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PROCESSES OF COMMUNITY DEVELOPMENT AND RESPONSES OF ECOSYSTEMS TO CLIMATE CHANGE

Progress Report
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ABSTRACT

Our studies focus on attempting to understand the role of decomposer-primary producer linkages in successional dynamics. We are testing a series of hypotheses that relate changes in plant species composition during succession to changes in activity and structure of the soil microfloral and faunal community, dynamics of soil organic matter, and availability of soil nutrients. As these successional patterns are identified, they are being applied to understanding specific processes and mechanisms involved in ecosystem development during recovery from moderate and severe disturbances. These findings are then being used in conjunction with simulation models to assess potential effects of climate change on ecosystems.

Our research involves field studies in northwestern Colorado and southeastern Washington, laboratory studies, and simulation modeling. Ongoing projects include studies of response patterns of primary producer and soil microbial communities to nutrient additions (N, P, and sucrose), the function of mycorrhizal fungi in plant community development, and the dynamics of litter decomposition under semiarid conditions. New studies are being implemented to investigate the significance of nutrient transfers from VAM fungi to plants and plant-root exudate interactions, and to relate this to understanding their roles in succession.

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INTRODUCTION

Our hypotheses are based on the premise that plant community development is closely linked to the coupling of decomposers (soil microflora and fauna) with primary producers through direct and indirect mutualistic interactions. This coupling governs nutrient acquisition by plants and nutrient utilization by decomposers. The rate of recovery of an ecosystem is related to the degree to which different components of the primary producer and decomposer subsystems are disrupted and to the rates at which these components and their interactions are re-established. Our research is testing a series of hypotheses that relate changes in plant species composition during plant community development to changes in the 1) density, activity, and community structure of the soil microflora and fauna; 2) organic matter, quality, quantity, and decomposition; and 3) nutrient availability. In addition to identifying successional patterns, our work also seeks to identify specific processes and mechanisms relevant to ecosystem development following severe and moderate disturbances. Results from our experiments are being used in conjunction with simulation models to assess the potential effects of climate change on ecosystems.

Our research is divided into two parts: 1) field and laboratory experiments to study processes important during community development and for ecosystem response to climate change, and 2) models to forecast ecosystem responses to climate changes in semiarid regions. The experimental component of our research is primarily process-level work in Colorado along with a comparative study at our Colorado site and the Arid Land Ecology Site on the Hanford Research Park in Washington. Data from these studies will be used to compare aspects of plant community development and food web architecture at each site and to parameterize simulation models. In the modeling component, we will apply our experimental data to a hierarchy of existing simulation models to explore how climate changes are likely to affect ecosystem development and to guide us in developing future field and laboratory studies. Modeling appears to be the best means of linking climate and ecosystem changes because of the practical difficulties in manipulating temperature, water, nutrient levels, and CO_2 availability, and because of the gradual, long-term nature of climate change.

METHODS

Site Description

The field studies are located in the Piceance Basin, approximately 70 km northwest of Rifle in northwestern Colorado. Elevation of the site is 2020 m, and mean annual precipitation is approximately 282 mm with about half of that occurring as snowfall. Mean annual temperature is approximately 6.8°C. The climate is semiarid and is characterized by a relatively dry period from mid May to mid September (Stark 1983).

The soils in the study area belong to the Piceance and Yamac series and support a big sagebrush shrubland. This community is composed primarily of big sagebrush (Artemisia tridentata tridentata), western wheatgrass (Agropyron smithii), junegrass (Koeleria cristata), thickspike wheatgrass (A. dasystachyum), Sandberg bluegrass (Poa secunda), needle-and-thread (Stipa comata), Hood's phlox (Phlox hoodii), roughseed cryptantha (Cryptantha flavoculata), and Englemann fleabane (Erigeron engelmanni).

Experimental Design

Experimental plots were initiated in the fall of 1984. We are using manipulative field experiments to study secondary succession in a semiarid ecosystem. In order to initiate secondary succession, we imposed a major disturbance on the study site. Existing vegetation plus the top 10 cm of topsoil were removed with a bulldozer, and the remaining subsoil and topsoil was thoroughly mixed to a depth of 35 cm. This type of disturbance was chosen to simulate conditions that might exist following energy development.

Different treatment manipulations were applied to evaluate changes in ecosystem compartments during succession. Two types of treatments were used to address our questions and hypotheses: 1) fertilization experiments were initiated to study the effects of inorganic nutrient availability on structural and functional changes in primary producers and microflora during succession; and 2) fumigation experiments, as a means of initially decreasing soil microbial populations, were used to study the effects microbes play on regulation of nutrient availability.

Field experiments were organized in a randomized block design with four blocks (replications). Each block contained ten treatment plots, with each plot occupying an area of 500 square meters. In addition, there was an undisturbed control plot for each block.

The treatments were 1) annual fertilization with 100 kg N/ha and no seeding, 2) annual fertilization with 100 kg P/ha and no seeding, 3) annual fertilization with 100 kg N and 100 kg P/ha and no seeding, 4) annual nitrogen or sucrose additions, 5) soil fumigation with methyl bromide and no seeding, 6) fumigation and seeding early-successional species, 7) fumigation and seeding late-successional species, 8) no fumigation and seeding early-successional species, 9) no fumigation and seeding late-successional species, 10) control (no fertilization, fumigation, or seeding), and 11) undisturbed control (native sagebrush-grass vegetation).

RESULTS AND DISCUSSION

Fertilization Studies

Primary Producers

The addition of N reduced richness of perennial plant species during years 2-4 (1986-1988), and P reduced the number of perennial species in years 3 and 4. From year 1 to year 2, annual and biennial species richness declined on all treatments while biomass of annual species increased greatly. Added N increased production of annual species while it decreased production of most perennial species relative to the unfertilized control treatment. Community similarities were higher for the control and native vegetation than for other pairs of treatments, based on both species presence and plant production data. Nitrogen additions have retarded but not completely arrested secondary succession in this system.

The observed reduction in number of perennial plant species with N fertilization was consistent with findings of previous studies in climax vegetation and old fields. Tilman (1982) postulated a mechanism to account for such observations, namely that addition of a limiting resource would cause a shift in species composition, favoring species that are inferior competitors for that resource and that have a large growth response to its addition.

Experimental work by Parrish and Bazzaz (1982) and Tilman (1986) showed that annual and biennial species that dominated early-successional old fields were more responsive than perennial species to added N in terms of production. Redente et al. (1989) studied the response of early- and late-successional species that grow on our study site to N and P gradients under greenhouse conditions. They found that above- and belowground growth of early-successional species were more responsive to high levels of N and P than that of late-successional species.

The continued dominance of annuals through the fourth year after disturbance and the temporary increase of perennial plant production in year 2 followed by a decline in years 3 and 4 in plots that received N contrast with the findings of Tilman (1987) in a Minnesota sand plain. There, annual plant aboveground production increased greatly along an experimental N gradient during the first year following disturbance, but decreased significantly by the third year. Perennial plant production showed the opposite pattern, declining in response to added N the first year, but increasing by the third year. Our results do not support Tilman's (1987) postulate that added N could cause perennials to increase their energy and nutrient reserves during the second or third year after disturbance, thus leading to more early season growth and displacement of annuals.

Beneath the dense canopy of annuals in plots that received N fertilizer, the amount of light available to plants appeared to be greatly reduced in 1986 and 1987. Under high-nitrogen conditions, plant species that allocate a relatively high proportion of their resources to increase in height will be favored if light is a limiting resource, because they will capture more than their shorter-statured neighbors (Tilman 1985). Reduction in richness of perennial species may occur because some perennials may not be able to tolerate low-light conditions.

At present, it seems that increased N availability has slowed the invasion of Artemisia tridentata, the dominant plant of native plots. Production of A. tridentata was low for all treatments during the study, but was virtually zero for N and N+P treatments. In another study at this site we found that relative cover of A. tridentata increased from 0.3 to 2.8% during the 10 years following a similar disturbance but without N addition. Tilman (1987) suggested that invasion of woody plants may proceed very slowly on sites with low soil N levels. At our site, invasion of A. tridentata is not limited by low soil N, as evidenced by the vigorous growth of transplanted A. tridentata seedlings in adjacent plots that were also disturbed in 1984 but not fertilized. These transplants produced copious quantities of seeds in 1986 that led to thousands of seedlings in 1987, but only under or immediately adjacent to the parent shrubs. This indicates that rate of colonization by A. tridentata is limited by low seed dispersal ability.

The disturbance that we employed to begin secondary succession did not reduce the capital stock of soil N appreciably. Thus, we may have what Tilman (1987) terms succession on a rich site. On rich sites, he suggested that plant life history attributes, such as dispersal ability and maximum growth rate, should have more influence on secondary succession that soil fertility. While we cannot compare effects of plant life history traits and soil fertility on succession with this study, we did find that four years of N addition altered plant community composition and slowed the rate of secondary succession.

Rhizosphere Responses

Structural and functional responses of rhizosphere microbial communities, including estimates of soil nutrient resources, were evaluated during this funding period, using two plants, squirreltail bottlebrush (Sitanion hystrix) and western wheatgrass (Agropyron smithii), that had been studied the previous year and grown under field conditions in the Piceance Basin. In addition, experiments involving a wider range of plants have been initiated that will involve both laboratory and field experiments.

Based on results from 1988, fertilizer and plant type (early- versus late-successional) had no effect on total bacterial populations in the rhizosphere of these plants. In comparison, squirreltail (early-successional) had higher populations of active bacteria, and these higher populations of active bacteria were decreased with fertilizer presence.

The fungal hyphal length measurements also indicated that the squirreltail rhizosphere community was more sensitive to fertilizer presence than that of western wheatgrass, the late-successional plant. Western wheatgrass had hyphal lengths of approximately 130 meters/gram of soil which did not decrease in the presence of fertilizer. Squirreltail, however, had 142 meters/gram of hyphae without fertilization, and 57 meters/gram of soil with fertilization. This major difference in fertilizer response of squirreltail, in comparison with western wheatgrass, suggests that exudate release to maintenance of the rhizosphere microbial community is more flexible with the early-successional squirreltail than with the later succession wheatgrass. Greater amounts of exudates would be expected to be released by the early-successional plant to allow microbial nitrogen mobilization from soil organic matter, a process that is suggested to be decreased if mineral nitrogen is available. This process, if documented with a wider range of plants, could provide a framework for beginning to understand plant-microbe interactions in succession, in terms of exudate release, microbial mineralization-immobilization processes, and organic mater dynamics in the plant-soil system.

To obtain more information on this important point, microbial biomass, exudates, and soluble carbon resources in the rhizosphere of these plants were analyzed. Although there were no significant differences, squirreltail did show a decrease in organic carbon in the rhizosphere zone from 8.6 to 5.1 mg C/gram with fertilization, while the western wheatgrass value of approximately 7.0 mg C/gram soil was not changed. The microbial biomass values did not show responses to fertilizer presence or plant type, while the biomass nitrogen values did show distinct changes. With western wheatgrass, these values decreased, while with squirreltail, biomass nitrogen values were not significantly changed. The exudate carbon values for both plants were higher with fertilization, although these differences were not significant.

Similar studies of fertilizer effects on fungal community composition and diversity were also completed, using these two plants together with cheatgrass (Bromus tectorum). Without fertilizer, microbial populations and fungal diversity were similar for these three plants. Fertilizer resulted in decreased fungal diversity for squirreltail and cheatgrass that did not occur with late-successional western wheatgrass. These results again suggest that the microbial community in early-successional plants will be more responsive to nutrient presence than that of late-successional plants studied to date. Root and shoot growth responses of the species studied in this experiment also are of interest. For western wheatgrass, fertilization resulted in a significant decrease in shoot growth and a lower root growth. For squirreltail, in contrast, fertilization resulted in significant increases in both shoot and root growth, suggesting that less carbon was allocated to exudate release, with subsequent maintenance of nutrient-acquiring rhizosphere microorganisms, allowing more carbon to be allocated to plant tissue synthesis.

Nitrogen and Sucrose Study

Primary Producers

The dramatic increase in aboveground plant production with N addition and the accompanying decrease in production and richness of perennials prompted us to design a new study where N availability would be reduced as well as increased. A previous field study by H. W. Hunt, of our group, and simulation modeling indicated that a large addition of sucrose would reduce N availability by promoting the growth of microbes. A new study was initiated in September 1987 with three treatments: N addition (100 kg/ha/yr), sucrose addition (1600 kg C/ha/yr), and a control with no amendments. The amendments are added at several times during the growing season. The study design is a randomized complete block with 4 blocks. All plots (165-m^2 each) were seeded with a mixture of early- and late-successional plant species in order to make comparisons among particular species across the treatments. The amendments were begun in September 1987 and are continuing during each growing season of the study. Plant (% canopy cover, frequency, and density), microflora, microfauna, and N-mineralization data are being collected.

The first-year response to N was similar to that in previous studies, total canopy cover increased, and species richness decreased. Canopy cover was approximately equal between N and control plots for perennial grasses and shrubs (although amounts were very low in both cases), but was higher on N plots for annual forbs (61% and 33% respectively) and lower for annual grasses (3% and 7%). Density values followed the same pattern. Composition on the N plots consisted of 95% annual forbs (54% Kochia and 38% Salsola) and 4% annual grass (Bromus tectorum). Perennial forbs comprised only 0.8% on N plots. Composition on control plots consisted of 80% annual forbs (40% Kochia and 33% Salsola) and 17% annual grass. Perennial forbs comprised 2.4% on control plots. There were 13% fewer species on N plots than on control plots.

Sucrose plots had a lower plant density and less canopy cover (39% and 42% respectively) than did control plots, but had 9% greater species richness. Sucrose composition values were slightly lower for perennial grasses and slightly higher for perennial forbs and shrubs. Annual grasses were more abundant, and annual forbs less abundant, on sucrose plots. Kochia was most affected by sucrose treatment, exhibiting a 33% decrease in relative cover compared to control plots, and a 50% decrease compared to N plots.

Preliminary first-year data, therefore, appears to confirm the initial hypothesis. A response gradient is suggested, with N and sucrose plots on opposite ends of the gradient. Addition of N increases total canopy cover and decreases species richness. Sucrose decreases total canopy cover and increases species richness. Total plant density is highest on N plots, and lowest on sucrose plots. Annual forbs are favored by N addition, and annual grasses and perennial forbs decrease. Annual grasses, perennial forbs, and perhaps shrubs are favored by addition of sucrose, and annual forbs decrease.

Annual forbs dominate the first seral stage in secondary succession. Addition of N increases this dominance because the rapid growth rate of annuals allows them to dominate the flow of other resources (e.g., light and moisture) that then become limiting to other, slower growing species. The added energy source allows for competition for resources between two potentially rapid growth rate groups (annual forbs and microbes). Microbial production increases, consuming other resources such as N, which temporarily decreases availability to plants. As succession progresses, more nutrients become immobilized in organic matter and released with decomposition and mineralization. This favors species with slower growth rates (or at least decreases the advantage of rapid growth rates) since nutrient release takes place gradually during the growing season. Annuals are denied some of the resources early in the growing season, thereby decreasing (but not eliminating) their dominance. For annuals to continue to dominate the site, they must be able to monopolize resources during the initial growth pulse early in the season. Failure to do so, whether from microbial competition or climatic extremes, shifts the long-term advantage to perennials.

There exists both a temporal and a spatial component to competition. Perennials generally control the spatial by being able to carry over structure from previous years. For annuals to dominate, they must therefore control the temporal component. There are two strategies available to dominate the temporal: 1) be more efficient in gathering resources over time, or 2) secure resources more quickly than competitors. Most annuals are not able to effectively use the first against perennials. Therefore, dominance of a site by annuals is generally the result of the second.

Microbial Responses

For the nitrogen and sucrose study, bacterial and fungal populations in the 0-5 and 5-10 cm depths were completed in relation to variables of nitrogen and sucrose additions, using samples taken in June and August, 1988.

For the June, 1988 sampling, just after plots had been constructed, there were no significant differences in bacterial or fungal populations in relation to nitrogen and sucrose additions.

By the August, 1988 sampling, however, significant changes had occurred in relation to the treatment variables. The presence of nitrogen or sucrose resulted in significant increases in total bacteria at both depths. The sucrose treatment also resulted in a significant increase in active bacteria. At the August sampling, no significant changes in fungal hyphal lengths occurred. It was of interest that at the 5-10 cm depth, nitrogen addition resulted in a hyphal length decrease from 172 to 115 m. With larger sampling sizes and additional replications, it may be possible to identify significant differences suggested by these trends.

Mycorrhizal Fungi and Plant Nutrient Study

Recently, Reiners (1986) has suggested that elements in the environment do not cycle independently. In plants, they occur in distinct proportions in the protoplasm of cells. Certain ratios of elements (i.e., P/N, N/S, Ca/Mg. etc.) exhibit a limited range of values in algae, mosses, ferns, conifers, and flowering plants (Garten 1976 and 1978, Penning de Vries and Krul 1980). Nutrient ratios have been utilized in a crop tissue analysis technique termed the Diagnostic and Recommendation Integrated System (DRIS) that correlates ratios of element concentrations in crop tissue and maximum production data (Beaufils 1973). This system compares nutrient ratios in crop tissue and predicts the nutrient most limiting to plant growth. Ratios of elements in shoot tissue are being used to diagnose nutrient deficiencies in a variety of crops (Sumner 1978).

Nitrogen (N) and phosphorus (P) most commonly limit maximum growth or yield (Salisbury and Ross 1985). An approximate 1:10 ratio of P to N is common in diverse plant groups (Garten 1976).

Since a P/N ratio of about 1:10 is common for many plants, and since extensive results from greenhouse experiments support the conclusion that VA mycorrhizae enhance P concentrations in plants growing in P-deficient soils (Harley and Smith 1983), we designed an experiment to test the null hypothesis that: H_0 - under semiarid field conditions, VA mycorrhizae do not alter the P/N ratio of about 1:10 in native species. Experimental rejection of this hypothesis and support of the alternate hypothesis could have additional implications for success and stability of mycorrhizal species in semiarid habitats.

Correlations were made between VA mycorrhizal formation in roots and P concentrations, N concentrations, and P/N ratios in shoots of four semiarid grass species (<u>Koeleria cristata</u>, <u>Agropyron smithii</u>, <u>Stipa comata</u>, and <u>Sitanion hystrix</u>). The grasses were grown in the intensive study field plots in the Piceance Basin. These field plots included: 1) fumigated (methyl bromide), non-amended plots seeded with mixtures of either climax species or mixtures of early successional species; and 2) non-fumigated, non-amended plots seeded with mixtures of either climax species or mixtures of ruderal species.

Perhaps the most interesting results from this study are those that explain the relationship between mycorrhizal colonization and nutrient status of the host. Small increases (0-10%) in colonization are associated with large increases in tissue P concentration in the grasses. Changes in tissue P with varying levels of root colonization may be explained in several ways. The amount of P in shoot tissue may be a function of the actual proportion of active fungi. The life span of a functional arbuscule is estimated to be 4 to 15 days (Cox et al. 1980), and a functional mycorrhiza requires functional arbuscules (Hirrel and Gerdemann 1979). For a given root system, does an equilibrium exist between the amount of functional mycorrhizal hyphae and senescent mycorrhizal hyphae for which rates of hyphal growth equal the rates of hyphal senescence? Fine roots grow, die, and decay more rapidly than aboveground parts (St. John and Coleman 1983) and, as they decay, VA mycorrhizal fungi decay with them (Coleman 1976).

These results provide important information that other field studies have missed -- that low levels of colonization can yield significant nutritional benefits to the host. We contend that the lack of truly quantitative comparisons of colonization levels in other studies has contributed to inconsistent reports of the benefits of VA mycorrhizae in field grasses.

The potential for using the P/N ratio as a measure of plant vigor is suggested by the narrow range of values found at the sufficient nutrient level for plant growth (Dijkshoorn and Lampe 1980, Penning de Vries and Krul 1980). Ranges of P/N values deemed as sufficient to plant growth have been reported for a number of plants (Andrew and Robbins 1971, Small and Ohlrogge 1973, Dijkshoorn and Lampe 1980). A P/N ratio of 0.10 (%P/%N) was associated with maximal yields in several crop plants (Dijkshoorn and Lampe 1980). The P/N ratios in the four experimental grasses examined in our study range from 0.063 to 0.169. Optimal yield occurred when tissue P/N values were ca. 0.150 for each grass. In August, 1987, P/N ratios of colonized grasses approached or exceeded 0.150 and were significantly higher than non-colonized grasses. These results suggest that P/N ratios are good indicators of mycorrhizal benefit to grasses in a semiarid environment.

P/N ratios in plants in natural environments may yield information that cannot be gained from other data. The P/N ratio may be a reliable index to measure mycorrhizal responsiveness (Reeves 1987), and differences in P/N ratios between treatments may indicate which nutrient is most limiting to growth. If the P/N ratio of a plant is less than a certain optimum range of values, the plant is most likely limited by P; if the P/N ratio is higher than optimum, then the plant is most likely limited by N. We believe that growth of mycorrhizal grasses studied in the Piceance Basin is limited more by N availability than P availability, since the P/N ratios exceed an estimated optimum P/N value. The reverse may be true for non-mycorrhizal grasses with significantly lower P/N ratios. Non-mycorrhizal grasses are potentially at a distinct disadvantage, both in terms of nutrient status and water relations, to grasses colonized by VA mycorrhizal fungi if P or moisture levels are low.

The role of VAM on plant growth may be viewed on at least two different scales: 1) the community level with respect to higher plant competition, and 2) the individual level with respect to plant metabolism. Following a land disturbance, composition of the plant community exhibits change. Over time, there is a gradual change from a community composed of fast-growing annuals to a community composed of slow-growing perennials. The proportion of mycotrophic species increases as the plant community matures. If mycorrhizal fungi are absent, community development may linger at a more ruderal stage. The benefit to plant metabolism may be mediated directly through enhanced P uptake or indirectly through the influence of improved P-nutrition on water relations.

Litter Decomposition Study

Until the present time, only the total bacteria and active bacterial analyses have been completed on the sagebrush litter study. In relation to the variables of under versus between plant placement of materials, and whether native or climax materials were used, no significant block of main effects were observed in the first season of the experiment.

Modeling and Climate Change

Climate Change

Our grassland ecosystem model, GEM (referred to as the TOST model in the proposal and previous progress report) was used to investigate effects of elevated CO_2 and climate change on plant production and ecosystem function (Hunt et al. 1989). GEM simulates seasonal dynamics of shoots, roots, soil water, mycorrhizal fungi, saprophytic microbes, soil fauna, inorganic nitrogen, plant residues, and soil organic matter. Modeled processes include evapotranspiration, photosynthesis, respiration, nutrient uptake, allocation between shoots and roots, exchange between roots and mycorrhizal fungi, plant organ death, herbivory, decomposition, nutrient mineralization/immobilization, and trophic transfers among microbes and fauna.

The model was adapted to data from two grasslands: a native shortgrass steppe dominated by _Bouteloua gracilis_ (blue grama, a native perennial C4), and a 40-year-old stand of _Agropyron cristatum_ (crested wheatgrass, an introduced perennial C3). Parameters in the plant and water flow models were adjusted to achieve a fit to data for live and standing dead shoots, transpiration rate, root biomass, and soil water. The model correctly simulated greater live shoot biomass for the crested wheatgrass community (Fig. 1), and greater standing dead biomass for the native shortgrass community (Fig. 2). The model predicted the timing and amount of spring growth, but total shoot biomass in the fall was overestimated. Predicted daily average transpiration showed the same seasonal pattern as mid-day measurements (Fig. 3). The model correctly predicted that the native community had drier soil, greater transpiration in spite of smaller live shoot biomass, and greater root biomass.

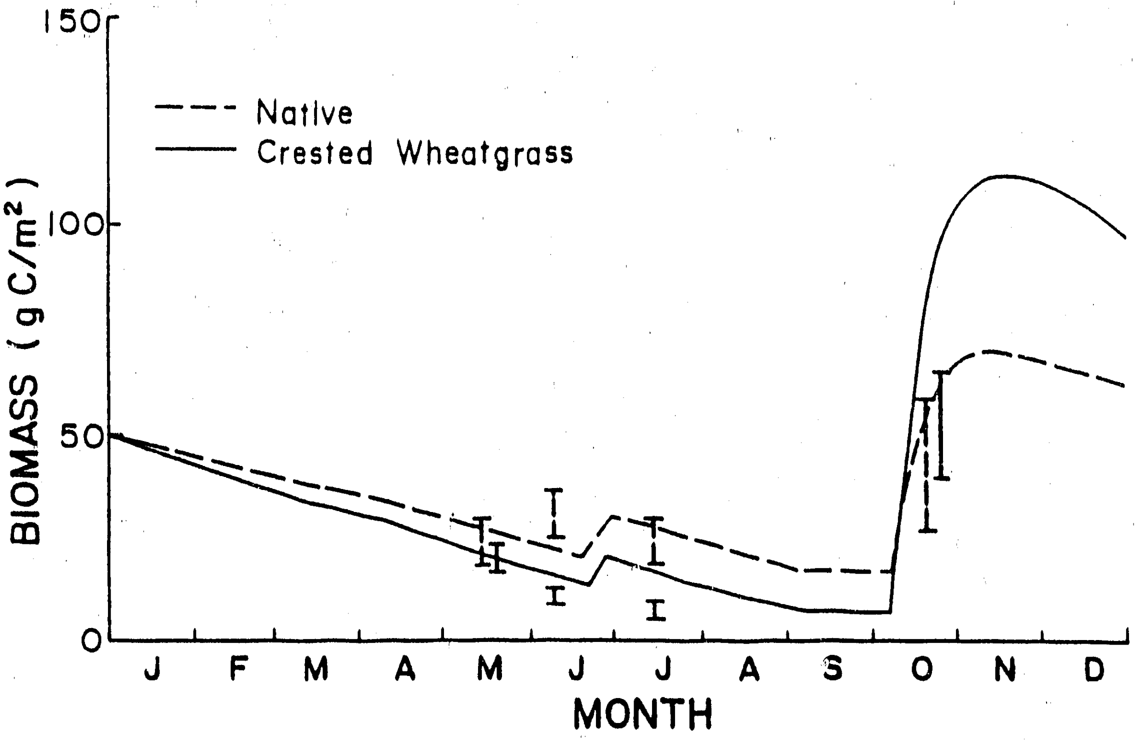

Figure 1. Predicted and observed (95% confidence intervals) dynamics of live shoots in the crested wheatgrass community and the native shortgrass community.

The fit of the model to the above data was achieved by adjusting parameter values. Validation tests consisted of additional comparisons between model predictions and data not used in model development. The model correctly predicted that the native site had a lower litter level and smaller fungal biomass, that soil organic carbon increases with precipitation and decreases with temperature, that increased precipitation leads to decreased shoot nitrogen, water use efficiency, and root:shoot ratio, that elevated relative humidity increases NPP, and that elevated CO_2 increases NPP, water use efficiency, and mycorrhizal fungal biomass. These successes increase our confidence in model predictions.

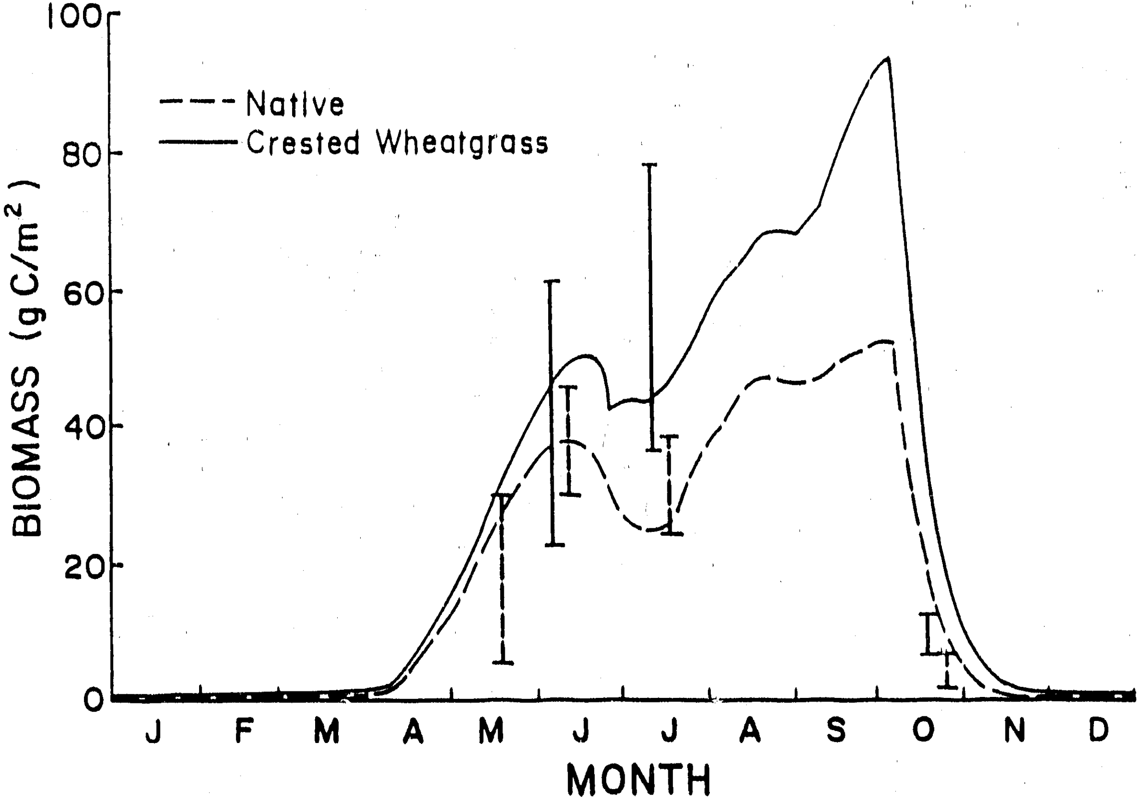

Figure 2. Predicted and observed (95% confidence intervals) dynamics of standing dead shoots in the crested wheatgrass and native shortgrass communities.

We used information from general circulation models of the atmosphere (Schlesinger and Mitchell 1987) to construct a series of climate change scenarios. These consisted of all combinations of two levels of atmospheric CO_2 (present-day levels and doubled), two levels of temperature (present-day and elevated by 3°C), and three levels of precipitation (present-day, -50%, and +50%). Both the native and crested wheatgrass versions of the model were run for 40 years to simulate long-term ecosystem response. In general, precipitation was the most important factor in determining system response to climate change, followed by CO_2 level, and plant species.

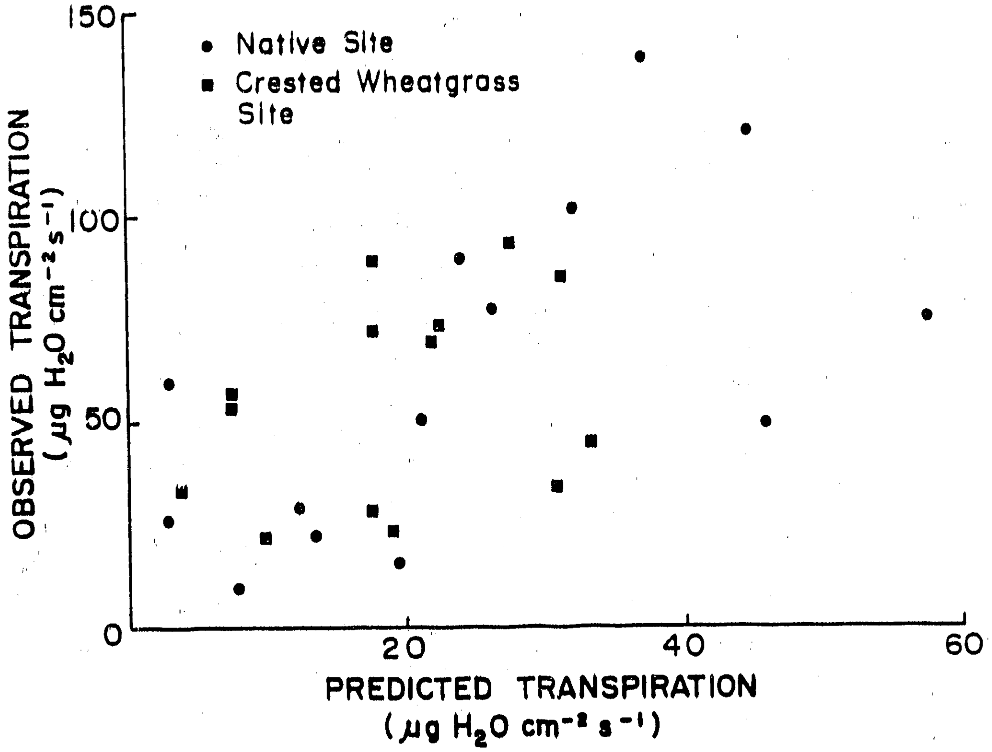

Figure 3. Correlation between predicted daily transpiration and observed mid-day transpiration for the native and crested wheatgrass communities. There was no significant difference between regression lines for the two communities. Treating the data as a single group, the equation is: observed = 30.0 + 1.32 * predicted ($R^2 = 0.30$, $P < 0.003$).

Net primary production (NPP) increased from 110 to 257 to 288 g C m-2 y-1 as annual precipitation increased from 23 to 46 to 69 cm. Doubling CO_2 increased NPP of crested wheatgrass by 53%, and of blue grama by 36%. Riechers and Strain (1988) found 35% greater biomass in blue grama seedlings after 7 weeks exposure to doubled CO_2. The response of crested wheatgrass to doubled CO_2 apparently has not been determined, but C3 grasses generally show a greater response than C4's (Riechers and Strain 1988). Temperature had little effect on total annual NPP, which was surprising because temperature effects pervade the model. However, elevated temperature had appreciable effects on the seasonality of primary production. Figure 4 shows two-fold and greater increases in net photosynthesis in spring and fall, and decreases of up to one-third during summer when the temperature exceeded the optimum for photosynthesis. These increases and decreases tended to cancel out over a year, and accumulated net photosynthesis of crested wheatgrass under control and elevated temperatures was 372 and 364 g C m-2 y-1, respectively. Blue grama, under control and elevated temperatures, showed increased production in spring, fall, and some periods in summer, and accumulated photosynthesis was 13% greater than in the control (311 versus 276 g C m-2 y-1).

Water use efficiency was greater with elevated CO_2 and less precipitation, which agrees with results for wheat (Gifford 1979). The CO_2 effect was greater with less precipitation. Two factors contribute to this interaction: 1) with more moisture, nitrogen was more limiting, and the additional C supply had a smaller effect; and 2) the vapor pressure deficit and CO_2 gradient are affected differently by increases in stomatal resistance resulting from lower precipitation.

Total C in the system was 320 g C m-2 greater under elevated CO_2, and excess atmospheric CO_2 was being sequestered at 4 g C m-2 y-1 after 40 years. The amount of atmospheric CO_2 in the air above 1 square meter is increasing by about 6 g C m-2 y-1 (Ramanathan 1988). These results suggest that our grassland sites could sequester about two-thirds of their share of excess atmospheric

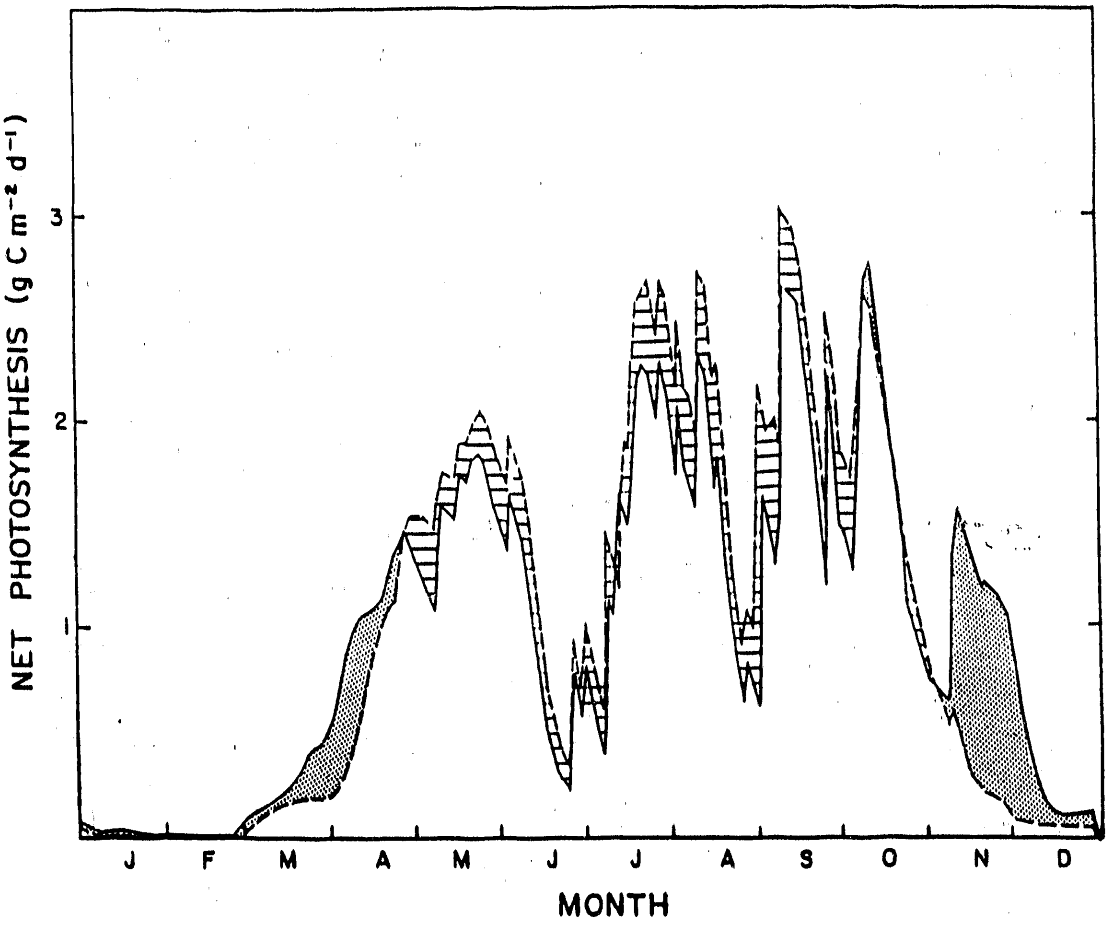

Figure 4. Simulated net photosynthesis of crested wheatgrass under control (dashed line) and elevated (solid line) temperature regimes.

CO_2. This amount and rate of storage is smaller than estimates of Lugo and Brown (1986) for forests undergoing normal development (not subjected to climate change).

Adaptation of GEM Model to Shrubs and Annuals

We have completed the literature review of shrub models, and are presently evaluating alternative modeling approaches. The model has been adapted to represent growth of pine seedlings as part of a USDA project, and this effort will speed our progress on the shrub model. We have initiated a literature search of models for annual plants.

NEW STUDIES BEGUN IN 1989

Piceance-Hanford Study

Nutrient acquisition by perennial grasses appears to be improved by direct nutrient transfers from VAM fungi to plants. Such nutrient transfers may be most important during the establishment phase of a plant's life cycle, particularly where seedlings grow in a matrix of competitive annual plants. We expect that the benefits of this direct mutualism between fungi and plants would be greater for late-successional species, that probably are adapted to grow under low-nutrient availability conditions, than for early-successional species. We also want to test responses of the grass seedling establishment to VAM and annuals under different climatic and edaphic conditions to determine if responses are localized or of a general nature.

Four perennial grass species (<u>Sitanion</u> <u>hystrix</u>, <u>Poa</u> <u>secunda</u>, <u>Stipa</u> <u>comata</u>, <u>Agropyron</u> <u>spicatum</u>) characteristic of different seral stages will seeded in large cylinders buried in the field. There will be four treatments in a factorial design: annual weeds (<u>Bromus</u> <u>tectorum</u>, <u>Salsola</u> <u>iberica</u>) present, annual weeds removed, high MIP (mycorrhizal infection potential) soil, and low MIP soil. The experiment will be conducted at two sites, the Piceance Basin and the Hanford Research Park in southeastern Washington. Soil with low MIP will be obtained by fumigating soil at each site with methyl bromide. Roots and attached soil debris from mycorrhizal corn plants grown in the greenhouse will be added to the fumigated soil to create high MIP soil. There will be 5 replicates (cylinders) of each treatment combination. Because this study is designed to investigate the establishment phase of the plant life cycle, the study will run for one year. Variables to be measured include aboveground plant biomass, N and P concentration of aboveground perennial plant material, and mycorrhizal colonization of perennial grasses. Rhizospheres of perennial grasses growing without the presence of annual weeds will be examined for organic matter accumulation, microbial biomass, and soluble components. In conjunction with this study, we will collect data on bacteria, fungi, and soil fauna to develop food webs that will be compared for the two sites.

Contacts with personnel at Battelle Pacific Northwest Laboratories have been made, and the field site on Hanford's ALE site selected. Soil samples have been returned to Fort Collins, and mycorrhizal populations characteristic of the Hanford site are being cultivated. Plans are underway to have the cylinders ready on both sites by September 1989. Plantings are planned for September-October 1989 in order to allow the Hanford site plants to begin growth during the growing season that begins there in the fall. The cylinders are to be harvested at the end of the respective growing seasons (May-June 1990 at Hanford, and August-September 1990 at Piceance).

Root Exudate Study

This study, begun in the spring of 1989, involves the growth of <u>Sitanion hystrix</u>, <u>Stipa comata</u>, <u>Poa secunda</u>, and <u>Agropyron spicatum</u> under greenhouse conditions, where nitrogen level and microbial communities can be controlled using a Root Microcosm System (RMS). These studies are intended to expand upon field experiments that have been completed to data, and will allow for development of a more detailed understanding of plant-plant exudate interactions with nitrogen availability. In addition, more detailed field studies are planned that will include plant-plant root interactions and competition for nutrient resources.

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