20b	21b	47ab	29b
Total perennial grasses	18cd	60a	50ab	39abc	8d	25bcd	21cd
Total perennial forbs	5ab	2bc	1bc	9a	1c	4bc	1bc
Total biennial forbs	0a	0a	0a	1a	ta	1a	ta
Total annual grasses	ta	ta	2a	22b	46c	11ab	21b
Total annual forbs	ta	1a	1a	9ab	24ab	12ab	28b
Late-seral species	77a	55c	67b	5d	6d	4d	1d
Mid-seral species	20b	41a	29ab	59a	22b	62a	33ab
Early-seral species	3c	4c	4c	36b	72a	34b	66a
Number of species	17ab	13bc	11c	19a	13bc	18ab	13bc

Table 11. Main effect treatment means of relative biomass variables from the fumigation experiment. Values are means of 24 plots per fumigation treatment and 16 plots per seeding treatment sampled in 1991. Within treatment category means followed by the same letter are not significantly different (P < 0.05).

Variable	Fumigation Treatment		Seeding Treatment		
	Non-fumigated	Fumigated	Climax	Control	Ruderal
Shrubs	34 a	32 a	41 a	21 b	38 ab
Perennial grasses	42 a	26 b	55 a	24 b	23 b
Perennial forbs	5 a	1 b	2 b	5 a	3 b
Biennial forbs	t a	t a	0 a	1 a	1 a
Annual grasses	11 b	23 a	1 c	34 a	16 b
Annual forbs	7 a	17 a	1 b	16 ab	20 a
Late-seral species	16 a	20 a	61 a	5 b	2 b
Mid-seral species	59 a	33 b	35 a	41 a	48 a
Early-seral species	24 b	47 a	4 b	54 a	50 a
Artemisia tridentata	11 a	16 a	38 a	2 b	1 b
Chrysothamnus nauseosus	11 a	11 a	1 b	15 a	18 ab
Gutierrezia sarothrae	12 a	5 b	2 b	4 b	20 a
Agropyron smithii	9 a	5 a	16 a	4 b	2 b
Agropyron spicatum	6 a	5 a	15 a	1 b	0 b
Bromus tectorum	11 b	23 a	1 c	34 a	16 b
Koeleria pyramidata	3 b	4 a	7 a	2 b	t b
Oryzopsis hymenoides	8 a	1 b	3 b	7 a	3 b
Sitanion hystrix	3 a	7 a	0 b	1 b	13 a
Stipa comata	9 a	4 a	11 ab	7 a	2 b
Kochia scoparia	3 b	15 a	1 a	12 a	15 a
Salsola iberica	3 a	t a	t b	3 a	1 ab

Table 12. Main effect treatment means for total aboveground biomass, number of species, decomposition rate, and soil chemical variables from the fumigation experiment. Values are means of 24 plots per fumigation treatment and 16 plots per seeding treatment sampled in 1991. Within treatment category means within the same row followed by the same letter are not significantly different ($P < 0.05$).

Variable	Fumigation Treatment		Seedling Treatment		
	Non-fumigated	Fumigated	Climax	Control	Ruderal
Total biomass (g/m^2)	125 a	96 a	82 b	144 a	105 b
Number of species	16.6 a	12.1 b	11.8 b	15.9 a	15.4 a
Organic matter (%)	1.9 a	1.8 a	2.0 a	1.7 b	1.9 a
pH	7.5 b	7.5 a	7.5 a	7.5 a	7.5 a
Total N (%)	0.11 a	0.10 a	0.10 ab	0.11 a	0.10 b
NO_3-N (mg/kg)	3.38 a	3.08 a	2.94 b	3.94 a	2.81 b
NH_4-N (mg/kg)	17.0 a	19.1 a	22.4 a	12.0 b	19.8 a
P (mg/kg)	2.25 a	2.03 a	1.78 b	2.27 a	2.37 a
EC (mmhos/cm)	0.49 b	0.52 a	0.50 a	0.51 a	0.51 a
Decomposition (%)	51.8 a	41.1 b	51.7 a	38.7 b	48.8 a

FIGURE LEGENDS

Figure 1. Schematic illustration of the Mahalanobis-D^2 distances between multivariate means of the control plots, by year (85-91), as determined by discriminant analysis. Multivariate means were computed from annual aboveground production values of 10 major species with 8 replications per year.

Figure 2. Changes in aboveground tissue N concentration (%), by lifeform, on control plots (1987-91) during secondary succession as compared to values within the undisturbed community (Und).

Figure 3. Changes in aboveground tissue N concentration (%), by lifeform and by relative seral position of the species, on control plots (1987-91) during secondary succession as compared to values within the undisturbed community (Und).

Figure 4. Comparison of annual aboveground production (g/m^2) by lifeform between nitrogen (N) and control (C) plots during the first seven years of secondary succession within a disturbed sagebrush community. Significant differences between treatment means within the same year are indicated by different letters ($P < 0.05$).

Figure 5. Comparison of total annual aboveground production (g/m^2) and number of species (m^2) between nitrogen (N) and control (c) plots during the first seven years of secondary succession within a disturbed sagebrush community. Significant differences between treatment means within the same year are indicated by different letters ($P < 0.05$).

Figure 6. Relative canopy cover (%) of lifeform groups and species richness on nitrogen (N), control (C), and sucrose (S) plots. Confidence intervals ($P < 0.05$) of the means are given by the vertical lines.

Figure 7. Nitrogen concentrations (%) of five major seral species from nitrogen (N), control (C), and sucrose (S) pltos, September 1990. Confidence intervals ($P < 0.05$) of the means are given by the vertical lines.

Figure 8. Soil NO_3-N, NH_4-N, total N (%), and organic matter (%) concentrations (0-15 cm depth) within undisturbed (U), control (C), and nitrogen (N) plots in August 1991. Significant differences between treatment means for each variable are indicated by different letters ($P < 0.05$).

Figure 9. Conceptual model of available N dynamics and decomposer subsystem redevelopment during secondary succession in a disturbed sagebrush ecosystem in northwestern Colorado.

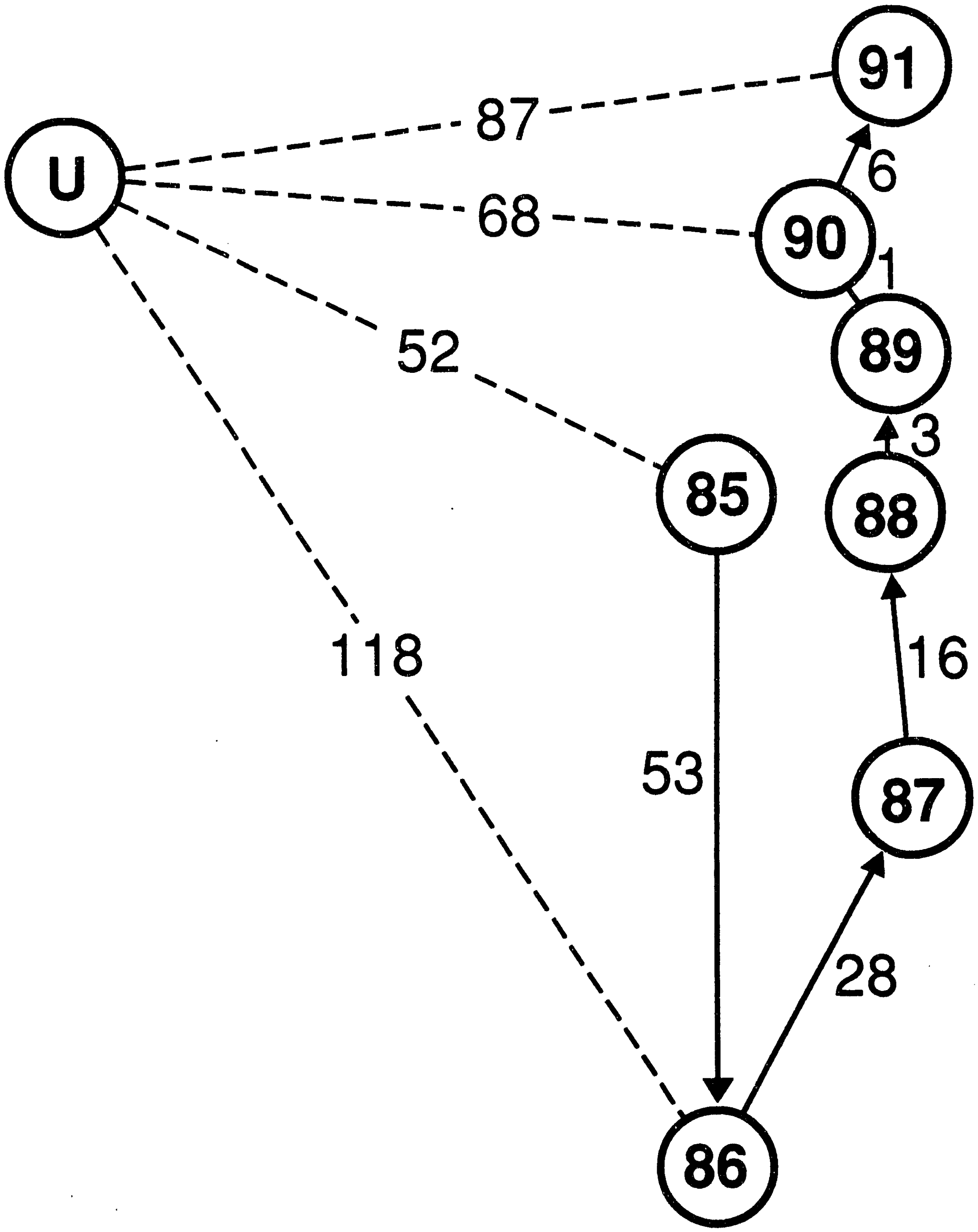


Figure 1

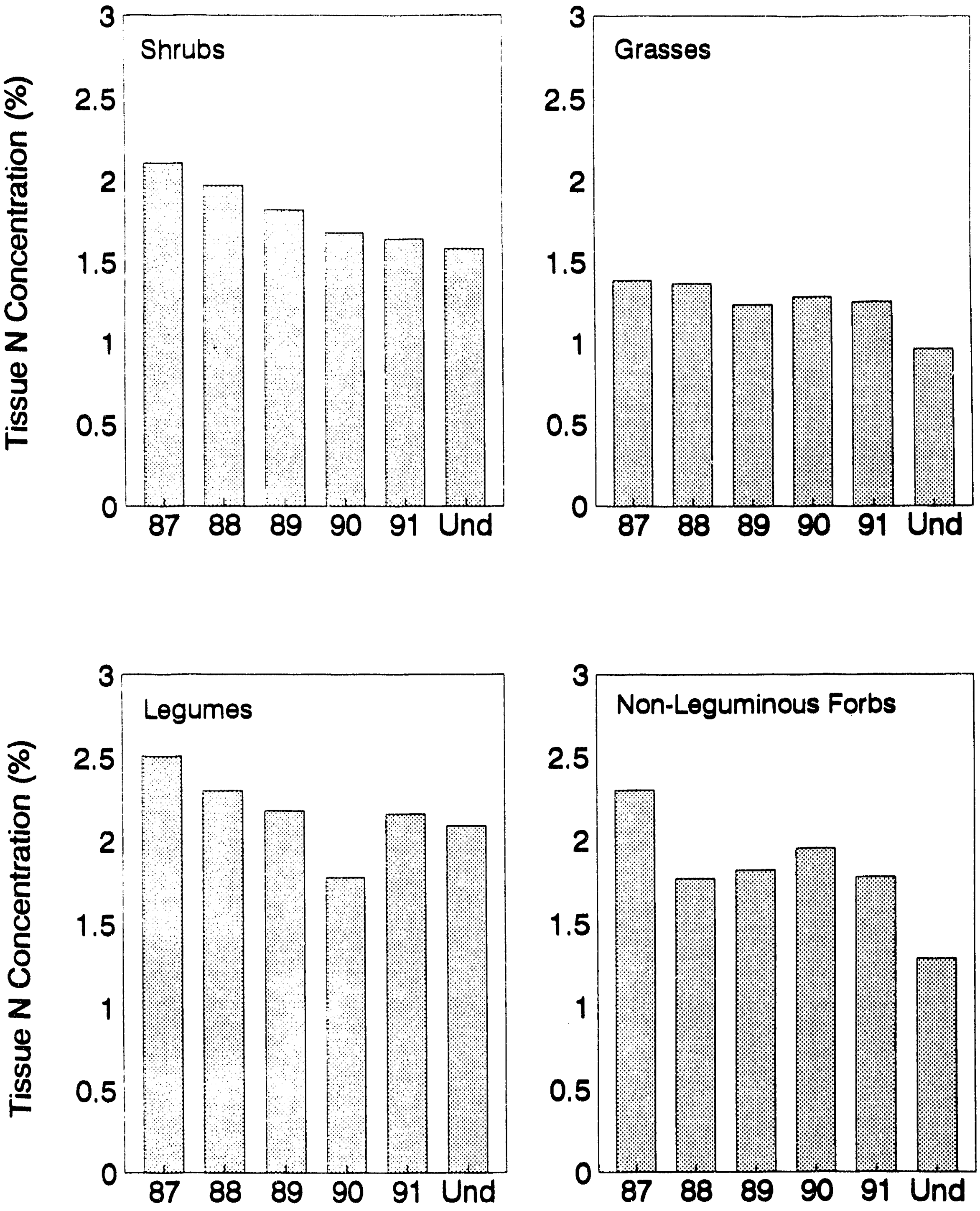

Shrubs
Grasses
Legumes
Non-Leguminous Forbs
Tissue N Concentration (%)
Tissue N Concentration (%)
0
0.5
1
1.5
2
2.5
3
87
88
89
90
91
Und

Figure 2

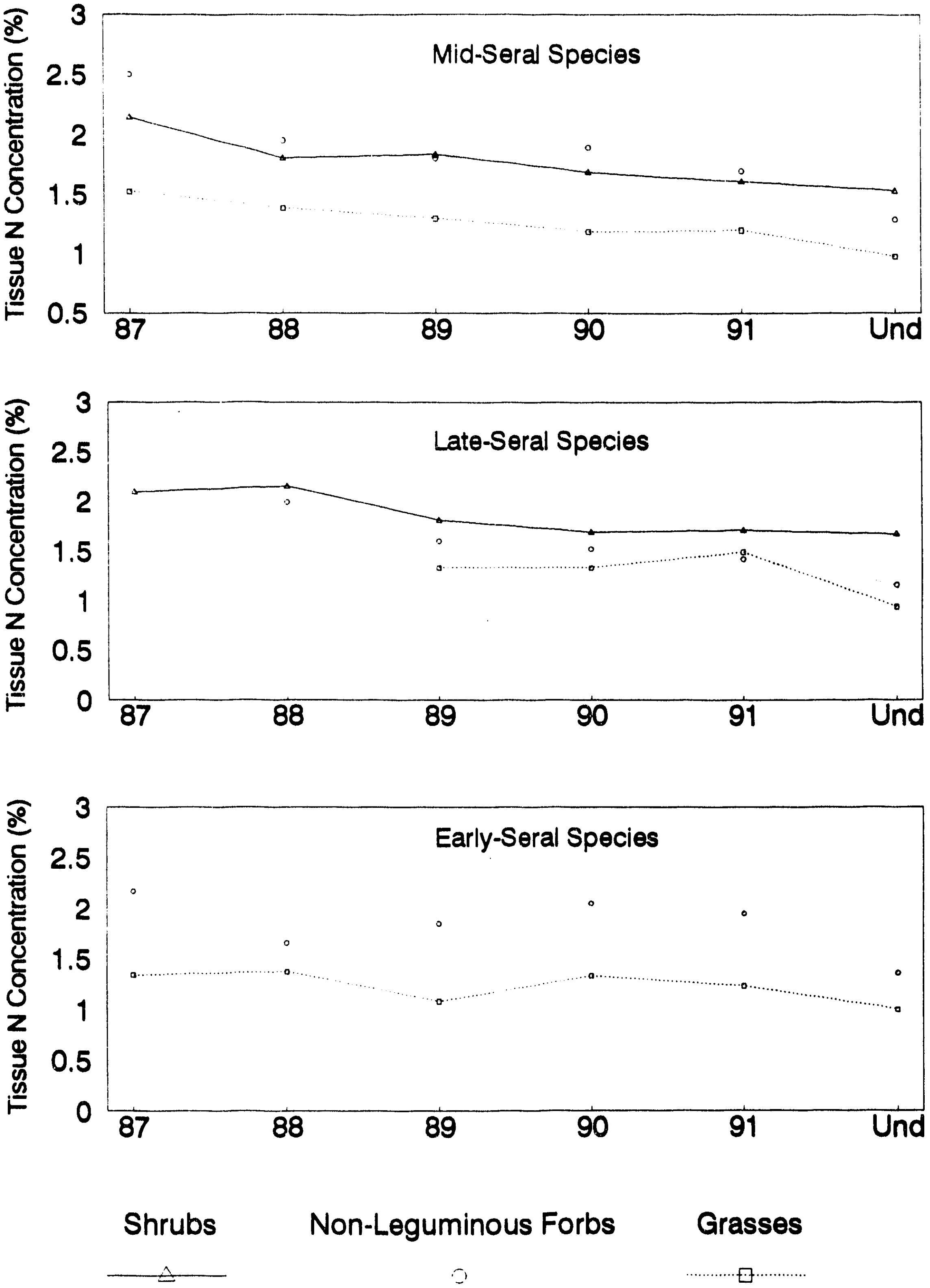

Mid-Seral Species
Late-Seral Species
Early-Seral Species
Tissue N Concentration (%)
3
2.5
2
1.5
1
0.5
0
87
88
89
90
91
Und
Shrubs
Non-Leguminous Forbs
Grasses

Figure 3

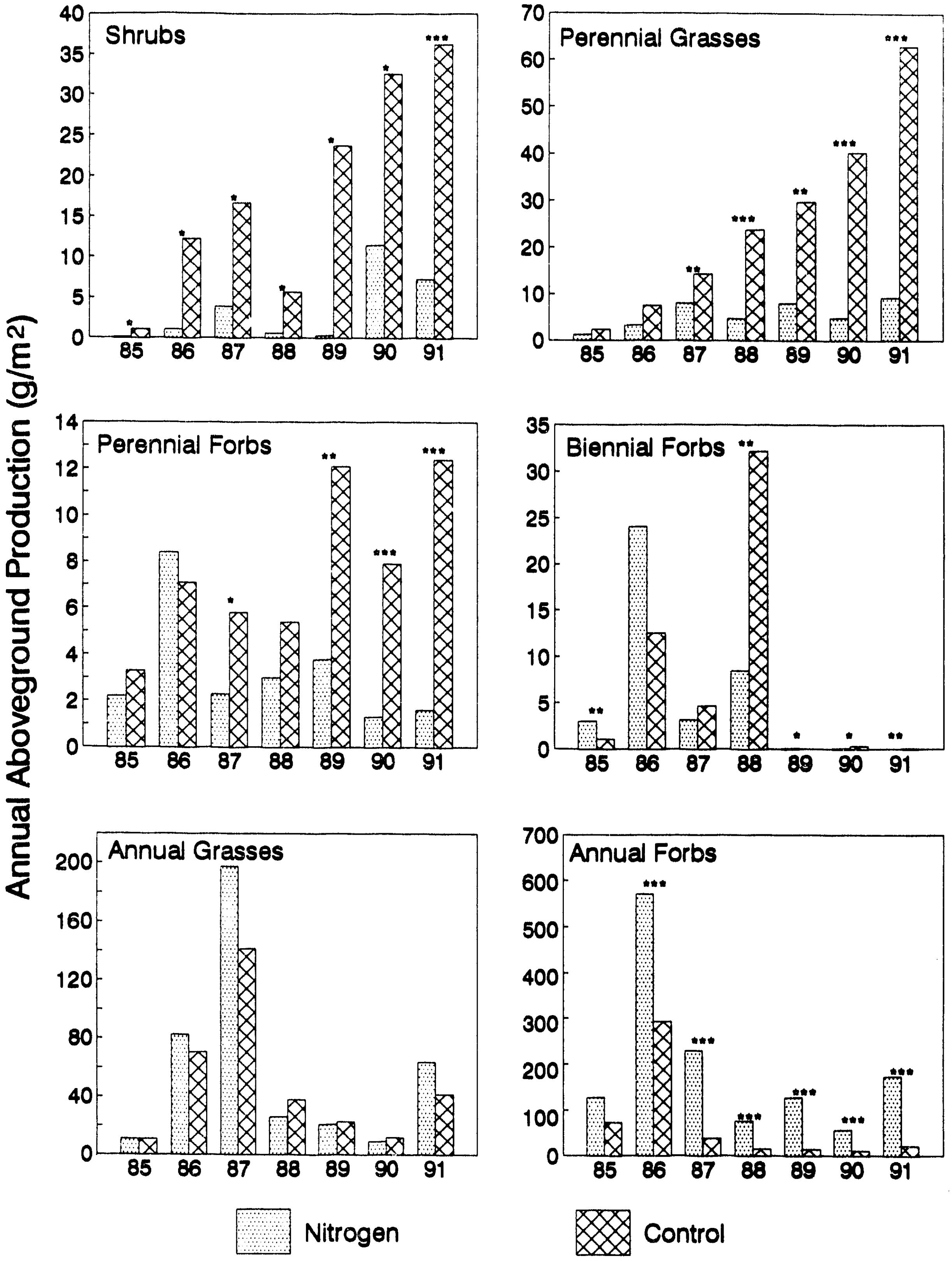

Annual Aboveground Production (g/m²)
Shrubs
0
5
10
15
20
25
30
35
40
85
86
87
88
89
90
91
*
*
*
*
*
*
***
Perennial Grasses
0
10
20
30
40
50
60
70
85
86
87
88
89
90
91
**
***
**
***
***
Perennial Forbs
0
2
4
6
8
10
12
14
85
86
87
88
89
90
91
*
**
***
***
Biennial Forbs
0
5
10
15
20
25
30
35
85
86
87
88
89
90
91
**
**
*
*
**
Annual Grasses
0
40
80
120
160
200
85
86
87
88
89
90
91
Annual Forbs
0
100
200
300
400
500
600
700
85
86
87
88
89
90
91
***
***
***
***
***
***
Nitrogen
Control

Figure 4

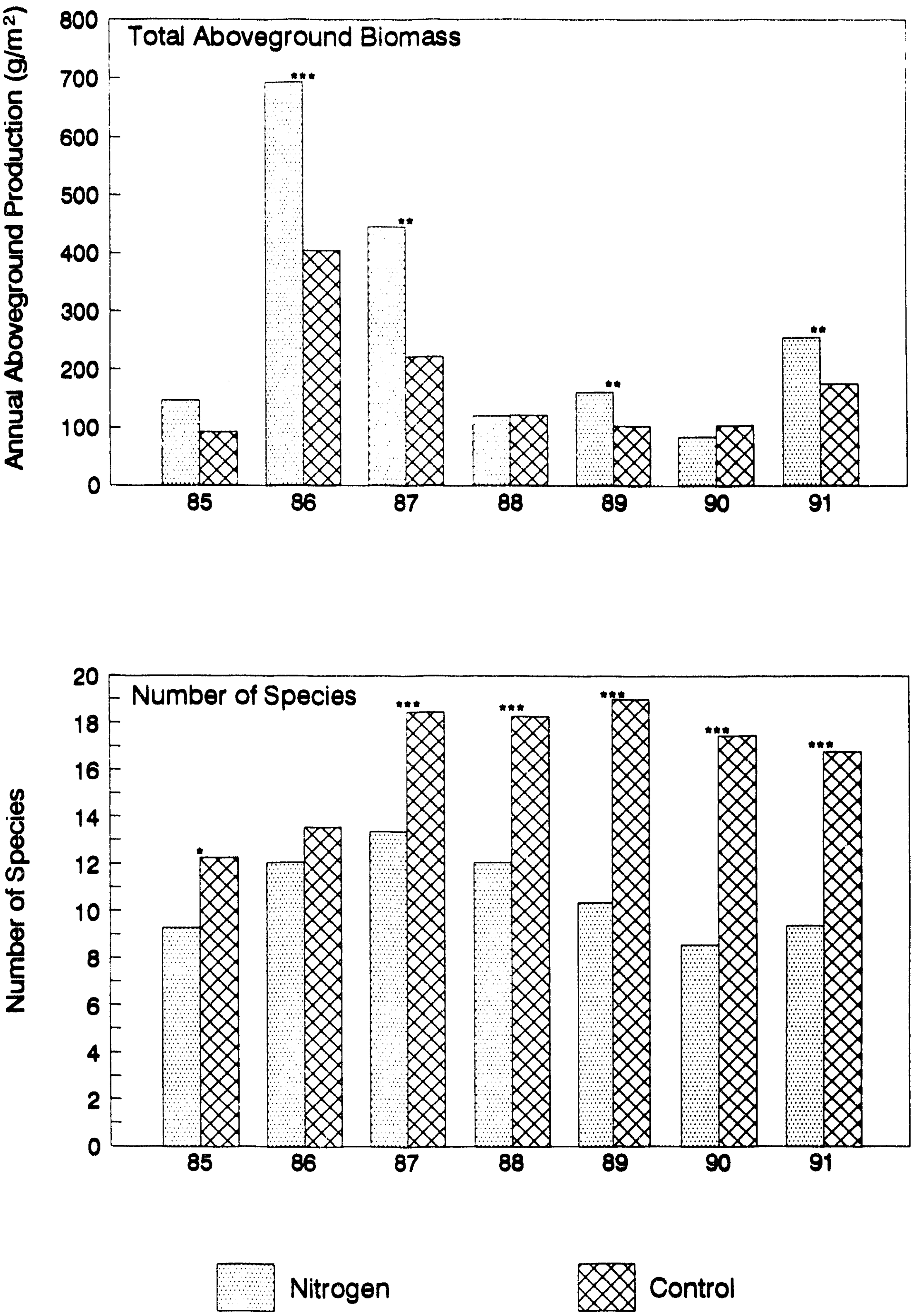

Total Aboveground Biomass
Annual Aboveground Production (g/m²)
0
100
200
300
400
500
600
700
800
***
**
**
**
85
86
87
88
89
90
91
Number of Species
Number of Species
0
2
4
6
8
10
12
14
16
18
20
*
***
***
***
***
***
85
86
87
88
89
90
91
Nitrogen
Control

Figure 5

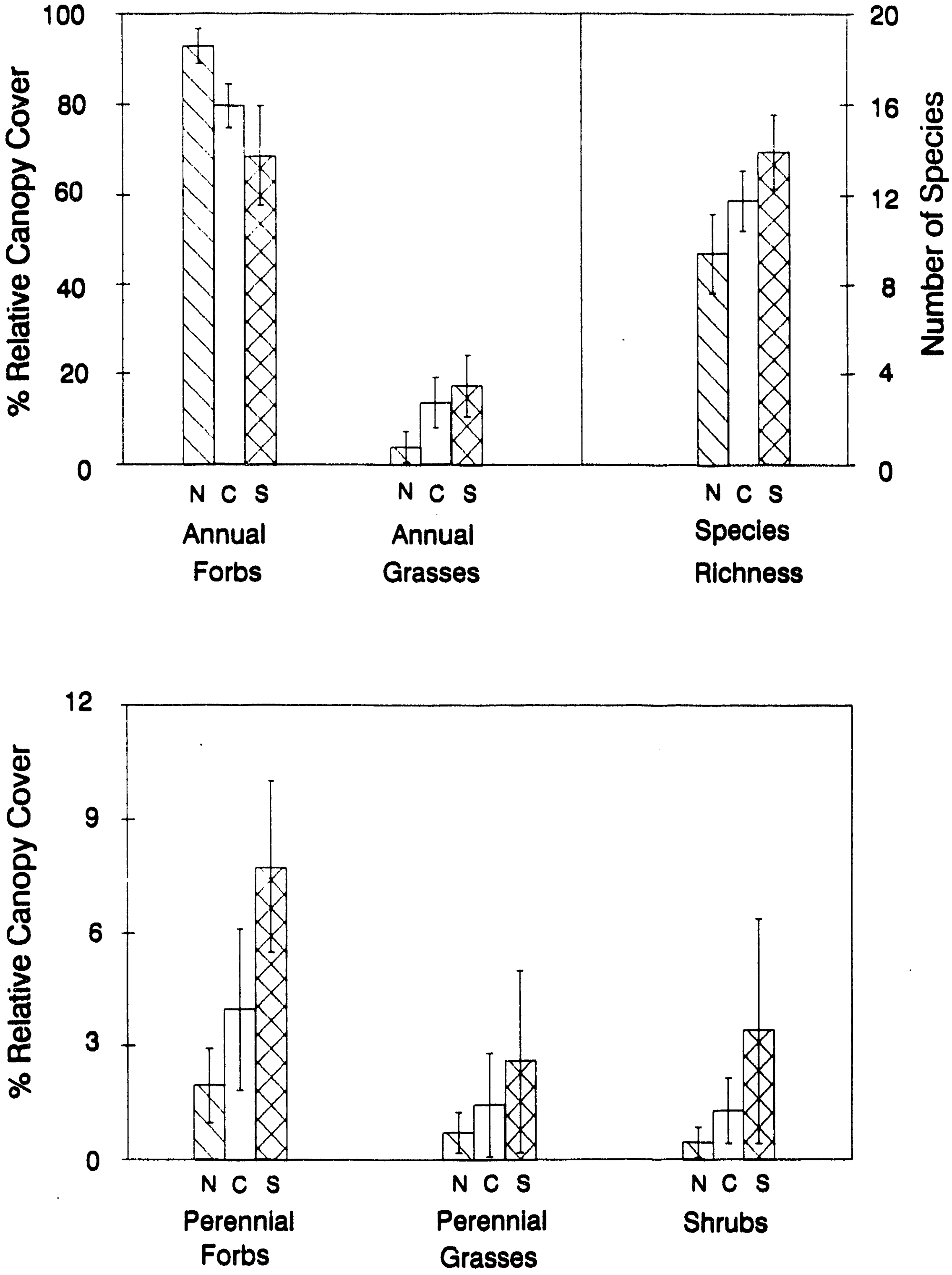

% Relative Canopy Cover
100
80
60
40
20
0
Number of Species
20
16
12
8
4
0
N C S
Annual Forbs
N C S
Annual Grasses
N C S
Species Richness
% Relative Canopy Cover
12
9
6
3
0
N C S
Perennial Forbs
N C S
Perennial Grasses
N C S
Shrubs

Figure 6

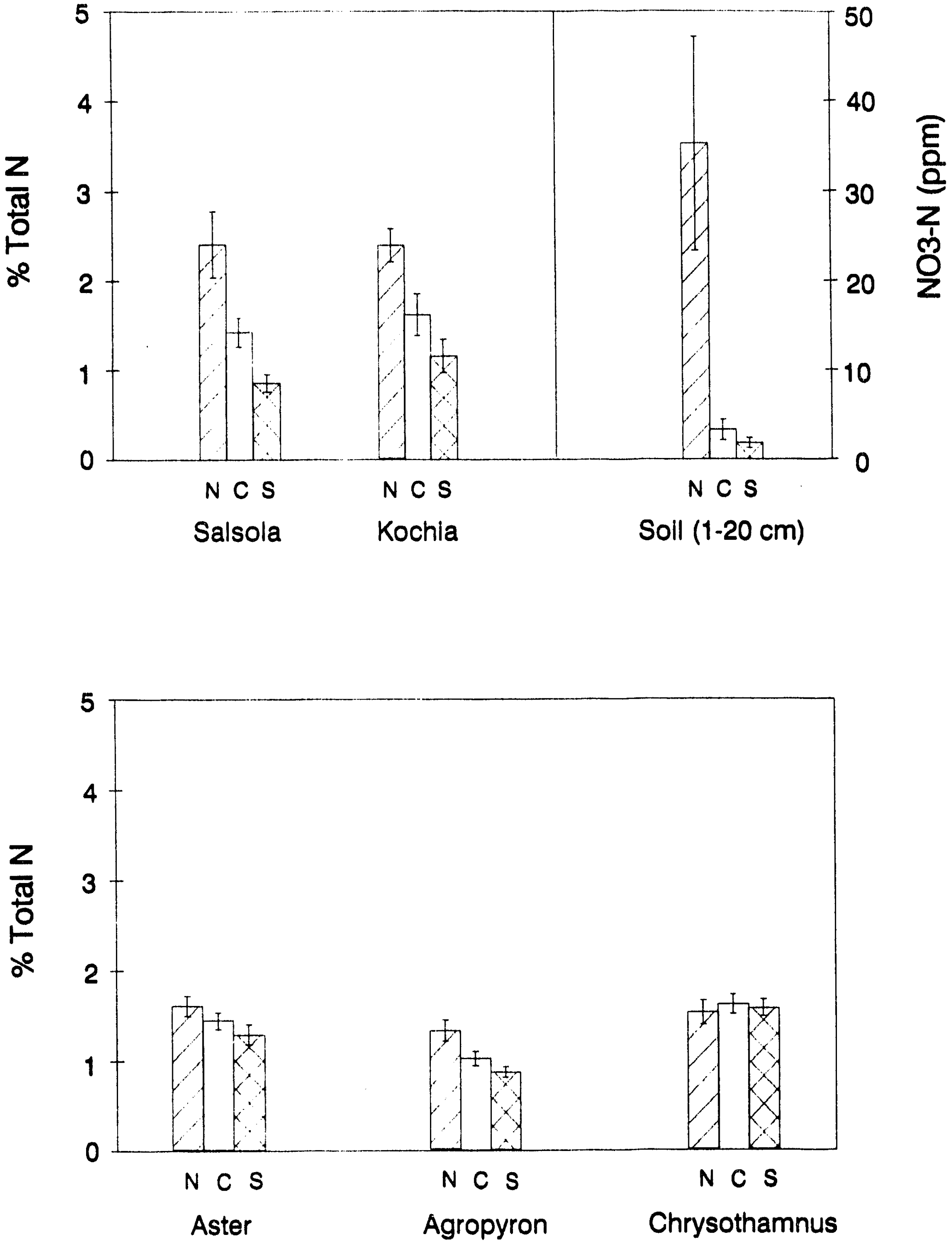
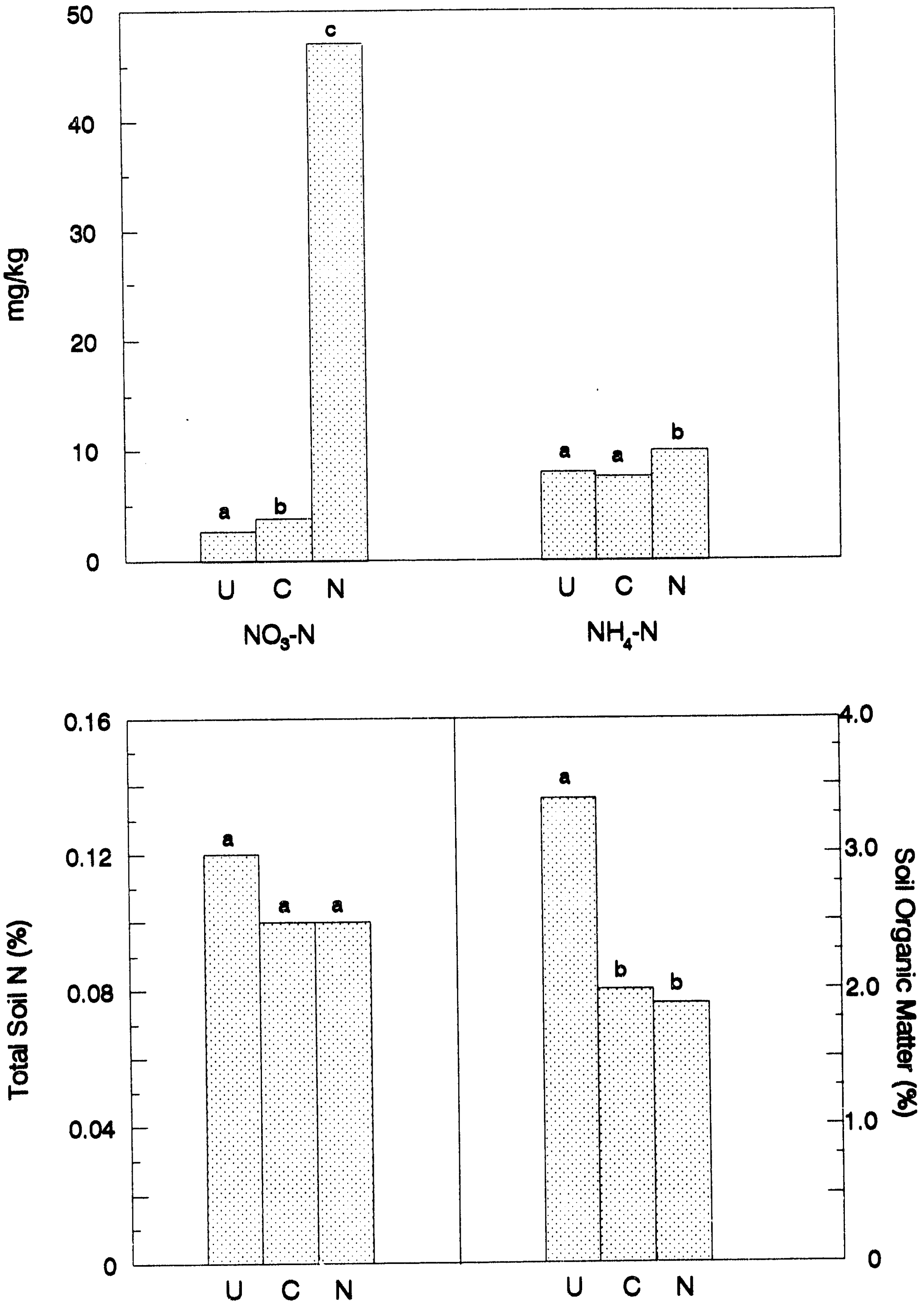
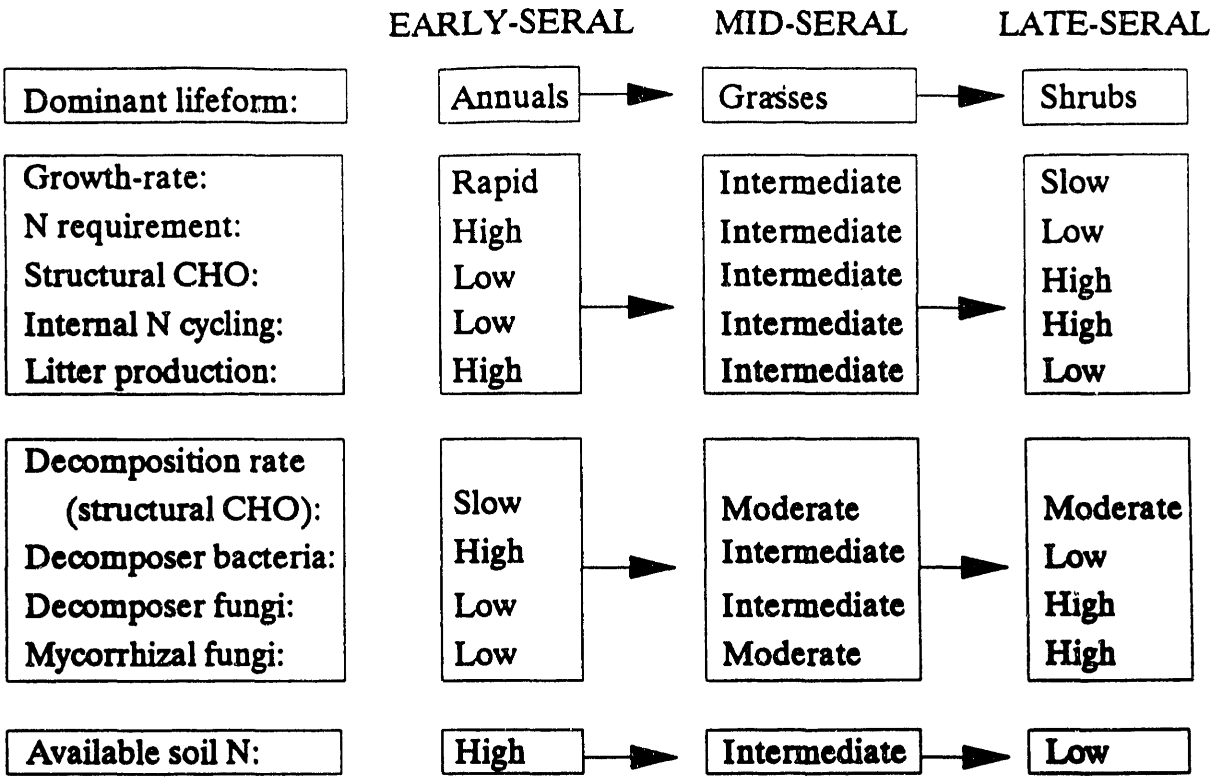

5
4
3
2
1
0
% Total N
50
40
30
20
10
0
NO3-N (ppm)
N C S
Salsola
N C S
Kochia
N C S
Soil (1-20 cm)
5
4
3
2
1
0
% Total N
N C S
Aster
N C S
Agropyron
N C S
Chrysothamnus

Figure 7



50
40
30
20
10
0
mg/kg
a
b
c
a
a
b
U C N
U C N
NO_3-N
NH_4-N
0.16
0.12
0.08
0.04
0
Total Soil N (%)
a
a
a
a
b
b
4.0
3.0
2.0
1.0
0
Soil Organic Matter (%)
U C N
U C N

Figure 8



	EARLY-SERAL	MID-SERAL	LATE-SERAL
Dominant lifeform:	Annuals	Grasses	Shrubs
Growth-rate:	Rapid	Intermediate	Slow
N requirement:	High	Intermediate	Low
Structural CHO:	Low	Intermediate	High
Internal N cycling:	Low	Intermediate	High
Litter production:	High	Intermediate	Low
Decomposition rate (structural CHO):	Slow	Moderate	Moderate
Decomposer bacteria:	High	Intermediate	Low
Decomposer fungi:	Low	Intermediate	High
Mycorrhizal fungi:	Low	Moderate	High
Available soil N:	High	Intermediate	Low

Figure 9

END

DATE
FILMED

12 / 8 / 92