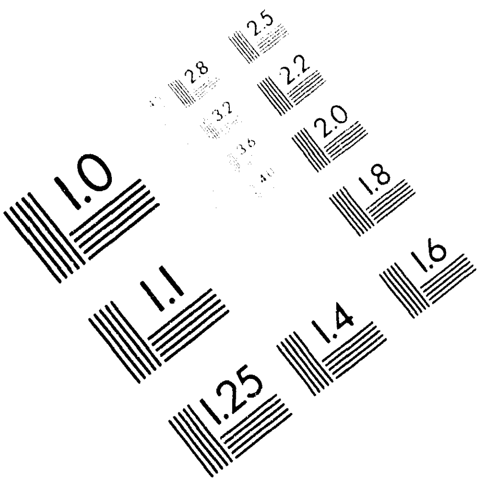

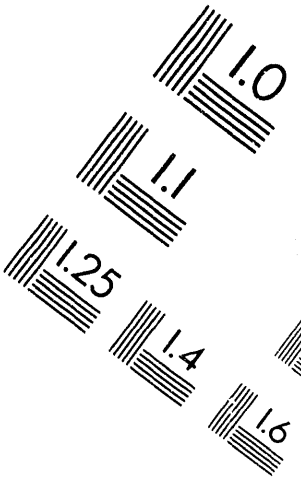

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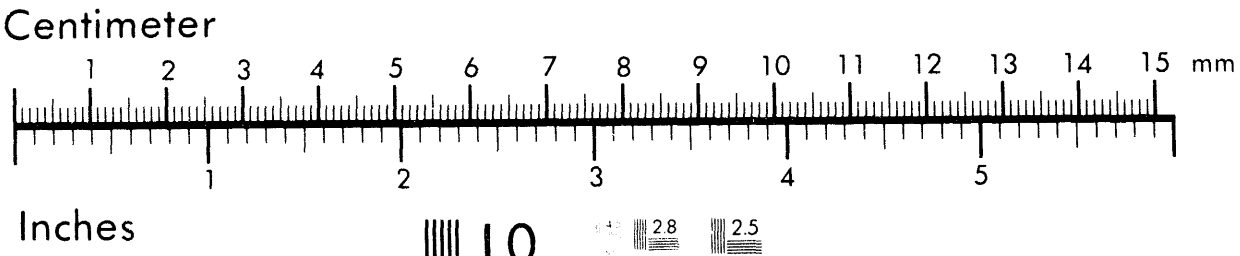

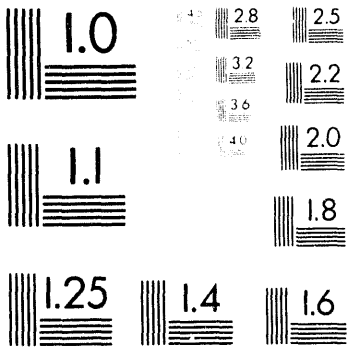

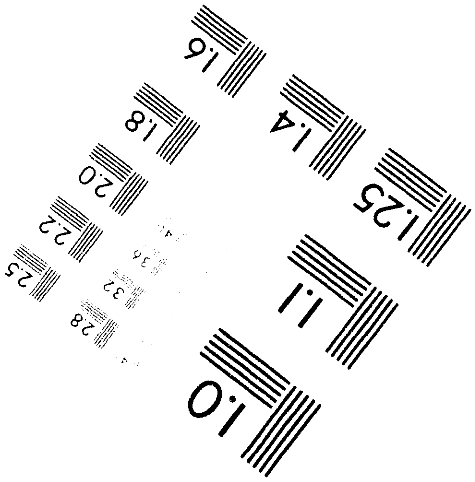

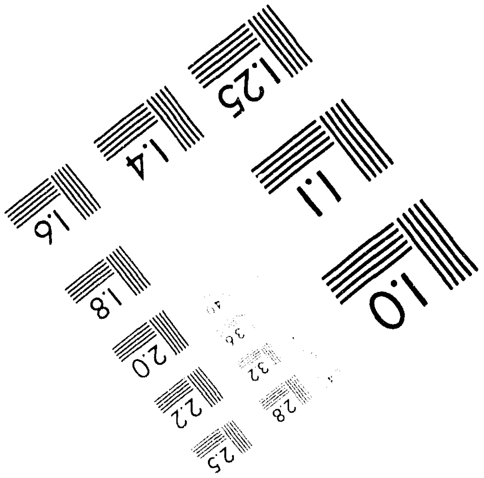

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DOE/ER/60490--T2

FINAL TECHNICAL REPORT

United States Department of Energy,
Carbon Dioxide Research Division,

AWARD NUMBER: **DE-FG 0386ER60490**

TITLE: **Response of Plants and Ecosytems to CO_2 and Climate Change**

Principal Investigator: **James F. Reynolds**

1.0 INTRODUCTION

In recognition of the important role of vegetation in the bio-geosphere carbon cycle, the Carbon Dioxide Research Program of the U. S. Department of Energy established the research program: *Direct Effects of Increasing Carbon Dioxide on Vegetation.* Our ultimate goal is to develop a general ecosystem model to investigate, via hypothesis testing, the potential responses of different terrestrial ecosystems to changes in the global environment over the next century. Our approach involves the parallel development of models at several hierarchical levels, from the leaf to the ecosystem. At the plant level, we have stressed mechanism and the direct effects of CO_2 in the development of a general plant growth model, **GEPSI** - GEneral Plant SImulator. At the ecosystem level, we have stressed the translation of CO_2 effects and other aspects of climate change throughout the ecosystem, including feedbacks and constraints to system response, in our development of a mechanistic, general ecosystem model **SERECO** - Simulation of Ecosystem Response to Elevated CO_2 *and* Climate Change.

The strength of our approach, and what distinguishes us from other modeling groups, is that we are *simultaneously* conducting research (and publishing) at multiple hierarchical levels, thus permitting a joint "bottom-up" and "top-down" approach. The primary models and modular components of our research are illustrated in Figure 1. Each module or submodel is independently used to address specific questions appropriate at its particular hierarchical level. Since all the levels are being developed simultaneously, advances at one level are not necessarily implemented immediately or directly into higher level models. For example, we have shown that phosphate limitations to photosynthesis can be important in some circumstances and we have developed ways to include this in our leaf level photosynthesis model. Yet, the higher level models

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do not yet include this result. Indeed we may consciously decide to exclude this detail in our whole-plant model while deciding that it is of significance in the canopy model. Questions like this are part of the art of complex model building and depend on our understanding of the process of scaling up.

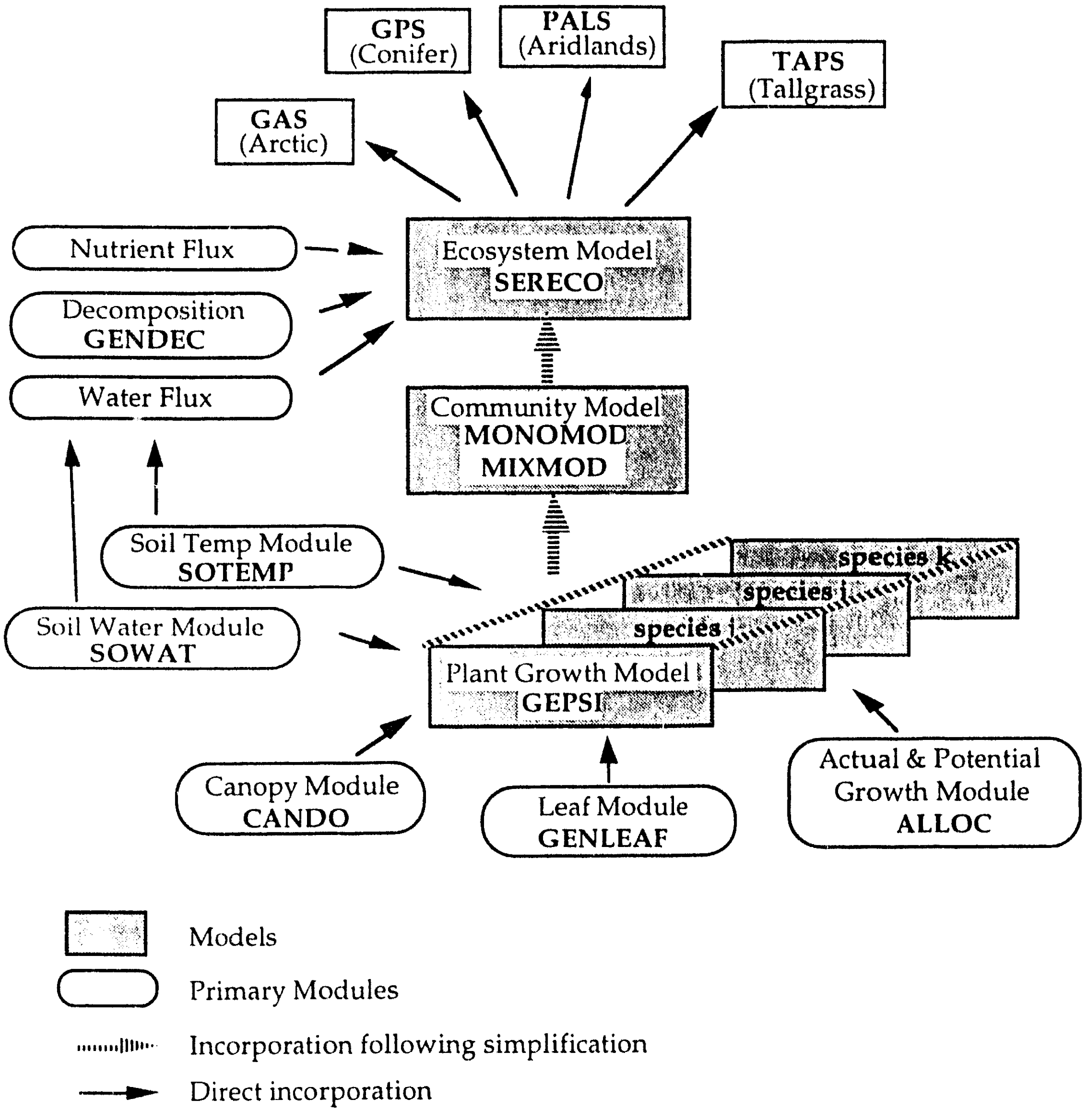

Figure 1.: Modules and models of our program arranged hierarchically.

Our philosophy is that each level in the hierarchy has its own characteristic set of processes and special modeling challenges that can be worked on in relative isolation from work at other levels. This reflects the principle from hierarchy theory that levels in nature are relatively discrete: whole-plant growth, for example, is more or less insensitive to the precise biochemical behaviors occuring in the leaves but, rather, responds to the daily production of assimilate.

Assimilation may be limited by external variables such as light or temperature, or by internal sink limitations, or many other constraints with the resulting growth pattern being the same in all cases.

As a consequence of this decomposability of complex systems we can move ahead on all fronts simultaneously, e.g., temporarily using a simplified photosynthesis model rather than the full model. For example, one of the major challenges in modeling whole-plant growth is the development of a flexible and realistic allocation model; in our allocation modeling work, we can temporarily ignore the interesting and important details of photosynthesis that are the subject of our leaf model. Eventual inclusion of the better photosynthesis model will strengthen our plant model, but modeling the processes that are unique to the whole-plant level can proceed without waiting for a final version of the leaf or canopy model. The same can be said for the development of models at all levels.

Developing a hierarchy of models in this way, each suited to a particular scale while drawing on insights and output from lower levels, is an effective way of accounting for the effects of elevated CO_2 and climate change as they progress from the physiological level of organization to the ecosystem level. Furthermore, this allows us to answer numerous basic, fundamental questions directly at each level of interest. While much of the work involved in actually integrating these models remains as the challenge for the future, it is important to see this work as a whole and consider the scaling related issues that involve the interaction of more than one level. These hierarchical levels do interact in nature and the ecosystem level impacts of elevated CO_2 and climate change primarily result from the complex interactions that begin at the leaf level and culminate in altered ecosystem structure and function.

1.1.1 Plant Modeling

The general research objectives of our plant modeling efforts have been: 1) To construct generic models of leaf, canopy, and whole-plant response to elevated CO_2 and climate change; 2) To validate predictions of whole-plant response against various field studies of elevated CO_2 and climate change; 3) To use these models to test specific hypotheses and to make predictions about primary, secondary and tertiary effects of elevated CO_2 and climate change on individual plants for conditions and time frames beyond those used to calibrate the model. and 4) To provide information to higher-level models, such as community models and ecosystem models.

These objectives lead to immediate design decisions for **GEPSI**. Objective #1 requires that the modules in **GEPSI** explicitly contain plant physiological mechanisms. CO_2 and other environmental variables (temperature, moisture, nutrients, etc.) affect plants through the interactions of physiological mechanisms. While overall plant response to elevated CO_2 (the sum of primary-tertiary effects) is poorly understood, the primary effects have been well characterized. By coupling detailed modules for the expression of primary CO_2 effects with modules for other processes, the effects on these other processes can be modeled. Similarly, Objective #2 implies that the plant modules should use physiological detail to make statements about different sets of conditions. As mentioned above, extrapolation of model results is possible only with models that include information on mechanisms. Objective #3 is based on the goal of building the general ecosystem model **SERECO** with a plant simulator as a central component. This objective requires that we consider how the results of the plant models will be summarized and aggregated to ecological levels higher than the single plant. A mechanistic plant model cannot simply be iterated for each plant in an ecosystem simulation.

1.1.2 Ecosystem Modeling

There are 4 general (necessarily overlapping) objectives of our ecosystem level modeling efforts: 1) To incorporate models of plant responses to elevated CO_2 into a generic ecosystem model in order to predict the direct and indirect effects of elevated CO_2 and climate change on ecosystems; 2) To validate model predictions of total system-level response against various ecosystem field studies of elevated CO_2 and climate change; 3) To use the ecosystem model to test specific hypotheses and to make predictions about primary, secondary and tertiary effects of elevated CO_2 and climate change on ecosystems for conditions and time frames beyond those used to calibrate the model; and 4) To use the ecosystem model to study effects of change in CO_2 and climate at regional and global scales; ultimately, this will involve linking to models of landscape dynamics and global carbon balance models.

1.1.3 Modules and the Importance of Generality

As stated above, both our plant and ecosystem level modeling is based on the development of general modules that represent various subsystems of interest. Just as it is impossible to perform all possible combinations of experiments, it is not feasible to develop new *ad hoc* models for each plant species or ecosystem of interest. However, by general, we are not suggesting that it is possible to build a single, all-purpose model that can address the entire suite of objectives in the DOE direct effects program. Rather, the goal is to build models that are based on general modules derived from classes of general flow descriptions that are fundamentally similar across different plants and ecosystems. These models, by emphasizing generality as opposed to concentrating on the unique and different, may also contribute to the evolution of a comprehensive ecosystem theory.

The use of general modules offers an alternative to conventional model-building, in which subdivisions of the model represent many forms of simplification. A general, modular structure groups related processes in submodel components and the function of each module and the variables to be calculated for output is explicitly defined. In the case of **GEPSI** (which is itself a module of the ecosystem model), general processes common to all plants, e.g., photosynthesis, respiration, nutrient and carbon allocation, etc., are modules. Modules are parameterized for specific species, related groups of species, life form classes, or broader groups depending on how variable the process is across certain groupings and the level of variability that is acceptable for the question being investigated. Higher levels of organization, i.e., population, community, and ecosystem, are simulated through coupling of organism - process modules, as well as development of new modules which represent higher level interactions, such as competition, herbivory, and decomposition. Economy of effort is obtained when a general model provides an alternative to developing *ad hoc* models for each plant and site of interest; economy of understanding is the result of building onto general flow descriptions that are fundamentally similar across different types of organisms and systems. The general approach forces the modeler to determine general properties of the class of systems and to see specific systems as variations on a theme rather than as separate entities.

2.0 TECHNICAL SUMMARY OF RESULTS

Here we provide brief summaries and overviews of our major findings to date with regard to the development of **GEPSI** and **SERECO**.

2.1 Conceptual Framework for Scaling Ecophysiological to the Ecosystem

We argue that complex global change issues, such as elevated atmospheric CO_2 and its effects on plants and ecosystems, are especially difficult to address since they involve many scales. While the direct effects of a particular change may be focused primarily at a single scale, the potential ramifications of the change are likely to be seen at many higher, and possibly, lower scales. Understanding these interactions and making predictions at larger scales will require modeling. However, in our view, models can not be expected to span all scales, so an effort must be made to develop mechanistic models that are effective at particular scales and that can also be used to provide information to models at larger scales. We must go beyond the naive view that mechanisms exists solely at a single level, e.g. biochemical or molecular. The processes and elements that constitute the model's mechanism must be dictated by the level (scale) of focus of the model. Mechanistic interactions of the systems components can best be represented at one, or at most, two levels lower than the focal level. In Reynolds et al. (1992) we present the conceptual framework for accomplishing this and give an example of how ecophysiological information on CO_2 *x* nitrogen interactions, which operate on a daily time frame, can provide meaningful information to a stand succession model, which operates on an annual time frame.

2.2 Leaf Level

At the level of the leaf, the short-term and long term responses to elevated CO_2 must be distinguished. In the short-term, stomata respond to changes in ambient CO_2 but the biochemical properties of the leaf are fixed. When plants are maintained in an elevated CO_2 atmosphere for a period of days to weeks, changes in leaf biochemistry occur, typically resulting in reduced photosynthetic capacity. Depending on the extent to which both stomatal conductance and photosynthetic capacity are reduced, the long-term response of net photosynthesis to a doubling of CO_2 may be substantial or relatively small. In some cases, net photosynthesis of plants grown and measured at 680 µbar is actually less than that of 340-grown plants.

The photosynthesis model (named **GENLEAF**, Fig. 1) has been validated under current CO_2 levels (Harley *et al.* 1986; Harley and Tenhunen 1989) and responds realistically to short-term increases in CO_2, although the stomatal function necessarily remains empirical. We believe that the model, properly parameterized, is equally capable of simulating photosynthetic behavior of leaves following long-term exposure to elevated CO_2.

We stress the importance of utilizing a mechanistic demand function which enables one to distinguish between three potential limitations to carboxylation and assimilation, i.e., the amount and activity of Rubisco itself, the rate of RuBP regeneration in the Calvin cycle, or the rate of triose phosphate utilization and simultaneous release of inorganic phosphate. If we are to take advantage of the potential of this model, the physiological basis of the photosynthetic changes associated with long-term exposure to elevated CO_2 must be determined, and the findings incorporated into the model structure.

The observed change in the shape of the demand function represent a reallocation of limiting resources, primarily nitrogen [N], within the individual leaf or within the plant as a whole. This affect cannot be evaluated at the leaf level of organization alone. If N is re-allocated to new shoot meristems, the question must be placed in the context of the plant canopy; if additional N is allocated to other sinks, such as roots or reproduction, a whole plant perspective is required. The analysis of optimal leaf N and the phenomenological allocation model provide criteria to predict *a priori* the total shoot N content while the analysis of optimal distribution of N within the canopy (Section 4) can predict the spatial distribution of this shoot N. Feedback inhibition and N reallocation are not mutually exclusive of course; if the leaf is incapable of utilizing all the carbohydrate produced, one might expect N to be withdrawn from photosynthetic processes and allocated to either carbohydrate utilization or other leaf (or plant) processes.

2.3 Canopy Level

The canopy module (Reynolds et al. 1993) (named **CANDO**, Fig. 1) is being used to investigate components of within-canopy interactions important for predicting whole-plant photosynthetic response to elevated CO_2. Preliminary results suggest that a more complex formulation of the light-interception calculations included in the Caldwell *et al.* (1986) version of the model is necessary for predicting photosynthetic and transpirational response to elevated CO_2. This more complex formulation entails considering several separate classes of sunlit leaves (distinguished on the basis of azimuth with respect to the sun) instead of using average conditions for sunlit leaves in a layer. Thus, more precise calculation of gas exchange in leaves that are nearly light-saturated is possible; such leaves exhibit highly nonlinear responses to light and CO_2. Further complexity in the light interception module (such as that provided by considering several classes of leaf inclinations) is deemed less valuable for refining estimates of gas exchange, particularly at elevated CO_2. More value is attributed to the inclusion of leaf and canopy energy balances, since gas exchange response to elevated CO_2 is highly dependent on temperature.

Additional work with the canopy model is focusing on the interactive effects of canopy acclimation to growth at high CO_2 (e.g. increased leaf area), leaf acclimation (reduced photosynthetic capacity due to changes in leaf N), and whole-plant photosynthesis. Conclusions to date include: 1) canopy gas exchange is sensitive to the acclimation to elevated CO_2, 2) leaf acclimation reduces the enhancement of canopy photosynthesis from that expected from elevated CO_2 alone, and 3) canopy acclimation can partially offset this adjustment. Simulations with acclimation of leaf function (decreased carboxylation capacity) and of canopy structure (increased LAI and leaf size) produce canopy photosynthesis estimates intermediate to the estimates resulting from ambient CO_2 and elevated CO_2 without acclimation. This model is quite effective in describing the aggregate behavior of a population of leaves with known properties.

2.4 Whole-plant Level

Two important conclusions can be drawn from our work at the whole-plant level: 1) reduced leaf N concentrations may result in higher growth rates for plants growing at high CO_2 concentrations; and 2) phenomenological allocation models (collectively referred to as **ALLOC**, Fig. 1) are effective in predicting changes in root:shoot ratio, leaf photosynthetic capacity, and plant growth at high CO_2 despite the lack of a complete mechanistic understanding of allocation.

As generally observed in experiments, optimal leaf nitrogen is predicted to decrease at elevated carbon dioxide levels. This response appears to be adaptive since the relative growth rate that the plant maintains under these circumstances is greater than that which would occur if high leaf nitrogen concentrations and high photosynthetic capacity had been maintained. Photosynthetic capacity is reduced at high carbon dioxide levels but this is preferable to paying the higher cost of increased root:shoot ratios necessary for higher leaf nitrogen concentrations. Optimal root:shoot ratios are also predicted to increase when plants are grown at elevated carbon dioxide concentrations. While it is difficult to generalize from the available data, our model predictions are consistent with empirical results.

The prototype version of **ALLOC** used in **GEPSI** is effective at predicting root:shoot ratios but is not designed to predict altered photosynthetic rates due to changes in leaf N concentration. This is due to a limitation of the allocation module used in **GEPSI** where the efficiencies of resource assimilation were not mechanistically predicted. This is a general limitation of all root:shoot partitioning models (Reynolds and Thornley 1982). They require that specific root and shoot activities be specified as parameters. We have developed a new allocation module (**ALLOC**) that distinguishes degradable components in the leaves (primarily proteins) from non-degradable components such as cell walls. This model simulates changes in root:shoot allocation as well as allocation of N to photosynthetic enzymes in the leaf. With this model it is possible to predict the changes in photosynthetic capacity, root:shoot ratio, and growth rate of plants growing at various levels of CO_2, light, and N availability. The effects of water availability needs to be included as well. This allocation module is particularly important because it provides feedbacks between the whole-plant, canopy, and leaf level processes. Along with root and shoot biomass, the photosynthetic characteristics are predicted for plants exposed to a wide range of environments.

2.5 Plant Population and Community Level

Initially, our plant community model was adapted from the SPUR ecosystem model. SPUR incorporates generalized growth responses of plant functional groups to a suite of environmental variables (light, temperature, soil water, and nitrogen). However, SPUR is very simplistic in its treatment of plant interaction (plants affect one another by their preemptive use of soil water and nitrogen, but all plants use resources in exactly the same way) and CO_2 is neither directly nor indirectly involved in any of the phenomenological growth functions.

We have now developed a new, mechanistic community model. We decompose the system (community) into its component parts, i.e., individual plants, populations of single species (**MONOMOD**, Fig. 1) and populations of mixed species (**MIXMOD**, Fig. 1) and describe the behavior of the system through the interaction of these parts. Implicit in this approach is the assumption that effects of elevated CO_2 and concomitant climate change exert their direct effect at the level of the organism and below, rather than directly at the level of the community or ecosystem. Changes in community structure and function result indirectly from the interaction of individual organisms.

In developing this model we have devised a theoretical framework of the problem of plant community structure and function with respect to variable CO_2 and climate change. The plant community ecology literature is replete with studies of intraspecific competition, plant distribution, nearest-neighbor effects, resource abundance, niche dimensions, etc., but there is little unifying theory on the functioning of plant communities, particularly in the context of environmental and global change. Our theoretical investigation of this problem attempts to bridge the gap between population and physiologically-based explanations of plant competition and interaction and, as such, contributes to the goal of linking population biology and physiological ecology of plants. Most importantly at this stage, we have developed a method for predicting mortality and alterations in plant morphology as a function of density that can be used along with more complex plant models such as **GEPSI**.

2.6 Ecosystem Level

Our ecosystem-level research to date has involved 1) development of the framework for scaling up information through the ecosystem hierarchy, 2) development of preliminary ecosystem-level models, and 3) preliminary model simulations of long-term (decades or more) ecosystem response to ambient and/or perturbed climate or other abiotic factor. Our modeling at the ecosystem level presently emphasizes primary production (using **GEPSI**), nutrient cycling, and water balance in the ecosystem.

The goal of the ecosystem level modeling research is the development of models that can successfully predict long-term responses of ecosystems, and, particularly, responses to perturbations that might be associated with elevated carbon dioxide and global climate change. A fundamental model validation technique that we are using to assess our achievement of this goal is that of comparing simulation results with documented responses of ecosystems to natural or human-induced perturbations. We have preliminary results of the response of four different systems--tall grass prairie, aridlands (desert shrubland), lobolly pine forest, and arctic tundra--to changes in the abiotic environment. In each case, we have adapted various elements of the **GEPSI/SERECO** models to the specific ecosystems. For convenient reference, we refer to these ecosystem models as: **GAS** (arctic), **TAPS** (tallgrass prairie), **PALS** (aridlands), and **GPS** (loblolly forest). These models are being developed and - as illustrated in Fig. 1 - utilize the various modules of **SERECO** differently and in varying degrees of complexity.

GAS (General Arctic Simulator)

The effect of climate change on peak biomass (overwintering biomass plus seasonal production) in *Eriophorum* (a tussock-forming sedge) was explored using a simplfied version of **GEPSI** with a temporal resolution of one year. The model was validated against data from short-term experimental manipulations of nutrients, temperature, and shading. The model was then used to predict responses of the sedge to a 50 year period of increased temperature, longer growing season, and elevated CO_2. Results indicate that all three factors would have very little effect on peak biomass because production in these Arctic systems is limited to a large extent by nutrients (mostly nitrogen). A simulated doubling of nitrogen availability resulted in a 70% increase in peak biomass at the end of 50 years. Thus, climate change will affect *Eriophorum* production only indirectly through changes in nitrogen availability. These results reveal that a simple simulation model, which accounts for the important limiting processes that govern a system, may be able to provide adequate predictions of the systems response.

GPS (General Pine Simulator)

This work has produced the first truely modular version of **GEPSI** combined with some modules of **SERECO (SOWAT, SOTEMP)**. The C++ object-oriented programming language is an ideal and powerful tool for modeling . Preliminary comparison of model output for dry weight of stems, leaves and roots and height of loblolly pine seedling against experimental data at CO2 concentrations of 350, 500, and 650 ppm were good.

TAPS (TAllgrass Prairie Simulator)

Two long-term vegetation records from central Kansas document changes in tall-grass and mixed-grass prairie in response to an extended drought period of the 1930's. Predictions using the simulation model **TAPS** were generally consistent with historical records and reveal that the model is capable of making long-term predictions of grassland response to relatively strong climatic shifts. However, some of the changes were not reproduced by the simulation model, indicating that further development is needed before we can successfully predict ecosystem response to future climate change. We conclude that successfully "predicting" historical vegetation changes that have been induced by climate is a requisite to successfully predicting future responses to climate change.

PALS (Patch AridLands Simulator)

This work examined the response of arid/semi-arid ecosystems (dominated by xerophytic sclerophyllus shrubs) to variability in rainfall. Model simulations were conducted with **PALS** for the Jornada Basin of Southern New Mexico. **PALS** showed that total annual primary production was quite variable from year to year under ambient climate--more than twice as variable as rainfall. However, this variability was associated primarily with production of herbaceous annual species. Production of shrubs was relatively constant from year to year. Simulated changes in rainfall variability revealed that there was a magnification in variation of vegetation production compared to variation in rainfall. This was, again, observed to be the result of variation in production of herbaceous species. Changing the frequency of rainfall types was observed to have a direct effect on herbaceous annual species by impacting a specific group of annuals specialized for utilizing a particular pattern of rainfall, such as summer annuals that use monsoonal rainfall. Shrub production was not observed to change over the length of the simulation. **PALS** simulations are not only consistent with the finding of high variability of production in desert ecosystems, but offer an explanation for this variability. In addtion, we adapted the **GEPSI** modules **GENLEAF** and **CANDO** of **PALS** for use in Mediterranean oaks systems in France and Portugal, which are characterized by xerophytic sclerophyllus plants. Presently, component submodels function on a variety of time scales: minutes (leaf level response), hourly (canopy and plant water balance), and daily time step (plant growth and soil processes). Eventually, by understanding how submodels operating at fine time scales are affected by longer-term changes in stress factors, nutrient availability, and development, these research efforts will permit formulation of simplified submodels. Focusing on monospecific systems such as the *Quercus coccifera* garrigue and the *Quercus ilex* forest will allow us to refine a generic sclerophyll shrub model and define controls and constraints on resource capture potentials.

Experimental data being collected at the ecosystem-level at several research sites in North America also form an important part of the ecosystem model development. These are the first experimental manipulations of atmospheric CO_2 at the level of the ecosystem. They will provide data necessary to parameterize and validate each of the modules within the ecosystem model and will give us a new perspective on the whole-system response to elevated CO_2.

Process	**Ecosystem Level: Our Modeling Approach and Capability**
Total above ground biomass; productivity	Models can predict responses of dominant plant species of grassland, desert, and Arctic tundra ecosystems to environment changes of moderate duration (ca. 1-10 years).
Ecosystem physiognomy; biome classification	Changes in ecosystem physiognomy is accounted for by changes in dominance among those growth forms included in the model (this is done in **TAPS**).
Species diversity	The extent to which diversity is modeled at the ecosystem level is limited to the simplistic case of recording losses of any of the species or growth forms that are included within a particular model formulation .
Succession	Successional aspects of ecosystems are implicitly accounted for in models if the successional species are included in the model formulation (this is done in **TAPS**).
Plant-animal interactions	Presently, only herbivory is included in ecosystem models; herbivores remove vegetation according to prescribed choices. The rate of removal based on quality.
Rates of decomposition & nutrient cycling	Decomposition (and thus nutrient cycling) is a direct function of microbial activity (not important it seems) and nutrient concentration of litter, and is responsive to changes in litter quantity and quality.
Evapo-transpiration	Both soil evaporation and plant transpiration are accounted for on a daily basis, and so changes in soil water, atmospheric demand, and plant transpiration can all be effectively simulated in response to CO2 and climate change.
Hydrology	Distribution of water in soils can be predicted from a combination of soil, plant, and atmospheric factors that are fully coupled in **SERECO**
Bio-geochemical carbon cycling & storage	Our capability in **SERECO** is limited to determining total organic carbon for a patch; however, the scale of the model is not well suited to answering this question *directly*, particularly over the long term. Could be used as input to carbon based models.

4.0 Publications: Publications supported wholly or in part by DOE Grant DE-FG03-86ER60490 from 1989-93.

Description	Product
MODULAR MODEL RATIONALE--A modular structuring of models is suggested as a way to identify key processes of the model and help focus the needs of data collection around those key processes. This will facilitate the development of plant & ecosystem models responsive to global change.	Reynolds, J.F., B. Acock, R.L. Dougherty, & J.D. Tenhunen. 1989. A modular structure for plant growth simulation models. In: J.S. Pereira and J.J. Landsberg (eds.), *Biomass Production by Fast-Growing Trees.* Kluwer Academic Publ., Boston, MA, pp 135-168. Acock, B. & J.F. Reynolds. 1990. The rationale for adopting a modular generic structure for crop simulators. **Acta Horticulturae** 248:391-396.
MODEL STRUCTURE--Programming structure and language has important consequences for integration of data into model and linking of models. Object oriented language has advantages over traditional languages for developing complex programs and linking programs of different disciplines.	Acock, B. & J.F. Reynolds. 1990. Model structure and database development. In: R.K. Dixon, R.S. Meldahl, G.A. Ruark, & W.G.Warren (eds.), *Forest Growth: Process Modeling of Responses to Environmental Stress.* Timber Press, Portland, OR, pp. 169-179. Chen, J.L.. & J.F. Reynolds. 1993. A general plant simulator (GEPSI) in object-oriented language. **Ecol. Modelling** (submitted) J.F. Reynolds, B. Acock, and R. Whitney. 1993. Linking CO2 experiments and modeling. In: Design and Execution of Experiments on CO2 Enrichment, D. Schulze and H. Mooney (eds.), Springer-Verlag. In Press.

Description	Product
SCALING--Discusses the problems and methods of scaling up from the source of effects of elevated CO_2--the plant--to the point of accumulation of effects--ecosystem.	Reynolds, J.F., D.W. Hilbert, & P.R. Kemp. 1993. Scaling ecophysiology from the plant to the ecosystem: a conceptual framework. In: J. Ehleringer & C. Field (eds.), *Scaling Ecophytiologic Processes: Leaf to the Globe.* Academic Press, NY, pp. 127-140. Hilbert, D.W. & J.F. Reynolds. 1992. The response of plants to global change: the modeling challenge. Bull. Ecol. Soc. Amer. ESA abstract for Hawaii meetings.
BOUNDARY ANALYSIS--BA is a powerful tool for identifying shifts and discontinuities in data, and will help establish climate-induced changes in ecosystems boundries.	Cornelius, J.M. and J.F. REYNOLDS. 1991. Determining the significance of discontinuities identified by boundary analysis. **Ecology** 72:2057-2070.
BOUNDRY ANALYSIS--This study reveals the importance of dramatic shifts in climate states in the prairie and their potential to obscure gradual climate change and its effect on grassland ecosystems.	Kemp, P.R., J.M. Cornelius, & J.F. Reynolds. 1993. . Discontinuities in precipitation patterns of the North American prairie during the period of meteorological record. **Inter Journal of Climatology** (submitted)
GENLEAF--Stomatal conductance module based on Ball et al. (1987) relationship. Responds to radiation, temperature, humidity, & CO_2.	Harley, P.C., R. Thomas, J.F. Reynolds, & B.R. Strain. 1992. Modeling the effects of elevated CO_2 and photosynthesis in cotton. **Plant Cell Environ.** 15: 271-282.
Application of **GENLEAF** model to sclerophyll shrubs.	Tenhunen, J.D., A. Sala-Serra, P.C. Harley, R.L. Doughterty, and J.F. Reynolds. 1990. Factors influencing carbon fixation and water use by mediterranean scherophyll shrubs during summer drought. **Oecologia** 82:381-393.

Description	Product
GENLEAF--Generic leaf photosynthesis module, based on biochemical mechanisms. Responds to radiation, temperature, humidity, & internal CO_2.	Harley, P.C. & J.D. Tenhunen. 1991. Modeling the photosynthetic response of C_3 leaves to environmental factors. In: K.J. Boote and R.S. Loomis (eds.), *Modeling Crop Photosynthesis - From Biochemistry to Canopy*. Spec. Pub. Am. Soc. Agron. Harley, P.C. & T.D. Sharkey. 1991. An improved model of C3 photosynthesis at high CO_2: reversed CO_2 sensitivity explained by lack of glycerate reentry into the chloroplast. **Photosynthesis Res.** 27:169-178. Harley, P.C., F. Loreto, DiMarco, G., & T.D. Sharkey. 1993. Theoretical considerations when estimating the mesophyll conductance to CO_2 diffusion from analysis of the response of photosynthesis to CO_2. **Plant Physiology** (In press)
An application of **PALS - GENDEC** and **CANDO** for the prediction of canopy gas exchange in *Quercus* species based on water status and time of season. Potential reaponse to elevated CO_2 is predicted.	Tenhunen, J.D., J.F.Reynolds, O.L. Lange, R.L. Doughterty, P.C. Harley, J. Kummerow, & S. Rambal. 1989. QUINTA: A physiologically-based growth simulator for drought adapted woody plant species. In: J.S. Pereira & J.J. Landsberg (eds.), *Biomass Production by Fast_Growing Trees*. Kluwer Acad. Publ., Boston, MA, pp. 123-134.
CANDO--Simplified version of canopy microclimate model. Predicts canopy response to elevated CO_2 based on single leaf response within canopy	Reynolds, J.F., J.L. Chen,, P.C. Harley, & D.W. Hilbert, and J.D. Tenhunen. 1993. Modeling the effects of elevated carbon dioxide on plants: Exptrapolating leaf response to a canopy. **Agric. For. Meteor.** 61: 69-94 Chen, J.L., J.M. Norman, & J.F. Reynolds. 1993. A comparison of models of bidirectional transfer of radiation in canopies. **Agric. For. Meteor.** (Submitted)

Description	Product
CANDO--Canopy microclimate model that includes the distribution of leaf N among the leaves within different canopy layers	Chen, J.L., J.F. Reynolds, J.D. Tenhunen, & P.C. Harley. 1993. Coordinated leaf photosynthesis model and its relation to optimum daily canopy assimilation. **Oecologia** 93: 63-69 Kemp, P.R., J.F. Reynolds, and C. Owensby. 1993. Effects of elevated atmospheric CO2 and soil nitrogen on canopy leaf area distribution in a tallgrass prairie. **Oecologia** submitted)
ALLOC--Whole-plant carbon and nitorgen allocation model.	Hilbert, D.W. 1990. Optimization of plant root:shoot ratios and internal nitrogen concentration. **Annals of Botany** 66:91-99. Hilbert, D.W., A. Larigauderie, & J.F. Reynolds. 1991. The influence of carbon dioxide and daily light reception on optimal leaf nitrogen concentrations. **Annals of Botany** 68:365-376. Hilbert, D.W. & J.F. Reynolds. 1991. Balanced activity through variable allocation to photosynthetic enzymes and root and shoot biomass. **Annals of Botany** 68:417-425.
GEPSI--Module for the simulation of growth of annual plants as a function of phenological response to environmental cues	Kemp, P.R. & J.F.Reynolds. 1993. A model for predicting growth and seed production of annual species based on environmental cues. **J. Ecol.** (In manuscript; to be submitted by July 1993)
SOTEMP--Module to simulate vertical soil temperature profile based on above surface conditions	Kemp, P.R., J.M. Cornelius, & J.F.Reynolds. 1992. A simple model for predicting soil temperatures. **Soil Science** 153: 280-287.

Description	Product
GENDEC, GAS --A general decomposition module is presented. Development and application to Chihuahuan desert supported by NSF; application to Arctic partially supported by CO2 project.	Moorhead, D. L. and J.F. REYNOLDS. 1991. A general model of litter decomposition in the Northern Chihuahuan Desert. **Ecological Modelling** 56:197-219. Moorhead, D. L. and J.F. REYNOLDS. 1992. Effects of climate change on decomposition in Arctic tussock tundra. **Holarctic Ecology** (Submitted).
SOWAT--Module to simulate vertical distribution of water in soil	Kemp, P.R., J. Brisson, & J.F. Reynolds. 1993. Simulation of soil water as a function of water loss through evaporation and transpiration: a comparision of three models. **Soil Science** (In manuscript; to be submitted summer 1993.)
MONOMOD/MIXMOD--Modules for simulating competition among species in response to elevated CO_2.	Hilbert, D.W. , J.F. Reynolds, and F. Bazzaz. 1993. Effects of carbon dioxide enrichment on plant communities: Models of competition in species mixtures based on scaling single plant responses. **Functional Ecology** (Submitted)
GAS: Current ecosystem simulations focus on predicting long term response of one of the principal plants in the Arctic--*Eriophorum*. The model includes effects of elevated CO_2 and nutrients and shows important interaction between the two.	Leadley, P.W. & J.F. Reynolds. 1992. Long-term response of an arctic sedge to climate change. **Ecological Applications** 2(4): 323-340.
PALS: Current ecosystem simulations focus on long term responses of arid ecosystems to variability in rainfall and potential responses to changes in rainfall.	Reynolds, J.F. et al. 1993.. The response of an arid ecosystem to climate change: spatial and temporal variability in rainfall. **Ecology** (Manuscript in prep.)

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