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MODELING THE RESPONSE OF ECOSYSTEMS TO CO₂ AND CLIMATE CHANGE

PROGRESS REPORT

For the Period September 1, 1992 - June 19, 1993

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EXECUTIVE SUMMARY

In recognition of the role of plants in the bio-geosphere carbon cycle, the Department of Energy (OHER) initiated a research program: *The Direct Effects of Increasing Carbon Dioxide on Vegetation*. This report describes the continuing research that we are conducting as part of this program. The ultimate goal of our research is to develop computer models capable of predicting responses of plants and ecosystems to the direct and indirect effects of atmospheric levels of carbon dioxide that are approximately twice those of the pre-industrial period. The understanding of ecosystem responses to elevated CO₂ necessarily depends on knowledge of responses of individual plants and their interactions with one another and their environment. Our research approach incorporates the study and modeling of response to CO₂ at all levels of the plant-community-ecosystem hierarchy, in an effort to understand the linkages and translation of effects of CO₂ from one level to another. The research results reported here focus at several different levels of this hierarchy, and are highlights of accomplishments for the period September, 1992 to June, 1993.

One of our principal objectives is the development of a modular, mechanistic plant growth model (GePSi). This model will serve as a template model to be used for predicting responses of a wide variety of plants to elevated CO₂. Section I describes the model development and structure. The model includes a great deal of physiological mechanism and structural reality in terms of leaf photosynthesis, canopy architecture, root architecture, and root nutrient and water uptake. The model was parameterized for loblolly pine and the predictions of the model are compared to some experimental results for pines grown under elevated CO₂. These results show that the model successfully predicts growth responses of pines under different CO₂ environments. Further work will be required to validate the model for other species and situations.

At the ecosystem level, our modeling research is focused on nutrient cycling and decomposition processes. An important indirect effect of CO₂ could be on the change in litter quality, root exudation, and nutrient uptake by plants. All of these factors could change microbial decomposition rates and nutrient availability in the rooting zone. Section II describes the modeling research that is being done to create a generic model of decomposition and nutrient availability that is mechanistic in terms of microbial metabolism and nutrient release in response to different chemical composition of litter.

Sections III through VI describe experimental research that is being conducted in order to answer questions that directly relate to our modeling research and can provide information about some missing links in understanding and modeling plant and ecosystem response to elevated CO₂. Section III describes that development of the tallgrass prairie canopy in response to elevated CO₂. This information is necessary to predict light distribution in the canopy and can aid in understanding plant competition and plant community response to elevated CO₂. The results show that elevated CO₂ produced larger canopies, but did not have a great impact upon the distribution of leaf material within the canopy.

Section IV describes the decomposition of leaf litter produced under different CO₂ levels and with or without nitrogen (N) fertilization. The litter produced under

different CO₂ levels did not differ significantly in its carbon chemistry or N concentration. Consequently, there was little difference in the rate of decomposition of the litter from different CO₂ treatments over a period of 18 months. However, there was a difference in the decomposition of litter from different species. Thus, if elevated CO₂ resulted in changes in species composition, there could be a change in decomposition and nutrient availability in the prairie.

Section V describes the growth and physiology of seedlings of 2 species of desert shrubs at elevated CO₂ and different root temperatures. Both shrubs responded to high CO₂ with increased photosynthesis and growth. This response was enhanced by high root temperatures. This suggests that the combination of high CO₂ and higher temperatures could make these shrubs very strong competitors in arid grasslands that are exposed to these invading shrubs.

Section VI describes the responses of loblolly pines to elevated CO₂, particularly root morphology and architecture. Although elevated CO₂ greatly increases total plant growth, there was little change in root/shoot ratio. The root architecture was changed by elevated CO₂, and this response was greatest when plants were grown at low N levels. High CO₂ increased the length of secondary lateral roots and increased the diameter of the primary tap root and laterals. At low N availability, CO₂ caused greater N stress and lowered tissue N levels.

The results of the above experiments reveal the important interactions that can occur between CO₂ and other environmental factors, particularly soil nutrients. Changes in soil nutrient levels can significantly modify the response of plant growth and morphology to elevated CO₂. Models must incorporate these significant interactions if they are to correctly predict the response of plants to elevated CO₂.

PUBLICATIONS – 1992-1993

1. Published:

- Chen, JiaLin, J.F. Reynolds, P.C. Harley and J.D. Tenhunen. 1993. Coordination theory of leaf nitrogen distribution in a canopy. *Oecologia* 93:63-69.
- Reynolds, J. F., D. W. Hilbert, and P. R. Kemp. 1993. Scaling ecophysiology from plant to the ecosystem: A conceptual framework. In: J. R. Ehleringer and C. B. Field (Eds.), *Scaling Physiological Processes*. Academic Press, San Diego. pp. 127-140.
- Reynolds, J. F., J.-L. Chen, P.C. Harley, D.W. Hilbert, R.L. Dougherty and J.D. Tenhunen. 1992. Modeling the effects of elevated dioxide on plants: extrapolating leaf response to a canopy. *J. Agric. For. Meteorol.* 61: 69-94.

2. In Press:

- Kemp, P. R., J. M. Cornelius, and J. F. Reynolds. 1993. Temporal discontinuities in precipitation in the central North American prairie. *Int. J. Climatol.*
- Moorhead, D. L. and J. F. Reynolds. 1993b. Changing carbon chemistry during decomposition of creosotebush fine litter in the northern Chihuahuan Desert. *Am. Midl. Nat.*
- Moorhead, D. L. and J. F. Reynolds. 1993a. Effects of climate change on decomposition in Arctic tussock tundra: A modeling synthesis. *Arctic Alpine Res.*
- Reynolds, J. F., B. Acock, and R. Whitney. 1993. Linking experiments and modeling. In: E. D. Schulze and H. A. Mooney (eds.), *Design and Execution of Experiments on CO₂ Enrichment*. Springer-Verlag.
- Reynolds, J. F., R. A. Virginia, and W. H. Schlesinger. 1993. Defining functional types for models of desertification. In: T. M. Smith, H. H. Shugart, and F. I. Woodward (Eds.), *Functional Types in Ecosystem Modeling*, Cambridge Univ. Press.

2. Submitted / In Review:

- Brisson, J. and J. F. Reynolds. 1993. The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. *Ecology*.
- Kemp, P. R., J. F. Reynolds, N. Adam, and C. E. Owensby. 1993. Effects of elevated atmospheric CO₂ and soil nitrogen on canopy leaf area distribution in a tallgrass prairie. *Ecol. Appl.*
- Larigauderie, A. J. F. Reynolds, and B. R. Strain. 1993. Root response to CO₂ enrichment and nitrogen availability in loblolly pine. *Plant and Soil*.
- Waldecker, D., P. Kemp, R. Virginia, J. Reynolds, and C. Owensby. 1993. Decomposition in a natural prairie environment of grass leaf litter produced under different levels of CO₂ and nitrogen fertilization. *Plant and Soil* (in review).

SECTION I.

A GENERIC PLANT GROWTH SIMULATOR (GePSi)

Description of GePSi

This Section reports the progress in developing a generic, totally modularized, and physically and physiologically oriented, plant growth model based on Object-Oriented Programming language, C++.

Structure of the Model

GePSi is divided into two major blocks, the ENVIRONMENT and the PLANT, as shown in Fig. 1. The ENVIRONMENT contains driving forces to plant growth. Plants are facing an above-ground aerial environment and a below-ground soil environment. The above-ground aerial environment contains two classes, Weather, which defines the weather conditions above a canopy, and MicroWeather, which defines the micro meteorological conditions in a canopy. The below-ground soil environment contains one class, Soil, which defines physical and chemical conditions of a soil column. The Weather acts as a driving force to the MicroWeather; the MicroWeather is closely linked to Canopy, and the Soil is closely related to RootSystem, as shown in Fig. 1.

The classes in PLANT are designed according to the hierarchical structure of a plant in the real world. At the top level, the class Plant is defined. At the second level, the class Canopy, which defines the above-ground part of a plant, and the class RootSystem, which defines the below-ground part of a plant are designed. At the lowest level, classes Leaf, Stem, Fruit, and Root are defined. The hierarchical structure of the PLANT part is shown in Fig. 1, which represents the ownership between classes. A Plant object will own one Canopy object and one RootSystem object. A Canopy object can own several objects of stems, leaves, and fruits, and the number of which changes during growth. When the canopy object updates itself, it can create new objects or destroy old objects and OOP makes it easy to do. A RootSystem object owns several root objects, and the number of root objects also changes with time and environmental conditions.

Some of the classes shown in Fig. 1 are stand-alone classes, such as Weather, MicroWeather, Soil, Leaf, Stem, Fruit and Root. That means, they can be used individually. For example, class Weather can be used, without referring to other classes, to analyze the annual, daily and diurnal patterns of the weather generated from theoretical and empirical formulas. Class MicroWeather incorporates full version of Norman's model of radiation transfer in canopy, and can be used by micro meteorologists to analyze profiles of radiation, temperature, wind speed, etc., and their response to different canopy structure. Class Soil is based on solving partial differential equations for heat, water and nutrient movement in soil and can be utilized individually by soil physicists and soil chemists to analyze their data obtained in laboratories and in fields. Class Leaf can be utilized by plant physiologists to analyze responses of attributes of Leaf class such as photosynthesis, stomatal conductance, and transpiration without referring to any other classes. Class Root can be used to analyze the characteristics of root water absorption and nitrogen uptake. While the class Canopy should be used in conjunction with classes Leaf, Stem and Fruit,

Figure 1. Diagram of principal elements of the model GePSi.

and the class RootSystem should be used together with Root, since without objects of Leaf, Stem, Fruit and Root, the objects of Canopy or RootSystem do not exist. For the same reason, the class Plant should be used with all classes shown in the PLANT block in Fig. 1.

Class Hierarchy

The class hierarchical structure is different from the ownership structure shown in Fig. 1. The class hierarchy presents the relationships among all classes. It is not a representation of the functional relationship of each class, but simply that of the descendancy among classes, like a family tree. In OOP, each class inherits all the behavior (modules) and all the attributes (instance variables) of its ancestors. The inheritance embodies one of the basic principles of OOP: to start with most general cases and then to go step by step into more specific cases. When we try to develop a class specific to loblolly leaf called, say, LeafLoblolly, we will first examine what are generic features all C3 leaves have. We will design a class LeafC3 first, which encompasses all the common features of C3 leaves, and then design the class LeafLoblolly as a subclass of LeafC3. We also examine what are the common features of all C3 and C4 leaves have, and put them together into a new class Leaf. Then the class LeafC3 becomes a subclass of Leaf, which contains only the special features C3 leaves have. Furthermore, we can compare leaf with stem, fruit and root, and find the features they have in common, and put them into a class Organ. The class Leaf becomes a subclass of Organ and contains only the features all leaves have which are distinct from stem, fruit and root. This example clearly shows that, when a class structure is developed in this way, a model based on it becomes truly generic. The class hierarchy of all classes in our generic plant growth model is shown in Fig. 2.

It can be seen from Fig. 2 that the class GObject, which is an abstract class, is at the highest class-hierarchical level. That means all the classes in Fig. 2 are descendants of the class GObject and inherit all behavior and attributes of it. The three classes Weather, MicroWeather and Soil shown in the ENVIRONMENT block of Fig. 1, and the three classes Plant, Canopy, RootSystem shown in the PLANT block of Fig. 1, are on the second class-hierarchical level. The class Organ also occupies the second class-hierarchical level and the classes Leaf, Stem, Fruit, and Root are subclasses of the class Organ, occupying the third hierarchical level. As we said, the lower class-hierarchical level a class occupies, the more specific properties it has. The classes Leaf, Stem, Fruit and Root are all Organs, but they have specific properties that make them different from each other.

After a generic plant growth model is developed, the application of it into more specific case can be done simply by designing more specific classes as subclasses to the existing classes. If we try to develop a plant growth model for cotton, what we need to do is to define classes PlantLoblolly, CanopyLoblolly, RootSystemLoblolly, LeafLoblolly, MainStemLoblolly, BranchLoblolly, FruitLoblolly, SuberizedRootLoblolly and ActiveRootLoblolly as subclasses of the corresponding classes, as shown in Fig. 2, while there is no need to change any existing classes. This feature of OOP greatly eases the efforts to expand the model, and avoids side-effects caused by modification of existing codes that are big headache to modellers.

Figure 2. Hierarchical relationships of all classes in the model GePSi

Interface Methods

There are two kinds of methods in each class: public and private. The public methods are accessible from outside of the class, while the private methods can only be seen within the class. For the users who are interested in application of the classes, they only need to know the interface methods in each class, which are part of public methods. Since the central task of plant growth model is to simulate plant growth, that is, to update the attribute variables of a Plant object and the related objects of Canopy, RootSystem, Leaf, Stem, Fruit, Root, Weather, MicroWeather and Soil, specially designed interface methods for updating are incorporated in each class shown in Fig. 2. There are four update methods on different time scales to meet various updating requirements: annual, daily, hourly and minutely. The annual update method is incorporated only in the class Weather which allows to read or generate arrays of daily weather variables on each day in a year once at a time. It simplifies calculations. In the same manner, the daily update method in class Weather reads or generates arrays of hourly weather variables at each of twenty four hours in a day. The update methods in each class update relevant attribute variables in the class, which are shown in the Tables 1 through 4. The related equations that will be explained in detail in the following section are also included.

Implementation of Plant Growth Model

The classes shown in Fig. 2 are the templates for various objects. The objects created from the same class have a same set of attribute variables and methods. These attribute variables can be updated on various time scales responding to corresponding update message sent to the object. When the design of the classes are completed, the implementation of a plant growth model requires only two things to do. The first thing is to create relevant objects from the classes, and the second thing is to send update message to the objects.

Fig. 3 shows how objects are created. For a plant growth model, single object of Weather, MicroWeather, Soil and Plant is created. When a Plant object is created, it automatically creates one object of Canopy and one object of RootSystem. In turn, when the Canopy object is created, it automatically creates several objects of Leaf, MainStem, Branch and Fruit, and when the RootSystem object is created, it automatically creates an object of SuberizedRoot and several objects of ActiveRoot, in accord with the initial status of the canopy and the root system, respectively.

Fig. 4 shows how the daily update message is sent to the objects. A daily update message is sent to the objects of Weather, MicroWeather, Soil, and Plant. When the Plant object receives the daily update message, it automatically sends a daily update message to the objects of Canopy and RootSystem, which in turn, send a daily update message to the objects of Leaf, MainStem, Branch, Fruit, SuberizedRoot and ActiveRoot. For the hourly and minutely update messages, the situation is similar to the daily update message.

Table 1: Annual update

Class	Variables Updated
Weather	Daily total short-wave radiation (each of 365 days) Daily total highest and lowest air temperature (each of 365 days) Daily mean vapor pressure (each of 365 days) Daily mean wind speed (each of 365 days) Daily total precipitation (each of 365 days)

Table 2: Daily update

Class	Variables Updated
Weather	Short-wave radiation (each of 24 hours) Direct and diffuse PAR and NIR (each of 24 hours) Air temperature (each of 24 hours) Relative humidity (each of 24 hours) Wind speed (each of 24 hours) Soil surface temperature (each of 24 hours) precipitation (each of 24 hours)
MicroWeather	Number of layers in the canopy, height of each layer Leaf area and stem area in each layer Extinction factors to diffuse radiation
Soil	Number of soil layers with roots
Plant	Age and physiological age
Canopy	Carbon and nitrogen supply to canopy and root system Leaf inclination distribution Carbon and nitrogen supply to each stem, leaf and fruit Heat sum for emergence of new stem, leaf and fruit Total biomass in stems, leaves and fruits Total nitrogen in stems, leaves and fruits Total leaf area and stem area Daily respiration rates of stems, leaves and fruits Daily photosynthesis and transpiration of all leaves
RootSystem	Carbon and nitrogen supply to each root Rooting depth Total biomass in suberized and active roots Total nitrogen in suberized and active roots Total root length Daily respiration rates of suberized and active roots Daily water and nutrient uptakes by all roots
Organ	Age and physiological age Biomass and nitrogen content Daily respiration
Leaf	Length, width, surface area, specific area, nitrogen content Daily photosynthesis and transpiration
Stem	Length, top and base diameter, surface area, volume Active biomass
Fruit	Length, width, volume
Root	Length, diameter Daily water and nutrient uptake

Table 3: Hourly update

Class	Variables Updated
MicroWeather	Profiles of CO ₂ concentration Profile of wind speed Profiles of air temperature and vapor pressure Profiles of direct PAR and NIR Profiles of downward diffuse PAR and NIR Profiles of upward diffuse PAR and NIR Profiles of downward and upward thermal radiation
Soil	Profiles of NH ₄ and NO ₃
Canopy	Hourly respiration rates of stems, leaves and fruits Photosynthesis and transpiration of sunlit leaves Photosynthesis and transpiration of shaded leaves Hourly gross and net assimilation of the canopy Hourly total transpiration
RootSystem	Hourly respiration rates of suberized and active roots Hourly water and nutrient uptakes by all roots
Organ	Hourly respiration
Leaf	Photosynthesis and transpiration Leaf boundary-layer conductance Stomatal conductance Interacellular CO ₂ concentration Leaf temperature
Root	Nutrient uptake rate

Table 4: Minutely update

Class	Variables Updated
Soil	Temperature, sensible and latent heat at surface Profile of soil temperature Profile of water potential Profile of volumetric water content
Canopy	Water potential and relative water content Total amount of water in the canopy
RootSystem	Water uptakes by all roots
Root	Water uptake

Figure 3. Creation of objects from classes.

Figure 4. Sending update message to objects.

Results

GePSi is parameterized for loblolly pine trees using the experimental data collected at Duke University. It is found through the experiments that the value of the key parameters in Farquhar's photosynthesis model and Ball's stomatal conductance model are different for the loblolly seedlings grown at current (350ppm) and elevated (650ppm) CO₂ concentrations. The class Leaf in GePSi incorporates modules of photosynthesis (Farquhar's model) and stomatal conductance (Ball's model), together with the modules of energy balance and leaf boundary layer conductance. Therefore class Leaf can simulate the integrated responses of a whole leaf to elevated CO₂. The results are given in Fig. 5, which show the response curves of photosynthesis, transpiration, stomatal conductance and leaf temperature against PAR at three CO₂ levels (350, 500 and 650 ppm). It can be seen that for a given PAR value, the photosynthesis of the leaf grown at higher CO₂ levels is larger, while the stomatal conductance and the leaf transpiration are smaller. The leaf temperature, however, shows little difference, since the leaf width is very small and the leaf boundary layer conductance are very large.

Elevated CO₂ also affects other aspects of loblolly growth. The leaves grown at elevated CO₂ concentrations become thicker and the specific leaf area become smaller. This response results in a smaller total leaf area of a canopy for a given total leaf biomass and will reduce the total canopy photosynthesis. The one of the major reasons for the leaf thickening found through experiments is the increase in the non-structural carbon in the leaf when grown at a elevated CO₂. The average non-structural carbon in a leaf grown at 350 ppm is about 8%, and that at 650 ppm is about 15%. In GePSi it is assumed that the ratio of the leaf area to the leaf structural carbon is the same for the leaf grown at either current or elevated CO₂ concentrations, and the decrease in the specific leaf area at the elevated CO₂ is solely due to the increase in the non-structural carbon in the leaf. The increase of the non-structural carbon from 8% to 15% accounts for about 8% decrease in the specific leaf area. GePSi shows that the effect of this decrease in the specific leaf area on the loblolly growth at elevated CO₂ concentrations cannot be neglected.

Experimental results show that loblolly seedlings grown at elevated CO₂ concentrations are taller than those grown at current CO₂ concentration. The growth of main stems in GePSi is simulated in the class Stem, in which the entire main stem is divided into several segments from each flush. It is assumed that the elongation of the main stem of each flush is controlled by two factors. One is the maximum daily elongation rate, which is a function of the physiological age of the main stem, and the other is the supply of the carboxylate to the main stem. The maximum elongation rate is a parameter in the class Stem and has a different value for the plants grown at current or elevated CO₂ concentrations. The carboxylate supply to a main stem depends on the total daily assimilation rate of the canopy, the maintenance cost of the whole plant, and the carbon allocation schemes.

In GePSi the carbon allocation scheme is described at three levels. The first level is at the whole plant level, and the allocation is between the canopy and the root system. The second level is at whole canopy or root system level, and the allocations are between fruits, stems and leaves within the canopy or between suberized roots and active roots within the root system. The third level is at organ level, and the allocation is between the organs (leaf, stem, fruit, root) of the same kind but with different ages. The experimental results do not show a strong effect of the growth CO₂ on the carbon allocation scheme of the loblolly

seedlings, so the carbon allocation coefficients at all three levels mentioned above are kept unchanged for all plants either grown at the current or at the elevated CO₂ concentrations. The simulated time courses of total stem biomass, total leaf biomass, total root biomass, total leaf area, and top height for the plants grown at 350, 500 and 650 ppm are given in Fig. 6, Fig. 7 and Fig. 8, respectively. The harvest data are also shown in the figures as filled circles with five repreca in each harvest. It can be seen that the results from GePSi gives a good agreement with the experimental data.

Figure 6. Leaf Response to PAR (3 CO₂ levels)

Figure 7. Time Courses of responses to ambient CO₂ (=350 ppm).

Figure 8. Time courses of response to elevated CO₂ (=500 ppm)

Figure 9. Time courses of response to elevated CO₂ (=650 ppm).

SECTION II.

GENERIC MODEL OF DECOMPOSITION AND NUTRIENT CYCLING IN RESPONSE TO ELEVATED CO₂ AND CHANGING NUTRIENT LEVELS

Objectives

Our objectives for modeling decomposition processes are: 1) to develop generic routines describing decomposition in a consistent manner for widely different ecosystems, 2) to examine the potential effects of changing environmental conditions on decomposition, and 3) to mechanistically link primary production and decomposition processes in an overall description of nutrient cycling. To meet these objectives, we are expanding a model of plant litter decay that previously was developed to study decomposition in a warm, dry desert (GENDEC; Moorhead and Reynolds 1991) and nitrogen mineralization in a cold, wet tussock tundra (Moorhead and Reynolds 1993a). Although increasing concentrations of atmospheric CO₂ are unlikely to directly affect decomposer organisms, changes in the amounts and nutrient content of litter, as well as modifications in climate probably will. GENDEC responds to changes in climate, litter quality and quantity, and provides continuous estimates of nutrient release from litter turnover. The already successful application of this model to such widely divergent ecosystem types as tundra and desert demonstrate the flexibility of the approach.

GENDEC examines the interactions between buried litter, decomposer microorganisms, and C and N pools by interfacing microbial physiology and population dynamics with empirical observations of C and N pool dynamics, litter mass loss and changing system C:N ratios (Fig. 1). This combination of mechanistic and empirical bases provides us with the ability to predict effects of changing conditions (based on underlying mechanisms) while insuring reasonable model behavior (compared to empirical observations).

Modifications to GENDEC

We had proposed to expand GENDEC in three ways: 1) include a component to simulate recalcitrant material dynamics in more detail, 2) utilize changing litter quality to simulate changes in plant chemistry under CO₂ regimes, and 3) add a vertical dimension to the model, following patterns of surface and subsurface litter inputs and decay. Addressing the first of these changes, additional studies of litter decay in the northern Chihuahuan Desert demonstrated the importance of microbial products to

FIG. 1. Carbon flow diagram

interpreting patterns of litter decay (Moorhead and Reynolds 1993b). Therefore, GENDEC was modified to explicitly simulate the production and turnover of two distinct pools of dead microbial biomass: cell walls and cytoplasm (Fig. 1). This will provide a more accurate depiction of the transformations of individual substrates and a better estimate of overall dead organic matter dynamics, particularly for ecosystems in which significant quantities of recalcitrant soil organic matter are present.

Addressing the second of the proposed changes to GENDEC, a laboratory study of temperature-by-moisture-by-litter quality controls on plant litter decay was conducted during the autumn and winter of 1992-1993. These data are being used to test and refine model behavior for different litter types and climatic conditions (Fig. 2). Finally, differential patterns of surface and buried litter decay have been summarized for the northern Chihuahuan Desert (Moorhead 1993) and will be incorporated into an overall description of litter production and decomposition, within a vertically explicit spatial dimension, during the summer and autumn of 1993.

Plant-Microbe Interactions

Few data exist that can be used to quantify the dynamics of plant-microbe competition for mineral nutrients. Therefore, a small laboratory study is being conducted to provide this information for model development.

In this experiment, two common species of prairie and desert grasses (little bluestem and black gramma) are being grown in pots containing a nutrient-poor fine sand. Some of the pots will contain soil that is sterilized to remove mycorrhizae inocula. Small litter bags are being placed in some pots. Close monitoring of changing mass and nitrogen content of plants and litter will provide the means of estimating competitive interactions for available nutrients and to

FIG. 2. Mass loss of litter over time (mean values, $N=4$). A. creosotebush fine litter, B. tussock tundra fibric soil horizon, C. tussock tundra *Sphagnum* moss litter. Constant incubation conditions indicated in legend.

quantify the relationships between plant growth, litter decay and mycorrhizae development. This experiment will be completed by autumn 1993.

Other Ecosystems

GENDEC responds appropriately to the climatic and edaphic characteristics of the desert and tundra ecosystems addressed by this proposal (Moorhead and Reynolds 1991, 1993a,b). However, we also must simulate decomposition in other, less extreme environments. For example, the tall-grass prairies of central USA are warmer than the tundra and moister than the desert. A detailed litter decomposition experiment was recently conducted at the Konza Prairie LTER site, and data analyses are nearing completion. These data will be used to test and refine GENDEC for simulating litter decay in prairie ecosystems—validation studies are planned for autumn 1993. Decomposition simulations for forested ecosystems have not been attempted with GENDEC, although experimental studies to provide validation data are planned for the loblolly pine forests of North Carolina within the next year. Considerable information of this nature currently is available in the scientific literature for many forested sites throughout the USA.

Exoenzyme Activities

Microorganisms produce extracellular enzymes that catalyze the degradation of substrates in the immediate environment, but only recently has litter decay been expressed as a function of extracellular enzyme activities. In related studies, Sinsabaugh et al. (in review) demonstrated a strong empirical relationship between temporally-integrated measures of the activities of key lignocellulolytic enzymes and mass loss of various litter types. We proposed to develop a mechanistic description of recalcitrant organic matter dynamics based on the kinetics of such lignocellulolytic enzyme activities. We have started this work by utilizing a model of adsorption kinetics (Bader et al. 1992) for the key enzymes responsible for cellulose degradation (Fig. 3). Behavior of this model is consistent with culture data upon which underlying equations were

FIG. 3. Model of cellulose degradation via adsorption of endocellulase, exocellulase and cellobiase extracellular enzymes

developed. This model will be expanded to include a similar, general description of lignin degradation and the resulting lignocellulose simulator will be integrated with the empirical portrayal of lignocellulose degradation developed by Sinsabaugh et al. (in review) to provide a mechanistic model of litter decay.

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SECTION IV.

DECOMPOSITION OF TALLGRASS PRAIRIE LEAF LITTER GROWN UNDER ELEVATED CO₂ AND SUPPLEMENTAL N

(An experiment in collaboration with C. E. Owensby
at the CO₂ Enrichment Site, Manhattan, KS)

Introduction

This experiment was initiated in the autumn of 1990 in order to explore the potential for, and implications of, effects of increasing atmospheric CO₂ on several crucial aspects of the decomposition and nutrient cycling processes in the tallgrass prairie. We hypothesized that elevated CO₂ may cause changes in patterns of nutrient cycling and carbon storage through its indirect effect on litter quality or degradability. The process of decomposition depends upon the chemical makeup of the litter (Swift *et al.* 1979; Berg and Staaf 1980), and changes in atmospheric CO₂ could greatly influence the chemical composition of the plant tissues (Woodward *et al.* 1991), and quite possibly the resulting litter. Furthermore, accumulations of standing dead and litter within the tallgrass prairie can have a considerable influence on the amounts, productivity, and mixture of resident species (Knapp and Seastedt 1986). Thus, changes in rate of litter decomposition and release of limiting nutrients could be expected to play a critical role in controlling tallgrass prairie structure and function.

This study examines rates of decay and carbon chemistry during decomposition of litter from 3 principal grasses that had been grown under elevated CO₂ in a pristine tallgrass prairie ecosystem near Manhattan, Kansas (Owensby *et al.* 1990). The CO₂ enrichment study consists of the treatment of relatively large sample plots (ca. 16 m²) with open-top chambers that are fumigated with either ambient CO₂ (360 ppm) or twice ambient CO₂ (720 ppm). Within each CO₂ treatment, 2 plots were fertilized (45 kg N ha⁻¹) and 3 plots were not. There were also control plots with no chambers and with or without fertilization.

The objectives of the study were to: 1) *determine rates of mass loss of surface litter from grasses that were grown under the different CO₂ and N treatments (degradability), and 2) determine principal carbon components and levels of N and P of the decaying litter material (litter quality).*

Methods

The CO₂ enrichment study consisted of 15 experimental plots and 6 treatments. The treatments were: 1) Chamber, ambient CO₂, no N fertilization (3 reps); 2) Chamber, ambient CO₂, N fertilization (2 reps); 3) Chamber, elevated CO₂, no N fertilization (3 reps); 4) Chamber, elevated CO₂, N fertilization (2 reps); 5) No chamber, no N fertilization (3 reps); and 6) No chamber, N fertilization (2 reps). Chambers, and thus CO₂ fumigation, were maintained from April 1 to October 31. At the end of the growing season (November 1, 1990), the standing dead and green leaf litter from 3 grasses (big bluestem [*Andropogon gerardii*], Indiangrass [*Sorghastrum nutans*] and Kentucky bluegrass [*Poa pratensis*]) was harvested from every plot. All litter from each species and each treatment was combined to

produce a single homogen-eous sample. The litter was air dried for 5 to 7 days and then placed in a 10 x 10 cm, mesh (1 mm² opening), polypropylene bags. A total of 630 bags (210 per species) were made, each containing *ca.* 3.5 grams of grass litter. Ninety bags were randomly chosen for immediate chemical analysis (5 bags for each of 6 treatments and 3 species), and the rest (540) were placed into the field for subsequent retrieval. The field site was an area of undisturbed prairie adjacent to the CO₂ enrichment plots. Bags were positioned onto, and in contact with the mineral soil surface, by carefully removing the natural litter in an area the size of the bag. Bags were placed about 30 cm apart and the area between the bags was not disturbed (benches were used to place and retrieve bags). Ninety bags were retrieved from the field on each of the following sampling dates: March 1, May 1, August 1, and November 1, 1991, and May 1, 1992.

Litter samples were analyzed for the principal carbon constituents: solubles, cellulose, and acid resistant aromatics (lignin and tannins), and their concentrations of N and P. The method of extraction of the fractions is outlined in Figure 1.

Figure 1. Flowchart of chemical analyses used to obtain sample chemical fractions.

Results

Mass loss was similar for litter of both C_4 grasses, amounting to *ca.* 12% over the 18 month period (Fig. 2). Most of the loss of material occurred during the growing season. There were no significant differences among the C_4 litter from different growth treatments. Mass loss of *Poa pratensis* (C_3) litter was greater than that of the C_4 grass litter, and was significantly affected by N fertilization (Fig. 2). Mass loss was 19% for the non-fertilized plants and 16% for the fertilized.

Total Nitrogen concentration was similar for litter of both C_4 grasses, and increased from *ca.* 0.3% to 1.0% over a 12 month period (Fig. 3). Total N concentration of *Poa* litter was significantly greater than that of the C_4 grasses, and increased from *ca.* 1.1% to 2.0% over a 12 month period (Fig. 3). Total N of litter was unaffected by growth treatment of grasses.

Total Phosphorus concentration was similar for litter of both C_4 grasses (*ca.* 0.8 mg/gm) and changed little over the period from Nov., 1990 to Nov., 1991 (Fig. 4). Total P concentration of *Poa* litter was greater than for the C_4 grasses, averaging *ca.* 1.4 mg/gm over the 12 month period (Fig. 4).

Figure 2. Mass loss of litter through time. Symbols for this and subsequent figures are: filled symbols, no N; open symbols, N fertilization; triangles, no chamber; circles, chamber at ambient CO_2 ; squares, chamber at elevated CO_2 .

Figure 3. Total nitrogen concentration of litter through time.

Figure 4. Total phosphorus concentration of litter through time.

Carbon chemistry of the litter was generally similar among the species and was unaffected by the growth treatment of the grasses (Figs. 5, 6, & 7). There was one significant difference among the species: *Poa* litter had a higher fraction of solubles than the C₄ grasses initially, and a concomitant lower fraction of cellulose. This difference diminished after 6 months of decay in the field.

Figure 5. Fraction of solubles in litter through time.

Figure 6. Fraction of cellulose in litter through time.

Figure 7. Fraction of lignin in litter through time.

Discussion

Throughout the duration of this study, there was no difference among the litter from various growth treatments in mass loss, total N & P, or carbon fractions. The lack of CO₂-induced change in initial litter chemistry was probably a key factor governing the lack of differences in decay rates and subsequent litter chemistry. Curtis *et al.* (1989) also found no significant difference in litter chemistry in a salt marsh, even though elevated CO₂ had induced changes in chemistry of the green leaves.

The amount of mass loss in this experiment was lower than reported for a desert ecosystem (MacKay *et al.* 1987), but similar to that found in forest (Staaf and Berg 1982) and chaparral (Schlesinger and Hasey 1981) foliage litter. Mass loss in our study (12% to 19%) was somewhat less than the 25% reported by Seastedt (1988) for mixed foliage at a similar tallgrass prairie site. Our results also differ somewhat from Seastedt (1988) in that he reported increases in both N and P of foliage litter over a 2-year period. He concluded that foliage litter was a net sink for both elements. However, we found that only N increased with length of decay, while P remained relatively constant. Thus, there was no net mineralization of either N or P during the first year of decomposition, but neither did the foliage act as a sink for P.

Our results support the conclusion of Knapp and Seastedt (1986) that decomposition is slow in the tallgrass prairie and could be expected to control nutrient availability. The differences in rate of decomposition between C₃ and C₄ litter has important implications with regard to decomposition and nutrient availability. If elevated CO₂ and/or climate change induce changes in the species composition of the community, there could be a subsequent change in the overall time for decomposition and release of nutrients.

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SECTION V.

EFFECTS OF ELEVATED CO₂ ON SEEDLINGS OF TWO CHIHUAHUA DESERT SHRUBS AT DIFFERENT SOIL TEMPERATURES

Introduction

During the last 150 years, the woody shrubs of *Larrea tridentata* and *Prosopis glandulosa* have increasingly replaced the original grassland species of desert ecosystems in the southwest United States (Buffington and Herbel 1965, Gibbens and Beck 1987). These shrubs are likely to have a significant impact on the degree of desertification in many arid and semiarid ecosystems of North America given projected changes in the global climate (Schelesinger et al 1990). Although atmospheric CO₂ concentration (one of the major components of the global climate change) is expected to double by the mid or late 21st century (Conway et al 1988), the potential responses of these shrubs to elevated levels of CO₂ have not previously been studied. This study was therefore designed to investigate:

1. Growth and physiological responses of seedlings of *Larrea tridentata* and *Prosopis glandulosa* to a doubling of atmospheric CO₂ concentration.

Various investigators have reported that elevated CO₂ increases the proportion of biomass allocated to roots versus shoots (Curtis et al 1990, Fajer et al. 1991, Tolley and Strain 1984) and that the potential gain in total plant biomass due to increases in atmospheric CO₂ can be offset if root sink size is limited (Thomas and Strain 1991). Therefore, this experiment was also designed to investigate:

2. The potential interacting effects of CO₂ and soil (root) temperature on growth and productivity of these species.

Materials and Methods

Seedlings of *Larrea* and *Prosopis* were established from seeds collected from a field site at Jornada Experimental Range near Las Cruces, NM. Seedlings were grown in 4l pots containing a 1/1 mixture of gravel and vermiculite under greenhouse conditions receiving daily supplies of water and 1/2 strength Hoagland solution. At 2 and 4 months old (*Prosopis* and *Larrea* respectively), pots containing uniform sized seedlings of each species were placed in temperature controlled root zone cabinets [model R-I (M49) Environmental Growth Chambers, Chargin Falls, OH] and were placed in two growth chambers and were grown for the next 7 weeks under following treatment conditions: (1) constant root zone temperature of either 20 or 30°C; and (2) partial pressure of CO₂ in the chamber of either 350 or 700 ppm. Air temperature was maintained at a constant 25° C. The photoperiod was 16h at a light intensity of 700 $\mu\text{mole m}^{-2} \text{s}^{-1}$. Water and nutrients were supplied at an optimal rate.

Throughout the course of the experiment, plant gas exchange parameters were periodically determined with a LICOR 6200 photosynthesis system. Time course determination of xylem water potentials were also made during the course of this study

using a pressure chamber. At the end of the experiment, harvested plants were separated into root, shoot and stem, and the dry mass of each component was determined.

Results

Increased atmospheric CO₂ stimulated relative growth rate (g g⁻¹ d⁻¹) in both species regardless of the soil temperature (Figs. 1A and B). However, the stimulatory effects of CO₂ on growth was significantly higher at 30 than 20°C root temperature. The data also indicate that elevated CO₂ can fully (for *Larrea*) or partially (for *Prosopis*) compensate the inhibitory effects of low soil temperature on seedlings grown at ambient CO₂ (Fig. 1).

In both species, increases in biomass production resulting from elevated CO₂ at 20°C soil temperature were due to both enhanced photosynthetic rate (Fig. 2A) and increased photosynthetic area (Fig. 3A). In contrast, the enhanced growth responses to high CO₂ at 30°C root temperature were solely caused by increased assimilation rate since leaf area was unaffected by CO₂ treatment in either species. There were no significant differences in seedling xylem water potential among the treatments (Figs. 4A and B), indicating that CO₂-induced enhancement of growth was not due to changes in plant water status. However, the spontaneous values of water use efficiency (WUE; expressed as the ratio of assimilation rate over transpiration rate), indicates that WUEs were consistently higher for seedlings grown at high CO₂ levels (Figs. 5A and B).

Discussion

It has been suggested that in addition to changes in precipitation patterns, overgrazing, and other human activities, changes in atmospheric CO₂ concentrations during the last 150 years may have also contributed to the observed shift in the vegetation cover in the deserts of the Southwestern US (Polley et al. 1993). As stated earlier this shift has typically involved replacement of C₄ grasses by C₃ shrubs such as those studied here. Our study indicates that these shrubs have the potential to respond favorably to a doubling of the present atmospheric CO₂ concentration. Such information, combined with the reported lack of response of most C₄ species to elevated CO₂ (Bazzaz 1990, Patterson and Flint 1990), suggests that future CO₂-induced changes in the vegetation of the Southwestern US deserts may favor a continuous shift toward the dominance of shrubs such as those studied here.

Figure 1. Effects of CO₂ and soil temperature on plant relative growth rate calculated over the 42 d period of treatment exposure. Bars with different letters are significantly different at the $P = 0.05$ level by Scheffé tests.

Figure 3. Effects of CO₂ and soil temperature on total leaf area. Bars with different letters are significantly different at the $P = 0.05$ level by Scheffé tests.

Figure 2. Time course response of seedling assimilation rate (A) to CO₂ and soil temperature.

Figure 4. Time course response of seedling xylem water potential to CO₂ and temperature.

Figure 5. Time course response of seedling water use efficiency to CO₂ and temperature.

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