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DOE/ER-60490T-H1

March 1992

Prepared for
United States Department of Energy

Office of Energy Research
Office of Health and Environmental Research
Carbon Dioxide Research Program

Under Contract No. DE-FG03-86ER60490

TR054

Modeling the Response of Plants and Ecosystems to Elevated CO₂ and Climate Change

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DE92 009879

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Washington, DC 20585

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Modeling the Response of Plants and Ecosystems to Elevated CO₂ and Climate Change

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Under Contract No. DE-FG03-86ER60490

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PREFACE

It is well established that the concentration of atmospheric carbon dioxide (CO₂) is increasing and that, at the present rate, there will be a doubling of pre-industrial concentrations by the middle of the next century (Chen and Drake 1986; Schlesinger 1986; Ramanathan 1988). Carbon dioxide, one of the important greenhouse gases, plays a principal role in the warming of the atmosphere through the re-radiation of infrared energy (Tangle 1988). While the exact effects of elevated CO₂ on global climate are unknown, there is a growing consensus among climate modelers that global temperature and precipitation will increase, but that these changes will be non-uniform over the Earth's surface. In addition to these potential climatic changes, CO₂ also directly affects plants via photosynthesis, respiration, and stomatal closure (Strain 1985). Global climate change, in concert with these direct effects of CO₂ on plants, could have a significant impact on both natural and agricultural ecosystems (Committee on Global Change 1988). Society's ability to prepare for, and respond to, such changes depends largely on the ability of climate and ecosystem researchers to provide predictions of regional level ecosystem responses with sufficient confidence and adequate lead time (Dahlman 1985).

Although the primary cause of increased atmospheric CO₂ appears to be the combustion of fossil fuels (Rotty and Marland 1986), the increase represents a disequilibrium among all of the sources and sinks in the bio-geosphere carbon cycle (Woodwell et al. 1983; Chen and Drake 1986; Mooney et al. 1987). The effects that increased CO₂ will have on ecosystems -- and even broader questions, such as how much CO₂ will increase and how the various bio-geospheric pools of carbon will change -- are directly related to plants because of the fundamental role that they play in the global carbon cycle. Plants are a significant sink for CO₂ from the atmosphere and, at least for individual plants, their capacity as

sinks (i.e., for CO₂ uptake) is dependent upon the atmospheric concentration of CO₂. Plants form the base of terrestrial and aquatic food chains and all carbon available to the other organisms is directly or indirectly linked to productivity and carbon flow through plants. Thus, predicting the changes in Earth's vegetation in response to elevated CO₂ and climate change is crucial to understanding the future behavior of the atmosphere-biosphere-geosphere cycles of carbon (NRC 1982; Woodwell et al. 1983; Mooney et al. 1987).

In recognition of the role of plants in the bio-geosphere carbon cycle, the Carbon Dioxide Research Program of U. S./DOE initiated a research program on the Direct Effects of Increasing Carbon Dioxide on Vegetation (Strain and Cure 1985; Dahlman 1985). This report describes continuing research that we are conducting as part of the DOE/CO₂ program to develop a general ecosystem model to investigate the potential responses of different terrestrial ecosystems to changes in the global environment over the next century. The Committee on Global Change (1988) notes that such "generic ecosystem models" can only be useful for predicting responses of ecosystems to future global changes if they are linked to population-community models. Our research approach incorporates such efforts as part of a multi-investigator, multi-university, long-term research strategy developed with the ultimate goal of providing experimental data, modeling methodology, and models for predicting long-term, large-scale ecosystem response to global change.

The judicious use of modeling will allow a limited body of empirical knowledge to be greatly extended through simulation of complex combinations of environmental-biotic interactions. Mechanistic models further allow the extrapolation of results from short-term or small-scale studies to predictions of phenomena at larger time and spatial scales (Dahlman 1985, Reynolds and Acock 1985a,b).

Preface

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CHAPTER SUMMARIES

CHAPTER 1 : PROGRAM GOALS AND OBJECTIVES

We have established 2 principal working objectives to accomplish our goal of predicting the response of plants and ecosystems to climate change:

- 1) To understand and model the effects of elevated CO₂ and climate change at various hierarchical levels in the ecosystem, particularly at the plant and ecosystem levels, with an emphasis on generality; and
- 2) To develop techniques that will allow for aggregation of submodules (modules) and for scaling-up from one hierarchical level to the next.

The general research objectives of the plant modeling efforts are:

- 1) To predict primary, secondary and tertiary effects of elevated CO₂ and climate change on individual plants ;
- 2) To permit realistic simulations of plant growth at conditions beyond those used to calibrate the model;

- 3) To provide information to higher-level models, such as community models and ecosystem models.

There are 4 general objectives of the ecosystem level modeling effort:

- 1) To incorporate plant response to elevated CO₂ into an ecosystem framework in order to predict the primary ecosystem effects of global change;
- 2) To permit realistic simulations of ecosystem response to global change at conditions beyond those used to calibrate the model;
- 3) To validate the total system-level response against various ecosystem field studies of elevated CO₂ and climate change;
- 4) To use the validated ecosystem model to investigate specific hypotheses and make predictions about ecosystem response to global change that may or may not be discoverable within the time frame of the experimental data collection.

CHAPTER 2 : SCALING ECOPHYSIOLOGY FROM THE PLANT TO THE ECOSYSTEM: A CONCEPTUAL FRAMEWORK

Scaling issues greatly complicate investigation of the response of ecosystems to climate change. The spatial and temporal scales at which the plant carbon pool (e.g., tropical forests, coniferous forests, and grasslands) reaches equilibrium with other carbon pools of the bio-geosphere are vastly greater than the scale at which carbon dioxide directly affects plant growth via its effects on photosynthesis and stomatal aperture. Changes in leaf physiological processes leads to changes in allocation patterns, and other whole-plant properties, in turn, these effects feed back on lower hierarchical levels and are translated to higher hierarchical levels, e.g., plant - plant interactions and interactions among organisms of different trophic levels.

Addressing this problem of scale involves a careful match of scales of observation, theory, and models in order to develop models that are capable of

prediction at the scale of interest (e.g., leaf) while avoiding errors that occur when a model attempts to scale-up process and mechanism over too great a range. 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 argue that the processes and elements that constitute the mechanism of a model are 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. Developing a hierarchy of models in this way, each suited to a particular scale and drawing on insights and output from lower levels, is, in our opinion, the most effective way of accounting for the translation and ramification of effects from the physiological level of organization to the ecosystem level.

3.0.0 MODELING THE EFFECTS OF GLOBAL CHANGE ON LEAF LEVEL PROCESSES

Because CO₂ is fixed into the biosphere at the level of the individual leaf, we have chosen to incorporate as much mechanistic detail as possible into the models of photosynthesis and stomatal conductance. The model of C₃ photosynthesis is that of Farquhar et al. (1980) modified to include a potential phosphate limitation arising from the failure of starch and sucrose production to keep up with triose phosphate production in the Calvin cycle (Sharkey 1985a). This biochemical model is integrated with an empirical model of stomatal conductance (Ball et al. 1987) to predict the photosynthetic response of leaves to varying CO₂, irradiance, temperature and humidity.

The model structure, embodied in the equations describing the model, is applicable to leaves which develop under any environmental regime; resulting changes in the photosynthetic characteristics of leaves are incorporated through changes in the parameters of the model.

We describe the techniques of model parameterization using data collected from leaves of cotton plants grown under either ambient (350) or elevated (650 $\mu\text{l l}^{-1}$) CO₂. In the case of cotton, the photosynthetic characteristics of the leaves changed very little as a result of growth in a high CO₂

environment. Under the environmental conditions at which the plants grew, therefore, plants in 650 $\mu\text{l l}^{-1}$ CO₂ had photosynthesis rates approx. 25% greater than plants in 350 $\mu\text{l l}^{-1}$ CO₂, despite a reduction in stomatal conductance of approx. 23%.

We also describe two ways in which additional physiological detail may be incorporated into the model structure. It is demonstrated that if some fraction of the glycolate carbon which leaves the chloroplast in the photorespiratory pathway fails to return as glycerate, there is a net release of inorganic phosphate in the chloroplast. Under conditions where phosphate is limiting photosynthesis, this results in reversed sensitivity of photosynthesis to both CO₂ and O₂, as has been observed experimentally.

Finally, in most photosynthesis modeling efforts, it is implicitly assumed that the partial pressure of CO₂ at the site of fixation is equal to that in the intercellular air space, which implies that the mesophyll resistance to CO₂ flux is zero, an impossibility. We discuss two techniques for estimating the magnitude of mesophyll resistance, which appears to be approx. one-half of stomatal resistance, and therefore poses an additional diffusional limitation to CO₂ assimilation.

CHAPTER 4: MODELING THE PLANT CANOPY (CANDO)

The module CANDO simulates canopy photosynthesis and transpiration in response to a changing environment, especially elevated CO₂. CANDO is a scaling up from leaf level (GenLeaf) to canopy level. CANDO treats the whole canopy as a collection of leaves and stems with specific physiological properties and exposed to specific microenvironments. The whole canopy is divided into several horizontal layers, and the leaves in the same layer are grouped into sunlit and shade ones. The sunlit leaves are divided further into nine classes according to the irradiance level. This careful leaf classification takes care of the strong nonlinearity of the response of leaf photosynthesis to radiation. The current

version of CANDO also allows us to specify leaf nitrogen distribution within the canopy.

CANDO has been employed to investigate the effect of elevated CO₂ on photosynthesis and transpiration of a *Quercus coccifera* canopy. It was found that the daily total assimilation of *Quercus coccifera* canopy would be expected to increase by approx. 50-60% and transpiration to decline by 15-25% under short-term exposure to doubled CO₂. This would result in approximately a doubling of whole canopy water use efficiency. CANDO also has been employed to investigate the effect of simplifications of the canopy model on the accuracy of the calculated canopy photosynthesis and transpiration by aggregating several leaf classes together. It

was found that multi-layer canopy models with Gaussian integration for sunlit leaves and a single averaged class of shaded leaves gave excellent results. Multi-layer models with a single average sunlit and a single average shaded leaf class can satisfactorily describe canopy responses if errors of as much as 15% are acceptable.

The irradiance at the surfaces of leaves at different positions within a canopy affects canopy photosynthesis and transpiration strongly. So it is very important to model radiation transfer within a canopy carefully. The most detailed model of radiation transfer in a canopy was developed by Chen (KMC), and simplified models were developed by Norman (CUPID) and Caldwell *et al.* The performance of CUPID and KMC was examined, and the profiles of downward and upward diffuse radiation in a canopy, and the bidirectional

reflectance from a canopy, calculated from KMC and CUPID were compared. It was found that CUPID gives good approximations.

Adaptation of leaves to their environments is an important factor which effects long-term responses of the canopy photosynthesis and transpiration to the changing environment. A co-ordination theory is proposed, that leaves in different environments will adjust their nitrogen contents to keep a balance between two processes which limit leaf photosynthesis. It was found that the profile of leaf nitrogen contents in a canopy calculated from this theory is consistent with observations, and the resulting daily canopy photosynthesis was close to and even higher than that obtained from an optimal exponential distribution of leaf nitrogen within the canopy.

CHAPTER 5 : MODELING GROWTH AND ALLOCATION

Using a cost-benefit model, the leaf nitrogen concentration and root:shoot ratio that maximize whole-plant relative growth rate are determined as a function of the integrated daily photon flux density, the concentration of carbon dioxide at the site of fixation within the leaf, and the availability of soil nitrogen. The advantage of this approach is that it determines the adaptive significance of leaf physiology by considering the functional integration of leaves and roots. The cost of increasing tissue nitrogen concentration is found to be primarily related to an increase in allocation to roots. The predicted response to increasing daily photon flux densities is an increase in optimal leaf N concentration (N_{opt}) and a concomitant increase in root:shoot ratio. Increased carbon dioxide concentrations, on the other hand, reduce N_{opt} and only slightly change root:shoot ratio. Since these responses to light and CO_2 maximize the whole-plant relative growth rate, the

observed adjustments that plants make to light and carbon dioxide concentration appear to be adaptive. Predictions of the responses to soil nitrogen are consistent with previous theories and general empirical findings, suggesting that plants respond optimally to soil nitrogen.

A simulation model was also developed that considers the allocation of carbon and nitrogen substrates to a protein compartment in the shoots, shoot structural components, and root biomass. Inclusion of a shoot-protein compartment allows variation in shoot specific activity to be modeled as a function of leaf nitrogen concentration. Allocation to the biomass compartments is controlled by two partitioning variables that are defined by explicitly using the balanced activity hypothesis. The predicted patterns of both root:shoot ratio and leaf nitrogen concentration in response to environmental resource availability are qualitatively consistent with general trends observed in plants.

CHAPTER 6 : MODELING COMPETITION

We have developed a hierarchy of models to study the physiological and morphological effects of CO_2 on intra- and

interspecific competition in plants. Our approach is conceptually similar to Charles-Edwards (1984) who modeled crop growth as a function of the amount of light intercepted

by a canopy and the number of growth points that could be sustained by the resultant carbon uptake. Our models are based on whole-plant growth (rather than growth points) and utilizes 1) the behavior of isolated plants to model the dynamics of monocultures and 2) the behavior of monocultures to model the dynamics of mixed-species communities. Competition is realized through the dynamics of "sustainability," i.e., the number of individuals that can be sustained in either a monoculture or mixed-

species community considering canopy light interception, photosynthesis, partitioning of biomass between root and shoot, and competition for nitrogen. These models reproduce behaviors that are common in plant communities - such as Yoda's thinning relationship - and should prove useful in understanding the complex interactions among species in response to elevated CO₂ and the link between physiological ecology and population biology.

CHAPTER 7: ECOSYSTEM MODELING

Modeling at the ecosystem scale integrates results from the leaf, canopy, whole plant, and competition models with additional modules that simulate ecosystem level processes such as nutrient cycling, soil water, and decomposition. The goal of this research is to develop a generic ecosystem-level simulation model that can be used to investigate responses of different terrestrial ecosystems to changes in the global environment over the next century. Our first generation ecosystem model, SERECO, has been developed and used to simulate structure and function of three terrestrial ecosystems: grasslands, arid shrubland, and Arctic tussock tundra. Much of the simulation research currently involves model validation, particularly in the form of modeling historical ecosystem responses. A principal theme of research in grassland simulation is to understand the role of climate in influencing grassland structure and function. We have simulated the response of both tallgrass prairie and mixed prairie communities to historical weather patterns, including the widespread droughts of the 1930's and 1950's. Historic vegetation records suggest that the mixed prairie was more sensitive to climate effects than the tallgrass prairie. However, our simulation results do not show significant differences between the prairie types in response to drought. Thus, we are making further modifications to SERECO,

especially to account for the interaction of water and nutrients to control prairie species composition and production. Simulation of arid shrublands has focused on the importance of spatial and temporal variability of rainfall to control species composition and productivity in this ecosystem. Model simulations reveal that productivity in these shrublands is highly variable from year to year, even more variable than rainfall, a phenomenon noted in vegetation records throughout arid regions. Our model results help to explain this phenomenon by showing that plant phenological patterns play a key role in timing of plant responses in uncertain environments, and much of the variability in plant production can be attributed to the annual plants. Shrubs, on the other hand, have low annual variability in production. Simulation of Arctic tussock tundra has demonstrated the importance of nutrients in controlling productivity in this ecosystem. We examined the effect of increased temperature, increased CO₂, and increased growing season length on the growth of a principal tussock grass. The model revealed that over a 50 year period there would be little change in the annual biomass accumulation of this species. This was shown to be the result of nitrogen deficiency, which if alleviated, allowed for a doubling in biomass of the plant community over the 50 year period.

CHAPTER 8: SUMMARY AND GENERAL CONCLUSIONS

This chapter reiterates our general approach and describes the major conclusions from our modeling at each level of organization. A list of the major processes modeled at each level is given along with our modeling approach for these processes and the major limitations or uncertainties involved in modeling them.

While the ultimate goal of our research is to develop a general ecosystem model to investigate 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. Our philosophy is that each level has its own characteristic set of processes and special modeling challenges that can be worked on in relative isolation from work at other levels (see Table 8.1). 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 global change as they progress from the physiological level of organization to the ecosystem level.

At the level of the leaf, 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. In order to understand leaf response to environmental change, leaf level processes must be integrated into a whole plant context, in which canopy structure and resource allocation play a critical role.

The canopy module has been used to investigate components of within-canopy interactions important for predicting whole-plant photosynthetic response to elevated CO₂. This model is quite effective in describing the aggregate behavior of a

population of leaves with known properties. Further work, however, needs to be done that investigates the effects of altered photosynthetic capacity and morphological characteristics due to growth at high CO₂ concentrations.

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 CO₂ concentrations; and 2) phenomenological allocation models are effective in predicting changes in root:shoot ratio, leaf photosynthetic capacity, and plant growth at high CO₂ despite the lack of a complete mechanistic understanding of allocation.

In developing a new, mechanistic community model, we decompose the system (community) into its component parts (plants, populations, and species) and describe the behavior of the system through the interaction of these parts. Implicit in this approach is the assumption that effects of elevated CO₂ 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.

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 (based in large part upon the models and results discussed in previous sections), and 3) preliminary model simulations of long-term (decades or more) ecosystem response to ambient and/or perturbed climate or other abiotic factor. The ecosystem models will require considerable refinement in order to have the capacity to predict responses of communities and ecosystems to the combined effects of elevated CO₂ and climate change. Much of this refinement can be based on the modules currently being developed at the different levels of plant organization.

NOTE:

Much of the material in this progress report has been published, is in press, or has been submitted for publication. The reader should cite the appropriate reference when referring to this work.

1.0.0 PROGRAM GOALS AND OBJECTIVES

1.1.0 General Goals and Objectives

The ultimate goal of our modeling research is to *develop a general ecosystem model to investigate the potential responses of different terrestrial ecosystems to changes in the global environment over the next century*. We have established 2 principal working objectives to accomplish this goal:

- 1) To understand and model the effects of elevated CO₂ and climate change at various hierarchical levels in the ecosystem, particularly at the plant and ecosystem levels, with an emphasis on generality; and
- 2) To develop techniques that will allow for aggregation of submodules (modules) and for scaling-up from one hierarchical level to the next.

At the plant level, we have stressed mechanism in the development of our general plant growth model, GePSI - General Plant Simulator. At the ecosystem level, the phenomenon of translation of CO₂ effects and other aspects of global change throughout the ecosystem, including feedbacks and constraints to system response, have been stressed in our development of a mechanistic, general ecosystem model named SERECO - Simulation of Ecosystem Response to Elevated CO₂ and Climate Change.

One strength of our approach is that we are conducting research at several hierarchical levels simultaneously, thus permitting a joint "bottom-up" and "top-down" approach. The primary models and modular components of our research are illustrated in Figure (1.1). Each module or model is useful independently to address specific questions appropriate at its particular hierarchical level.

1.2.0 Plant Modeling

The general research objectives of the plant modeling efforts are:

- 1) To predict primary, secondary and tertiary effects of elevated CO₂ and climate change on individual plants;
- 2) To permit realistic simulations of plant growth at conditions beyond those used to calibrate the model;

- 3) To provide information to higher-level models, such as community models and ecosystem models.

These general objectives lead to immediate design decisions for GePSI. Objective #1 requires that the modules in GePSI explicitly contain plant physiological mechanisms. CO₂ and other environmental variables (temperature, moisture, nutrients, etc.) affect plants through the interactions of physiological mechanisms (Strain 1985). While overall plant response to elevated CO₂ (the sum of primary-tertiary effects, see Figure 2.1) is poorly understood, the primary effects have been well characterized. By coupling detailed modules for the expression of primary CO₂ 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 (Reynolds and Acock 1985a). 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.

1.3.0 Ecosystem Modeling

There are 4 general objectives of the ecosystem level modeling effort:

- 1) To incorporate plant response to elevated CO₂ into an ecosystem framework in order to predict the primary ecosystem effects of global change;
- 2) To permit realistic simulations of ecosystem response to global change at conditions beyond those used to calibrate the model;
- 3) To validate the total system-level response against various ecosystem field studies of elevated CO₂ and climate change;

Program Goals and Objectives

Figure 1.1: Modules and models of our program arranged hierarchically.

4) To use the validated ecosystem model to test specific hypotheses and make predictions about ecosystem response to global change that may or may not be discoverable within the time frame of the experimental data collection.

1.4.0 Modules and the Importance of Generality

In several publications we have described the utility of developing certain "classes" of models, called *modules*, in an attempt to clarify where similarities across ecosystems exist and to realize the full benefits afforded by the recognition of the existence of generality in biological and ecological systems (Reynolds *et al.* 1986, 1989; Acock and Reynolds 1989). 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. Thus, both our plant and ecosystem level modeling is based on the development of general modules that represent various subsystems of interest. 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 global change 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 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 (O'Neill and Reichle 1979).

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. (Criteria used to define modules, as well as the expected benefits of this approach, are described in Reynolds *et al.* [1989]) In the case of a plant growth model (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.

Model *transferability* is defined as the ability to apply a particular model to other functionally equivalent systems by re-parameterizing the model with system-specific parameters. (Haugh *et al.* 1983). Thus, a general plant growth model has the attribute of transferability to other functionally equivalent species by re-parameterizing the model with species-specific parameters. If a photosynthesis module is needed for a particular plant growth model, the modeler can choose from a number of previously built modules and place it into the model. To facilitate interchange, each module's function, variables, inputs and outputs must be explicitly defined. The principal appeal of general models is their economy, in terms of both modeling effort and understanding. 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.

1.4.0 Organization of Chapters

The chapters which follow describe the development of GePSI and SERECO during the period 1989 through 1991. Neither GePSI nor SERECO are completely developed and they currently exist in several preliminary versions. Our focus up to this point has been the development of their various component modules and the methods

Program Goals and Objectives

that will allow us to simulate the most important processes at each level of organization. Consequently, this book stresses the work at each level of organization rather than its eventual synthesis into more inclusive models. We begin with a chapter describing our conceptual framework and general modeling philosophy, especially with reference to the problem of scaling up information from the level of physiology within the leaf to ecosystem level processes. This is a major challenge for modelers involved in global change issues and an important part of our work includes the development of effective

methodologies to accomplish this scaling. The chapters then follow in the order of increasing scale from leaf to canopy to whole-plant to plant community and, finally, to the ecosystem. A final summary chapter summarizes the major results at each level of organization and list the major processes that are being modeled, our modeling approach for these processes, and the associated uncertainties or limitations.

2.0.0 SCALING ECOPHYSIOLOGY FROM THE PLANT TO THE ECOSYSTEM: A CONCEPTUAL FRAMEWORK

2.1.0 Introduction

There is a growing consensus among atmospheric scientists that global temperature and precipitation will increase due to increasing levels of atmospheric CO₂, although the exact magnitudes are unclear (Chen and Drake 1986, Schlesinger 1986, Ramanathan 1988, Kellogg 1991). Although the primary cause of increased atmospheric CO₂ appears to be the combustion of fossil fuels (Rotty and Marland 1986), this increase represents a disequilibrium among all of the sources and sinks in the bio-geosphere carbon cycle (Woodwell *et al.* 1983, Chen and Drake 1986, Mooney *et al.* 1987). In addition to these potential climatic changes, increased CO₂ also has a direct effect on plants via the physiological processes of photosynthesis, respiration, and stomatal closure (Strain 1985). Hence, global climate change, in concert with these direct effects of CO₂ on plants, could have a significant impact on both natural and agricultural ecosystems (Committee on Global Change 1988). Society's ability to prepare for, and respond to, such changes depends largely on the ability of climate and ecosystem researchers to provide predictions of regional level ecosystem responses with sufficient confidence and adequate lead time (Dahlman 1985).

The effects that increased CO₂ will have on ecosystems -- and even broader questions, such as how much CO₂ will increase and how the various bio-geospheric pools of carbon will change -- are directly related to plants because of the fundamental role that they play in the global carbon cycle. Plants are a significant sink for CO₂ from the atmosphere and, at least for individual plants, their capacity as sinks (i.e., for CO₂ uptake) is dependent upon the atmospheric concentration of CO₂. Plants form the base of terrestrial and aquatic food chains and all carbon available to the other organisms is directly or indirectly linked to productivity and carbon flow through plants. Thus, predicting the changes in Earth's vegetation in response to elevated CO₂ and

climate change is crucial to understanding the future behavior of the atmosphere-biosphere-geosphere cycles of carbon (National Research Council 1986, Woodwell *et al.* 1983, Mooney *et al.* 1987).

In essence, increasing atmospheric CO₂ is an Earth-scale experiment (Ramanathan 1988) since, at the present time, it is impossible to experimentally determine the long-term outcome of elevated CO₂ and climate change on ecosystems. To predict the outcome of this experiment is a daunting challenge, particularly across the various levels of organization in the bio-geosphere. For example, consider the multiple factors involved in predicting the response of single plants to elevated CO₂. Research has shown that not all plants are affected in the same way and that the way in which individual plants respond to CO₂ is greatly affected by the levels of other environmental resources (e.g., nutrients and water) and regulators (e.g., temperature and salinity) (see Strain and Cure 1985, Mooney *et al.* 1991). Since these resources and regulators are spatially and temporally variable over the Earth, large differences can be expected among regions or biomes in their response to elevated CO₂. These factors, coupled with the potential for climate change that will produce further changes in environmental factors, make it extremely difficult to design experiments that test more than a small fraction of the many different combinations of environmental conditions that may be involved in causing ecosystem change with elevated CO₂ (Reynolds and Acock 1985b). Even at very small scales (e.g., 1 m²), there are a many factors that make it difficult to experimentally determine the effects of elevated CO₂ on whole ecosystems, including long-term changes that may lead to a new homeostasis (Oechel and Strain 1985, Hilbert *et al.* 1987), potential herbivory feedbacks (Fajer *et al.* 1991), and multiple environmental stresses (Larigauderie *et al.* 1988).

Modeling has an essential role in developing an understanding of potential plant, community, and ecosystem responses to

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Figure 2.1: Physiological and ecological controls on translating effects of elevated CO₂ from leaf-level processes up to ecosystems. Adapted from Strain (1985).

simultaneous changes in atmospheric CO₂ and climate (Dahlman 1985, Reynolds and Acock 1985b). The judicious use of modeling will allow a limited body of empirical knowledge to be greatly extended through simulation of complex combinations of environmental-biotic interactions. The major challenge is how to build mechanistic models that are based on short-term or small-scale studies but are useful for extrapolating to predictions of phenomena at larger time and spatial scales (Reynolds and Leadley 1991).

Material in this chapter is taken from Reynolds, Hilbert, and Kemp (1991).

2.2.0 Hierarchy Theory and Scaling

2.2.1 The Problem of Scale

Scaling issues greatly complicate how we investigate the response of ecosystems to climate change (Rosswall, *et al.* 1988). The spatial and temporal scales at which the plant carbon pool (e.g., tropical forests, coniferous forests, and grasslands) reaches equilibrium with other carbon pools of the bio-geosphere are vastly greater than the scale at which carbon dioxide directly affects plant growth via its effects on photosynthesis and stomatal aperture.

The effects of enriched atmospheric CO₂ on ecosystems can be viewed in a hierarchical manner. Carbon dioxide directly enters the biosphere via plant leaves, affecting photosynthesis, respiration, stomatal conductance, and transpiration. Because these processes are reasonably well understood, the direct effects of elevated CO₂ can be predicted with a fairly high degree of confidence. However, the indirect effects of CO₂ are complex, as illustrated in Fig (2.1). Changes in leaf physiological processes leads to changes in whole-plant properties (Strain 1985, Hilbert *et al.* 1991). In turn, these effects feed back on lower hierarchical levels (e.g., altering leaf photosynthetic capacity) and are translated to higher hierarchical levels, e.g., plant - plant interactions (Bazzaz and Garbutt 1988) and interactions among organisms of different trophic levels (Committee on Global Change 1988). The plethora of interactions likely to occur will produce changes in the distribution of

resources and, ultimately, ecosystem structure and function (Mooney *et al.* 1991) and, thus, the global carbon balance (Post *et al.* 1990).

2.2.2 Scaling-up Mechanism Across Hierarchical Levels

How will climate change affect systems and processes at specific hierarchical levels and how will these effects be translated to higher levels of the hierarchy (Fig 2.1) Addressing this question will involve a careful match of scales of observation (pattern), theory (explanation), and models (description) in order to develop models that are capable of prediction at the scale of interest (e.g., leaf) while avoiding scaling errors that occur when a model attempts to scale-up process and mechanism over too great a range (e.g., leaf to ecosystem) (Patten 1983, O'Neill 1988, Woodmansee 1988). Furthermore, we suggest that mechanistic descriptions of systems are necessary for this scaling (Reynolds and Acock 1985a,b). We use the term *mechanistic* for models that decompose a system into its component parts and describe the behavior of the whole through the interaction of those parts (these types of models are also frequently referred to as "bottom-up", "explanatory", or "process" models). They are considered to be based on underlying mechanisms that give rise to the observed behavior of interest. Of course, "mechanism" is itself a scale-dependent concept: One person's "mechanism" is another person's empiricism!

The special characteristic of mechanistic models in our usage is that behavior of the system at *any* chosen level in a hierarchy (e.g., organ, whole plant, community, ecosystem, etc.) is modeled by representing the interactions of the component systems at one (or possibly, two) levels down, for example, modeling whole plant dynamics based on organ descriptions, modeling community dynamics based on whole plants, etc. Generally, mechanistic models are composed of both *empirical* and *phenomenological* equations that describe the component parts of the system (Thornley 1976). Empirical models are based on statistical formulations (e.g., multiple regression) that best correlate a set of

Figure 2.2: Examples of three types of models to describe the change in whole plant weight over time, $W(t)$. A) Empirical (degree day), where plant is treated as a "black box." B) Phenomenological, where functional form (logistic equation) is based on knowledge of plant growth. C) Mechanistic, where plant is decomposed into interacting components (root, shoot, carbon pool, and nitrogen pools). (Figure from Reynolds *et al.* 1991)

observed variables to some response variable of interest; these models are simple, readily built, easy to apply, but lack generality and their use must be restricted to the range of the data on which they are based (see Fig 2.2a). Phenomenological equations also describe the behavior of a system (the phenomena of interest) without decomposition into lower level subsystems (see Fig 2.2b). Phenomenological models or equations do not "plunge beneath the surface," but rather describe the process or system property directly at the level of interest (Spanner 1964, Thornley 1976).¹ In contrast to empirical models, the form of a phenomenological model is derived from a general understanding of the process or system of interest. Hence, the equation used for the model is meaningful and describes some logical or expected relationship between the variables.

An example of the use of phenomenological equations to build a mechanistic model is given by Reynolds and Thornley (1982). To develop a whole-plant growth model, they decompose the plant into four components (shoot biomass, root biomass, carbon substrate pool, and nitrogen substrate pool) and model plant growth as the interaction of these components (see Fig 2.2c). The equations they use to represent the behavior of each component in this mechanistic model are phenomenological. For example, the differential equation for the carbon substrate pool is formulated from a knowledge of the possible inputs and outputs to this component and the law of mass balance.

Hierarchy theory (Allen and Starr 1982, O'Neill *et al.* 1986) suggests that it is unnecessary to look further down than one level in the search for "mechanistic" explanations of a system's behavior. Ecological models that explicitly include processes and structures at several hierarchical levels (i.e., composed of

numerous coupled process models, having many interactions) tend to be very complex and are frequently hypersensitive to slight changes in parameters (Allen and Starr 1982). While such models have been successful in simulating specific short-term processes, they are not well suited for long-term simulations (Allen and Starr 1982). Models that include "mechanism" across a large range of hierarchical levels necessarily become very complex, are difficult to maintain and verify, tend to be unstable, and are usually not amenable to modification for new situations (Reynolds and Leadley 1991); ultimately, such models will "lose" their mechanism as noise (Rexstad and Innis 1985, Landsberg 1986, O'Neill 1988).

In our effort to build models that will enable us to predict ecosystem responses to global change, it is clear that only mechanistic models will permit us to extrapolate beyond our data with any degree of confidence (Reynolds and Acock 1985b, Strain and Cure 1985, Dahlman 1985). Yet, we must avoid building complex, "bottom-up", ecosystem models that attempt to directly include processes operating at many different levels of hierarchy. The conceptual approach we present is a hierarchical scheme where the level of focus (L) is modeled by describing the interactions among components that exist at any hierarchical level below L (typically one level below, i.e., L-1), but are themselves represented in the model as phenomenological relationships (Fig 2.3A,B). Thus, a fundamental focus is to understand the ways in which processes and system properties are aggregated and translated among and within subsystems. The mechanistic modeling of each hierarchical level is emphasized via the mechanism that occurs at the lower level, coupled with constraints from the level above (O'Neill 1988). We emphasize the hierarchical nature of our mechanistic modeling approach whereby modeling at each scale is based on information from lower scales (Fig 2.3) -- the model is parameterized with data collected at the subordinate scale, validated against data collected at the scale of focus, and constrained

¹ An example is the ideal gas law, $PV=nRT$, which accurately describes the behavior of gases over a wide range of conditions without any reference to (or even knowledge of) the molecules of which gases are composed.

Figure 2.3: Scheme to develop mechanistic models at level L. A) Whole plant model GEPSI (L) is based on the dynamics of organs (L-1) and whole-plant allocation of carbon and nitrogen substrates (L). B) Community model STAND (L) is based on relationships among components of community, e.g., shrub life histories (L), GEPSI (L-1), and organ dynamics (L-2). (Figure from Reynolds *et al.* 1991)

by data or information collected at the superior scale. In this way we continually test our ability to extrapolate from one scale to the next via mechanism or process.

2.3.0 Module Aggregation and Scaling Up

In the context of the above discussion, model aggregation and scaling is a parallel development of:

- 1) The *theory* of how CO₂ and climate effects are actually scaled up from levels where they have direct effects, such as on plant physiology and growth, to higher levels in the ecosystem where they act indirectly; and
- 2) The *technical aspects* of linkage, aggregation and information flow in the model.

The importance and utility of mechanistic modeling has been discussed in the context of predictive, system-level response models. Mechanistic modeling seems particularly applicable to global change questions. Perhaps most importantly, the examination of the effects of global change at several hierarchical levels will give us a greater understanding of how processes that operate at one level in a system are translated to or influence other levels in the system. A second justification for this approach is that most of the data regarding effects of CO₂ and climate change (mainly temperature, moisture, and nutrients) are for individual plant responses or responses of very small and simple "systems." It is necessary to scale-up these observations in order to make predictions for ecosystems, landscapes, regions, and ultimately the biomes of the Earth.

2.3.1 Using Model Simplification to Scale Up

Next, we present an example (Fig 2.3c) of how model simplification can be used to hierarchically scale up information. Our objective is to show that mechanistic information at lower hierarchical levels, for example, Level L-2, is valuable at higher levels, e.g., L+2, but only through a "filtering" or simplification process. A model of long-term stand dynamics in chaparral ecosystems was developed by Hilbert and Larigauderie (1990). This model (named

STAND, Fig 2.3c) includes PHENPLT, a simple phenomenological model of plant growth that has a fixed maximum relative growth rate (R_{max}); hence, PHENPLT was not built to be responsive to changes in resource availabilities, e.g., nitrogen (N), solar radiation, carbon dioxide, etc. However, in order to mechanistically understand *stand* level responses (i.e., L = Community, Fig 2.3c) to *altered* resource availability, we need to incorporate information about plant responses (i.e., L-1 = Plants, Fig 2.3c) to these altered resources. Yet, we cannot directly include all the detail of a mechanistic plant model (e.g., information from L-2 = Organs, Fig 2.3c) in such a formulation directly at level L. Rather, as illustrated in Fig 2.3c, we used components of GEPSI (Reynolds *et al.* unpubl.), a mechanistic plant growth model (equivalent to Fig 2.2c) to predict R_{max} as a function of light, CO₂, and N. GEPSI was run under a wide range of these resource availabilities to calculate a response surface for R_{max} ; a simple hyperbolic model (function g , Fig 2.3c) was then fit to this response surface. The R_{max} in PHENPLT is now an empirical function of CO₂, light and N (i.e., $R_{max} = g[CO_2, \text{light}, N]$). Information has been transferred up the hierarchy by substituting the empirical regression equation, developed from data generated by GEPSI (a model that has high extrapolation potential), into the phenomenological component (i.e., PHENPLT) of STAND.

We can now run STAND and investigate stand-level consequences of altered N or CO₂ availability. For example, the mortality rate of shrubs is accelerated under nitrogen stress and this affects the ultimate stand density and biomass (Fig 2.4). Interesting interactions between CO₂ and nitrogen availability emerge that would not have been predicted from the plant model alone. For example, total biomass and leaf area index are significantly increased by CO₂ only when the stand is strongly nitrogen limited. This contrasts to the behavior of individual plants, predicted from GEPSI, which suggests that growth rates are most stimulated by CO₂ when nitrogen is abundant. While this example is preliminary and requires more analysis, it

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Figure 2.4: Results from running STAND model at two levels of internal CO₂ (c= 240 and C= 500 μ bar) and low (n) and high (N) soil nitrogen availability. (Figure from Reynolds *et al.* 1991)

appears that the more open stands which develop under nutrient limitation are more responsive to CO₂ because they are less light limited. Stands with greater nutrient availability quickly attain a closed canopy where production is limited by competition for light.

Stand level effects of altered resource availability could not have been investigated in the original version of STAND because plant growth responses to resources were not represented. On the other hand, population and community effects of resource availability cannot be addressed by GEPSI since community level processes like mortality and competition among plants are not included. Each mechanistic model (GEPSI and STAND) is best at answering questions at its own level of focus. However, the method described here allows us to include information from a mechanistic model at level L-1 (GEPSI) into a mechanistic model at level L (STAND) without directly incorporating the complete model structure.

2.3.3 Danger of Direct Scaling

Scaling errors may be introduced if information obtained at a lower level of the hierarchy is used *directly* to make predictions at a higher level of the hierarchy, without incorporating the interactions between the components of an increasingly complex system. We present a simple example in Fig (2.5) to illustrate this. Fig (2.5) depicts the percent increase in critical states or processes at three hierarchical levels (leaf, whole-plant, and stand) in response to increasing atmospheric CO₂, where the responses are predictions based on the models (GEPSI, PHENPLT, and STAND) shown in Fig (2.4c). For the sake of this example, we assume constant climatic conditions.

At the *leaf* level, under saturating light and high nutrient status, the immediate short-term effect of increasing atmospheric CO₂ is substantial, resulting in a 51% increase in net photosynthesis when CO₂ rises from 340 to 680 μ bar (Fig 2.5a). During long-term exposure to elevated CO₂, leaf photosynthetic capacity generally declines and the modelled increase in net

photosynthesis at 680 μ bar is only 18% (Fig 2.5a).

The next step is to consider the results of the leaf simulations in a *whole-plant* context using GEPSI (which includes feedbacks to the leaves resulting from changes in carbon and nitrogen allocation to root and shoot. The whole-plant relative growth rates was calculated ($r_{\max}$, Fig 2.4c) and the effect of a doubling of CO₂ is an increase in $r_{\max}$ of 16% (Fig 2.5a).

These results were then included at the *stand* level following the scheme outlined in Fig (2.4c). At the stand level, there is a 20% increase in biomass predicted by STAND for a doubling of CO₂ (Fig 2.6b). (Note that this effect is contingent on several other factors, including soil nitrogen availability, which we do not consider here.)

The percent stimulation of these leaf, whole-plant, and stand processes at 680 μ bar is equivalent to the biotic growth factor (β -factor) of Bacastow and Keeling (1973), values of which are given in Fig (2.5). Although values of the β -factor obtained at the level of the individual leaf or small crop stand have been used to infer large-scale effects of increasing CO₂ (e.g., Gates 1985) we caution against such an approach. Information obtained from low levels of the hierarchy is certainly of value in understanding potential ecosystem responses, but if such information is to be incorporated into models at the next higher level, the potential interactions and feedbacks (positive and negative) which arise at the new level must be recognized and explicitly dealt with. To ignore them will result in potentially large errors in prediction. Jarvis and McNaughton (1986) present an analogous argument in discussing the problems of scaling measurements of evapotranspiration made at the leaf or plant level to make predictions at a regional or global scale.

2.4.0 Summary

In summary, we have argued that complex global change issues, such as elevated atmospheric CO₂, are especially difficult to address since they involve many scales. While the direct effects of a particular change may be focused primarily

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Figure 2.5: Predicted change in response to increasing atmospheric CO₂. β is the proportional change in each variable following a doubling of CO₂ concentration. (Figure from Reynolds *et al.* 1991)

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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 some single preferred level (e.g. biochemical) without denying that these lower levels have significant effects at

higher levels of organization (e.g. ecosystems). 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. Developing a hierarchy of models in this way, each suited to a particular scale and drawing on insights and output from lower levels, is, in our opinion, the most effective way of accounting for the translation and ramification of effects from the physiological level of organization to the ecosystem level.

3.0.0 MODELING THE EFFECTS OF GLOBAL CHANGE ON LEAF LEVEL PROCESSES

3.1.0 Introduction

Reynolds and Acock (1985a) reviewed plant growth models with respect to their ability to respond realistically to increasing CO₂ and associated climate change, and argued that if plant growth models are to be capable of prediction under elevated CO₂, they must be mechanistic or semi-mechanistic, at least in those areas where CO₂ directly affects plant behavior. Although elevated CO₂ has been shown to modify indirectly a multitude of plant processes (Strain 1985b), the direct effects occur at the level of enzymes and biochemistry, and manifest themselves at the level of the individual leaf through effects on photosynthesis and stomatal behavior. Highly mechanistic models incorporating considerable physiological detail are appropriate at this level of the hierarchy, where CO₂ is fixed by the plant into the biosphere. Knowledge gained from the leaf module will be used at the next hierarchical level, in conjunction with a model describing canopy structure and light interception (Section 4), to drive a model of whole-plant carbon gain under elevated CO₂ and associated climate change.

Much of the material included in this chapter has been published, or submitted for publication, elsewhere (Harley and Sharkey 1991; Harley and Tenhunen 1991; Harley *et al.* 1991a,b; Loreto *et al.* 1991).

3.1.1 Objectives

The objective of the leaf level model is to simulate the primary, first-order effects of increased CO₂ on plants which occur at the leaf-level (Strain 1985b). The model must simulate photosynthesis, photorespiration and stomatal conductance over the range of leaf temperatures and light intensities likely to be encountered, and these simulations must be projected into an elevated CO₂ environment. Given the impact of CO₂ on these important primary events, we have chosen to incorporate as much mechanistic

detail as practical into the model at this level of the hierarchy.

3.1.2 Modeling Approach

Varying the partial pressure of CO₂ (pCO₂) affects leaf photosynthesis in two fundamental ways, at the level of leaf biochemistry and at the level of CO₂ diffusion. The primary biochemical effect is on ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), the activity of which is dependent *inter alia* on the pCO₂ at the enzyme active site (C_c). This CO₂ dependency is formalized using Michaelis-Menten enzyme kinetics. Under steady-state conditions, the actual concentration of CO₂ at Rubisco is jointly determined by the rate of carboxylation ("demand" for CO₂) and by the rate at which CO₂ diffuses to the site of carboxylation ("supply" of CO₂). The rate of supply is determined by the CO₂ gradient between the ambient air and the site of fixation divided by the resistance to CO₂ flux which occurs along this gradient. Thus,

$$\text{Rate of CO}_2 \text{ supply} = (C_a - C_c)/R_t \quad (3.1)$$

where C_a is the pCO₂ in the air outside the leaf boundary layer and R_t is the total resistance to CO₂ flux between C_a and C_c. R_t is composed of several resistances in series (boundary layer, stomatal, mesophyll) of which only stomatal resistance responds directly to varying CO₂.

Fig (3.1), adapted from Farquhar and Sharkey (1982), depicts graphically the relationship between leaf biochemistry (the "demand" function) and diffusion processes (the "supply" function). The "demand" function is curvilinear and depicts CO₂ assimilation at any given value of C_c. The "supply" function, represented by Eqn (3.1), is a straight line with X-intercept at C_c=C_a and slope equal to -1/R_t. The intercept of the supply and demand functions determines the operational C_c and thus the rate of assimilation (A). Net CO₂ assimilation is inversely related to the resistance to CO₂ flux. To conform with common practice, we replace resistance with a conductance term

Figure 3.1: Graphical depiction of the interaction between leaf biochemistry ("demand") and CO_2 diffusion ("supply"), which determines the actual $p\text{CO}_2$ at the site of fixation (C_c) and the rate of CO_2 assimilation (A) for a given ambient $p\text{CO}_2$ (C_a), in this case approximately 350 μbar . (Adapted from Farquhar and Sharkey 1982)

($g_t=1/R_t$), which is related directly to assimilation. In the following, we assume that C_i , the $p\text{CO}_2$ in the intercellular air space, is equal to C_c . This involves the implicit assumption that the resistance to CO_2 flux between C_i and C_c is zero; although obviously not strictly valid (Evans *et al.* 1986), this assumption simplifies the analysis without affecting model predictions. The consequences of relaxing this assumption are considered in detail in Section 3.4.

In order to predict changes in photosynthesis in response to global change, the effect of CO_2 on both leaf biochemistry and stomatal resistance must be addressed. Furthermore, it is important to distinguish between immediate or short-term effects of increasing CO_2 on leaf performance and the longer-term effects resulting from growth in an elevated CO_2 atmosphere. CO_2 is a primary substrate of the photosynthetic reactions, and any change in the CO_2 concentration is immediately translated via biochemical reactions into an observed change in photosynthetic rate. This short-term CO_2 -dependency must be incorporated into the model structure (i.e., equations describing the biochemistry of photosynthesis) and applies equally to leaves of plants grown in an elevated or ambient CO_2 environment. Additionally, leaves of plants grown under elevated CO_2 frequently undergo quantitative changes in the amount of key photosynthetic enzymes, chlorophyll, etc. These long-term effects of growth at elevated CO_2 will be manifested as changes in model parameters. The challenge is to determine how model parameters change for different growth forms, species, etc., as a result of growth in an elevated CO_2 environment, and ultimately to identify those factors which control the way in which the photosynthetic apparatus responds.

3.1.3 Potential short-term effects of doubling CO_2

In the short term, stomata respond rapidly to changes in ambient CO_2 but the biochemical properties of the leaf, i.e. concentrations of enzymes, chlorophyll, etc.,

are fixed. Thus, the change in photosynthesis due to a sudden increase in ambient CO_2 depends on the shape of the demand function (fixed in the short-term) and the response of the supply function to changing CO_2 . Several possible results of a short-term doubling of CO_2 (from 340 to 680 μbar) are illustrated in Fig (3.2), which depicts two leaves with different demand functions. At 340 μbar CO_2 , for supply function (a), both leaves photosynthesize at a rate of 16-17 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at a C_i of ≈ 225 μbar . If we double CO_2 , but maintain the same rate of supply (b), the leaf in panel A attains a rate of only 22 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ($C_i \approx 525$) while leaf B achieves a rate of 30 ($C_i \approx 460$). Stomatal conductance typically decreases by approx. 40% when leaves are exposed to doubled CO_2 (Morison 1985), as depicted by supply function (c), leading to a small photosynthetic decline for leaf A (to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at $C_i \approx 410$) but a large reduction for leaf B (to 24 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at $C_i \approx 355$). This simple example illustrates the complexity of predicting leaf response to increasing CO_2 and the necessity of modeling the effects of CO_2 on both leaf biochemistry and stomatal behavior.

3.1.4 Potential long-term effects of doubling CO_2

When plants are maintained in an elevated CO_2 atmosphere for a period of days to weeks, changes in leaf biochemistry occur, often resulting in reduced photosynthetic capacity, i.e., the demand function is lower over the entire range of C_i values, as shown in Fig (3.3). Depending on the extent to which both the demand and supply functions are reduced, the long-term response of net photosynthesis to a doubling of CO_2 (ΔA in Fig 3.3) may be substantial (Fig 3.3A) or relatively small (Fig 3.3B). In some cases (not shown), the increase in C_i which occurs when plants are exposed to 680 μbar CO_2 is insufficient to compensate for the effects of a greatly decreased demand function, and net photosynthesis of plants grown and measured at 680 μbar is actually less than that of plants grown and measured

Figure 3.2: Supply and demand functions of photosynthesis as in Fig (3.1) showing the response to short-term doubling of CO_2 for two hypothetical leaves. Stimulation of photosynthesis may be relatively small (Panel A) or quite large (Panel B), depending on the shape of the demand function. Supply functions (a) and (b) represent identical values of leaf conductance. Supply function (c) represents a typical decline in leaf conductance associated with $C_a=680 \mu\text{bar}$.

Figure 3.3: Supply and demand functions of photosynthesis as in Fig (3.1), illustrating the combined effects of reducing both the supply and demand functions as a result of long-term exposure to doubled CO_2 . Stimulation of assimilation (ΔA) may be substantial (Panel A) or slight (Panel B), depending primarily on the amount of change in the demand function.

at 340 μbar (i.e., ΔA is negative).

The photosynthesis model has been validated under current CO_2 levels (Harley *et al.* 1986; Harley and Tenhunen 1991) and responds realistically to short-term increases in C_i . We believe that the model, properly parameterized, is equally capable of simulating photosynthetic behavior of leaves following long-term exposure to elevated CO_2 . However, the changes in photosynthetic response resulting from long-term exposure to elevated CO_2 , sometimes referred to as acclimation, are not yet predictable *a priori*, due largely to a data base neither sufficiently detailed to allow physiological mechanisms to be elucidated nor large enough to allow patterns of change to emerge. In Section 3.3, we describe results of an experiment to determine the changes in model parameters which occur in leaves of cotton grown at 650 vs. 350 μbar CO_2 . First, however, we describe the integrated photosynthesis and stomatal conductance models in detail.

3.2.0 Model Description

To model the biochemistry of C_3 photosynthesis, we use the model presented by Farquhar *et al.* (1980), modified to include a potential phosphate limitation arising from the failure of triose phosphate utilization (starch and sucrose production) to keep up with triose phosphate production in the Calvin cycle (Sharkey 1985a,b).

The demand function allows us to predict net photosynthesis for any value of C_i . As shown in Fig (3.1), however, the C_i at which a leaf operates results from the interaction of the demand function with a function describing the rate of CO_2 supply. This interaction is described by,

$$C_i = C_a - \frac{A \cdot 1.6}{g_s} \quad (3.2)$$

where g_s is stomatal conductance to water vapor and the factor 1.6 corrects for the difference in diffusivity between CO_2 and H_2O .

To be useful in predicting leaf response to varying environmental conditions, therefore, the model of CO_2 assimilation must be integrated with a model of stomatal

behavior. Whereas the biochemical processes underlying photosynthesis are well understood and provide a solid basis upon which to build a mechanistic model, the mechanism of stomatal action and the effects of irradiance, temperature, humidity and CO_2 remain unclear. Based on the observation that stomatal conductance and net assimilation are usually strongly correlated (Wong *et al.* 1979), we have adopted the empirical model of stomatal behavior proposed by Ball *et al.* (1987), in which conductance is assumed to be proportional to net CO_2 assimilation, modified by the ratio of relative humidity to CO_2 concentration at the leaf surface.

3.2.1 Modeling the Demand Function of Photosynthesis

Although CO_2 fixation in the chloroplast is a complex process, dependent on light energy absorption and transduction and a series of biochemical steps, a convincing case can be made that C_3 photosynthesis may be interpreted based solely on the kinetics of Rubisco (Woodrow and Berry 1988; Farquhar *et al.* 1980). The rate of carboxylation obeys competitive Michaelis-Menten kinetics, and depends on the partial pressures of the competing gaseous substrates, CO_2 and O_2 , and on the ratio of ribulose-1,5-bisphosphate (RuBP) concentration to enzyme active sites. The model incorporates the effects of irradiance on electron transport, and the effects of temperature on both electron transport and leaf biochemistry at the levels of Rubisco and RuBP regeneration in the Calvin cycle. In addition, the level of inorganic phosphate (Pi) may limit photosynthesis at elevated CO_2 and/or low temperatures (Sage and Sharkey 1987). The interaction of these potential limitations is depicted in Fig (3.4) for two values of irradiance. At low irradiance, the rate of RuBP regeneration, driven by electron transport, becomes limiting at high CO_2 ; at high irradiance and high CO_2 , phosphate limits the carboxylation reaction.

Net CO_2 assimilation (A) may be expressed,

$$A = V_c - 0.5V_o - R_d \quad (3.3)$$

Figure 3.4: Diagrammatic representation of the behavior of the "demand" function of photosynthesis. At low C_i , the activity of Rubisco limits carboxylation. As C_i increases, either RuBP (at low light, bottom panel) or inorganic phosphate (Pi) (at high light, top panel) becomes limiting. R_d is mitochondrial respiration continuing in the light. The point of transition between biochemical limitations is shown on each panel.

where V_c and V_o are rates of carboxylation and oxygenation at Rubisco, and R_d is the rate of CO_2 evolution in the light which results from processes other than photorespiration. The factor 0.5 reflects the fact that one molecule of CO_2 is released in photorespiration for each two oxygenations of Rubisco. Eqn (3.3) may be rewritten,

$$A = V_c \left(1 - \frac{0.5 \cdot O}{\tau \cdot C_i} \right) - R_d \quad (3.4)$$

where C_i and O are the pCO_2 and pO_2 in the intercellular air space, and τ is the specificity factor for Rubisco (Jordan and Ogren 1984). The rate of carboxylation, V_c , is assumed to be limited by one of three factors, discussed below; i.e.,

$$V_c = \min(W_c, W_j, W_p) \quad (3.5)$$

where $\min\{ \}$ denotes "the minimum of". Combining Eqns 3.4 and 3.5,

$$A = \left(1 - \frac{0.5 \cdot O}{\tau \cdot C_i} \right) \cdot \min(W_c, W_j, W_p) - R_d \quad (3.6)$$

W_c is the rate of carboxylation limited solely by the amount, activation state and kinetic properties of Rubisco, and obeys Michaelis-Menten kinetics, competitive with respect to CO_2 and O_2 ; i.e.,

$$W_c = \frac{V_{cmax} C_i}{C_i + K_c(1 + O/K_o)} \quad (3.7)$$

where V_{cmax} is the maximum rate of carboxylation and K_c and K_o are Michaelis constants for carboxylation and oxygenation, respectively. The rate of carboxylation limited solely by the rate of RuBP regeneration in the Calvin cycle, W_j , is mediated by the rate of electron transport (J).

$$W_j = \frac{J \cdot C_i}{4(C_i + O/\tau)} \quad (3.8)$$

Implicit in this formulation for W_j is the assumption that four electrons generate sufficient ATP and NADPH for the regeneration of RuBP in the Calvin cycle (Farquhar and von Caemmerer 1982).

W_p , the rate of carboxylation limited solely by inorganic phosphate, is expressed,

$$W_p = 3 \cdot TPU + \frac{V_o}{2} = 3 \cdot TPU + \frac{V_c \cdot 0.5 \cdot O}{C_i \cdot \tau} \quad (3.9)$$

where TPU is the rate of phosphate release in triose phosphate utilization (starch and sucrose production). This formulation, suggested by Sharkey (1985a) causes photosynthesis to become independent of both CO_2 and O_2 under conditions where P_i is limiting. This is contrary to considerable experimental data in which, under P_i -limited conditions, CO_2 assimilation is characterized by reversed sensitivity to CO_2 and O_2 ; i.e., assimilation decreases with increasing CO_2 and increases with decreasing O_2 . Harley and Sharkey (1991) developed a modified description of net photosynthesis when P_i is limiting, which qualitatively describes such behavior and is presented in abbreviated form in Sec. 3.4.

The only dependence on light (I) in the model is on electron transport, based on Smith (1937),

$$J = \frac{\alpha \cdot I}{\left(1 + \frac{\alpha^2 I^2}{J_{max}^2} \right)^{1/2}} \quad (3.10)$$

where α is the quantum efficiency of electron transport on an incident light basis (mol electrons/mol photons) and J_{max} is the light-saturated rate of electron transport.

The temperature dependence of the parameters K_c , K_o , R_d and τ is each described by an exponential function,

$$\text{Parameter} = \exp[c \cdot \Delta H_a / (R \cdot T_k)] \quad (3.11)$$

where "c" is a scaling constant, ΔH_a is the activation energy, R is the gas constant ($8.31 \text{ J K}^{-1} \text{ mol}^{-1}$) and T_k is leaf temperature ($^{\circ}\text{K}$).

Note that because τ is a declining function of temperature, its "activation energy" is negative. The temperature dependence of the parameters J_{max} , V_{cmax} and TPU is described as follows, after Johnson, Eyring and Williams (1942).

$$\text{Param} = \frac{\exp[c \cdot \Delta H_a / (R \cdot T_k)]}{1 + \exp[(\Delta S T_k - \Delta H_d) / (R \cdot T_k)]} \quad (3.12)$$

where ΔH_d is the energy of deactivation and ΔS is an entropy term.

A complete list of model parameters and their units is given in Table 3.1 in Section 3.3. Further detail is provided by Farquhar

et al. (1982), Sharkey (1985a) and Harley and Tenhunen (1991).

3.2.2 Modeling the Supply Function of Photosynthesis

Ball *et al.* (1987) developed the following empirical model to describe stomatal conductance:

$$g_s = g_0 + g_1 \cdot A \cdot \frac{h_s}{C_s} \quad (3.13)$$

where h_s and C_s are relative humidity pCO_2 , respectively, at the leaf surface (i.e., inside the leaf boundary layer). The parameter g_0 is the minimum stomatal conductance to H_2O vapor when $A=0$ at the light compensation point, and g_1 is an empirical coefficient which represents the composite sensitivity of conductance to assimilation, pCO_2 , humidity and temperature (Ball *et al.* 1987). We have modified this model by using C_a and RH (relative humidity in %) in the air outside the boundary layer. Thus,

$$g_s = g_0 + g_1 \cdot A \cdot \frac{RH}{C_a} \quad (3.14)$$

Because A and g_s are not independent, the value of C_i must be determined in an iterative fashion. C_i is systematically varied until a value is arrived at which yields values of A and g_s , calculated using Eqns (3.6) and (3.14), respectively, which simultaneously satisfy the relationship in Eqn (3.2).

3.3.0 Model Parameterization for Leaves of Cotton Plants Grown under Ambient and Elevated CO_2

In this section we demonstrate that the C_3 photosynthesis model described above is an excellent vehicle for describing the photosynthetic characteristics of cotton plants grown under both ambient and elevated CO_2 , and that the traits of leaves grown at ambient and high CO_2 may be compared by comparing the values of key model parameters. We also demonstrate that, as a result of the linear relationship between leaf N and key model parameters, measurements of leaf N concentration can be used to predict photosynthetic behavior of cotton. Material included in this section has

been accepted for publication elsewhere (Harley *et al.* 1991b).

3.3.1 Experimental Methods.

Seeds of cotton (*Gossypium hirsutum*) were planted in a mixture of vermiculite and gravel (1:1 by volume) in 3.5 l plastic pots and placed in a greenhouse at the Duke University Phytotron. After germination, seedlings were thinned to one per pot. Five days after planting, pots were placed in one of four CO_2 -controlled walk-in growth chambers, two of which were maintained at 350 μ bar CO_2 and two at 650 μ bar CO_2 . Air temperature was constant at 29°C in all chambers, and plants received a 14-hr. photoperiod, with daytime photon flux density (PFD) of $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. All pots were watered to saturation with 1/2 strength Hoagland's solution each morning and with distilled water each afternoon.

Photosynthetic measurements were conducted using an open infrared gas analysis system described previously (Thomas and Strain 1991) in which CO_2 exchange was measured using an infrared gas analyzer (Analytical Development Corp., Hoddesdon, UK) and water exchange using dew point hygrometers (General Eastern, Watertown, MA, USA). Except where noted, measurements were made on the youngest fully expanded leaves, and leaf temperature was maintained at $29.0 \pm 0.3^\circ\text{C}$, PFD at approx. $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and leaf to air vapor pressure deficit at approx. 1.8 kPa. In experiments to determine the temperature dependence of several model parameters, leaf temperature was varied between 18° and 35°C. Additional experiments to determine the nitrogen dependences of model parameters were conducted on leaves beyond the age of full expansion on plants up to 35 days old. Rates of net assimilation, transpiration, stomatal conductance and intercellular CO_2 were calculated following von Caemmerer and Farquhar (1981).

Six leaf disks to be used for leaf nitrogen assays were removed from all experimental leaves using a 0.65 cm^2 cork borer. Tissue used in nitrogen determinations was dried to constant dry weight at 70°C,

Table 3.1: List of model parameters and the parameters used to describe their temperature dependencies. Those parameters in parentheses are held constant in this version of the model; all other values must be determined for each leaf or group of leaves as described in the text. (Adapted from Harley *et al.* 1991b)

Parameter	Units	Temperature Parameters	Value 350 μ bar	Value 650 μ bar	Units
K_c	μ bar CO_2	$c(K_c)$ $\Delta H_a(K_c)$	(38.09) (80470)		-- J mol^{-1}
K_o	mbar O_2	$c(K_o)$ $\Delta H_a(K_o)$	(11.89) (14507)		-- J mol^{-1}
τ	--	$c(\tau)$ $\Delta H_a(\tau)$	(-3,9489) (-28990)		-- J mol^{-1}
R_d	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$c(R_d)$ $\Delta H_a(R_d)$	(Not used; $R_d=0.82$)		-- J mol^{-1}
V_{cmax}	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$c(V_{cmax})$ $\Delta H_a(V_{cmax})$ $\Delta H_d(V_{cmax})$ $\Delta S(V_{cmax})$	51.07 116,300 202,900 650	49.46 112,400 201,700 650	-- J mol^{-1} J mol^{-1} $\text{J } ^\circ\text{K}^{-1} \text{ mol}^{-1}$
J_{max}	$\mu\text{mol electrons m}^{-2} \text{ s}^{-1}$	$c(J_{max})$ $\Delta H_a(J_{max})$ $\Delta H_d(J_{max})$ $\Delta S(J_{max})$	37.08 79,500 201,000 650	32.88 69,100 201,100 650	-- J mol^{-1} J mol^{-1} $\text{J } ^\circ\text{K}^{-1} \text{ mol}^{-1}$
TPU	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	$c(\text{TPU})$ $\Delta H_a(\text{TPU})$ $\Delta H_d(\text{TPU})$ $\Delta S(\text{TPU})$	23.59 53,100 201,800 650	23.59 53,000 201,600 650	-- J mol^{-1} J mol^{-1} $\text{J } ^\circ\text{K}^{-1} \text{ mol}^{-1}$
α	$\frac{\text{mol electrons}}{\text{mol photons}}$	--	(0.24)		--
g_0	$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$	--	81.1	72.8	--
g_1	$\frac{\text{mmol H}_2\text{O} \cdot \mu\text{bar CO}_2}{\mu\text{mol CO}_2}$	--	95.8	89.2	--

then digested in a Technicon block digester using a sulphuric acid-hydrogen peroxide flux. Total leaf N was measured using a Technicon TRAACS 800 Continuous Flow Analytical System (Bran+Luebbe, Elmsford, NY, USA).

3.3.2 Model Parameterization Techniques

At a given temperature, the biochemical model incorporates eight parameters (Table 3.1). K_C , K_O and τ reflect intrinsic kinetic properties of Rubisco and are assumed to be the same for all C_3 species.

The enzyme specificity factor, τ , has been determined for several species, based on whole leaf gas exchange and *in vitro* enzyme assays, and is remarkably constant across C_3 species, varying only with temperature (Jordan and Ogren 1984; Woodrow and Berry 1988). On the other hand, *in vitro* determinations of K_C obtained from different C_3 species have shown considerable variation (Keys 1986; Evans and Seemann 1984). Parameterizing the model using only whole leaf gas exchange data, we are forced to accept published values for K_C and K_O .

Temperature dependences of K_C , K_O and τ used in our analysis (Table 3.1) are based on measured values of Jordan and Ogren (1984).

At high light and C_i values below approx. 250 μbar , Rubisco is assumed to be limiting. Thus, the rate of carboxylation is equal to W_c . Combining Eqns (3.4) and (3.7),

$$A = \frac{V_{c\max} C_i}{C_i + K_C(1 + O/K_O)} \cdot \left(1 - \frac{0.5 \cdot O}{\tau \cdot C_i}\right) - R_d \quad (3.15)$$

where $V_{c\max}$ and R_d are the only unknowns. Using only data collected at PFD greater than 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and C_i less than 200 μbar , non-linear least squares regression techniques were used to determine best fit values of $V_{c\max}$ and R_d in Eqn (3.15).

As C_i increases a point is reached at which carboxylation becomes limited either by the rate of electron transport (W_j) or by the turnover rate of inorganic phosphate (W_p). Having determined values for $V_{c\max}$ and R_d for a given curve, non-linear least squares techniques were used to fit entire A

vs. C_i curves to Eqn (3.6) in order to determine best fit estimates of $J_{\max}$ and TPU.

The efficiency of light energy conversion on an incident light basis, α , was not measured but is fixed at 0.24 mol electrons/mol photons, based on a typical quantum use efficiency (absorbed light basis) of 0.073 mol CO_2 /mol photons (Ehleringer and Björkman 1977) and a leaf absorptance of 83%.

The slope (g_0) and intercept (g_1) of the function in Eqn (3.14) may be determined graphically from a plot of g_s versus $(A \cdot RH/C_a)$, where g_s is allowed to vary with changes in PFD, C_a , leaf temperature and humidity of the incoming air.

3.3.3 Results

On the need to incorporate a phosphate limitation in the model. In previous studies (Harley *et al.* 1985, 1986) phosphate limitations did not play an important role, and it was possible to obtain adequate model fits to experimental data without invoking W_p (Eqn 3.9). In this study, net photosynthesis measured at 20 mbar O_2 increased rapidly with increasing C_i , attaining a maximum when $C_i \approx 200 \mu\text{bar}$. Photosynthesis then exhibited a gradual decline with further increases in C_i , resulting in a rapid convergence of A vs. C_i curves measured at 20 and 200 mbar O_2 (Fig 3.5). This lack of O_2 sensitivity indicates that Pi limits carboxylation at high values of C_i and high light (Sharkey 1985a,b). Attempts at fitting pairs of A vs. C_i curves measured at 20 and 200 μbar O_2 consistently resulted in large underestimates throughout the curved portion of the response at 200 mbar O_2 and overestimates at high C_i at 20 mbar O_2 (Fig 3.5, dashed lines) unless a Pi limitation (Eqn 3.9) was incorporated in the model (Fig 3.5, solid lines). All subsequent parameter estimates and model fits were made assuming that Pi becomes limiting at high C_i .

Model parameterization at the growth temperature. We measured A vs. C_i curves on 3 leaves from each treatment 17, 25 and 35 days after planting, and obtained

Figure 3.5: A vs. C_i response curves measured at both 20 and 200 mbar O_2 on a leaf of a representative cotton plant grown at 350 (A) and 650 $\mu\text{bar CO}_2$ (B). Dashed lines indicate model fit assuming no phosphate limitation to carboxylation; solid lines indicate model fits assuming a phosphate limitation at high CO_2 . (Adapted from Harley et al. 1991b)

Figure 3.6: Measured dark respiration as a function of leaf temperature for leaves of plants grown in 350 and 650 $\mu\text{bar CO}_2$, with fits to Eqn (3.11) using parameter values shown. Inset: Estimates of residual respiration (R_d), determined from A vs. C_i curves, plotted as a function of leaf temperature. (Adapted from Harley et al. 1991b)

least-squares estimates of V_{cmax} and R_d for each leaf (not shown). Estimates of R_d were quite variable, averaging 0.82 ± 0.44 . We elected to hold R_d constant and equal to 0.82, and obtained new estimates of V_{cmax} for each curve. Having set the values of V_{cmax} and R_d for each curve, estimates of J_{max} and TPU were also obtained (not shown).

Two-way analysis of variance applied to V_{cmax} , J_{max} and TPU, in which plant age and CO_2 treatment were the independent variables, indicated a significant effect of plant age ($P < 0.005$) with all parameters declining over time. There was no significant effect (95% confidence level) of growth CO_2 on any of the three parameters, although V_{cmax} was reduced in plants grown at high CO_2 at all three measurement times by an average 10.2% ($P = 0.064$).

Temperature dependence of model parameters. Measured dark respiration increased exponentially with temperature (Fig 3.6). However, R_d , estimated by least-squares fits to A vs. C_i curves, exhibited no such pattern (Fig 3.6, inset). Holding R_d constant at the mean value ($R_d = 0.82$), best fit estimates of V_{cmax} , J_{max} and TPU were obtained from A vs. C_i curves measured at different temperatures. These are plotted as a function of leaf temperature in Fig (3.7). Temperature data for each parameter were fit to Eqn (3.12), resulting in fits and parameter values shown. To simplify the fitting procedure, the entropy term ΔS was held constant at $650 \text{ J K}^{-1} \text{ mol}^{-1}$.

Nitrogen dependence of model parameters. To establish the relationship between model parameters and leaf N, we needed to evaluate leaves with as wide a range of N values as possible. Recognizing that photosynthesis and leaf N decline with leaf age beyond full expansion, we measured 20 additional A vs. C_i curves on leaves up to 30 days old, from both CO_2 growth treatments. Least squares estimates of parameter values obtained on these leaves were combined with values obtained previously from young leaves which had recently completed expansion, and plots of

V_{cmax} , J_{max} and TPU as a function of total leaf N, expressed on the basis of leaf area (g N m^{-2}), are shown in Fig (3.8). Analysis of covariance demonstrated no effect of CO_2 concentration during growth on the relationship between either J_{max} or TPU and leaf N; the slope of the relationship between V_{cmax} and leaf N however, was significantly lower ($P = 0.033$) for leaves of plants grown in high CO_2 (means of 60.0 vs. $52.8 \text{ } \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1} \text{ N}$). Parameter values plotted versus N on a leaf weight basis (g N g DW^{-1}) exhibited considerably more scatter [r^2 values: TPU=0.65; J_{max} =0.69; V_{cmax} =0.74] as well as a significant effect of growth CO_2 . This was clearly due to the confounding effect of leaf starch, high quantities of which accumulate in leaves of cotton plants grown under high CO_2 (Thomas and Strain 1991).

Leaf conductance model. For each growth CO_2 treatment, stomatal conductance data were pooled from a large number of gas exchange measurements, in which conductance varied in response to leaf temperature, measurement CO_2 and PFD. Stomatal conductance was plotted versus $(A \cdot RH / C_a)$ and the intercept, g_0 , and slope, g_1 , were determined by linear regression (Eqn 3.14). The relationship was more robust if data with $C_a < 300 \text{ } \mu\text{bar}$ were excluded, and such data for both CO_2 treatments are plotted in Fig (3.9). The slope of the response for plants grown at $650 \text{ } \mu\text{bar}$ was slightly lower, but the difference was not significant at the 95% confidence level ($P = 0.064$).

Model validation. The model was parameterized using young fully-expanded leaves of 25-33 day old cotton plants. Because most of the data collected was used to parameterize the model, a true validation against an independently measured data set was not possible. However, pooling all the data, for which C_a , PFD, temperature and humidity all varied, and comparing measured values of net CO_2 assimilation, stomatal conductance and C_i with values predicted by the model (Fig 3.10), we could visually assess the ability of the model to simulate measured data. Model predictions were obtained as follows. Inputs to the model

Figure 3.7: Estimates of V_{cmax} , J_{max} and TPU, obtained by non-linear least squares regression, for leaves of plants grown in 350 and 650 μbar CO_2 , plotted as a function of leaf temperature. Curves are least-squares fits to Eqn (3.12) for each growth treatment, using parameter values shown. (Adapted from Harley et al. 1991b)

Figure 3.8: Estimates of V_{cmax} , J_{max} and TPU, plotted versus total leaf N. Square symbols are estimates obtained from recently fully-expanded leaves; round symbols are from leaves up to 18 days after full expansion. For V_{cmax} , independent linear regressions were obtained for leaves grown in 350 (open symbols) and 650 μbar CO_2 (filled symbols). Regressions to J_{max} and TPU use combined 350 and 650 μbar CO_2 data. (Adapted from Harley et al. 1991b)

included C_a , PFD, leaf temperature and relative humidity. Biochemical model parameters were obtained using Eqns (3.11) and (3.12) and the appropriate temperature parameters in Table (3.1), and the appropriate slope and intercept of the conductance model were used. For each set of inputs, the model then iterated for that value of C_i which satisfied simultaneously Eqns (3.2), (3.6) and (3.14). Given that C_i value, A and g_s were calculated. Due to the limitations of the conductance model, only data for which $C_a > 300 \mu\text{bar}$ were used.

In addition, we assessed the potential of the model to predict CO_2 assimilation based only on measured leaf N values. In this case, values of V_{max} , J_{max} and TPU were derived on the basis of the linear regressions in Fig (3.8). Model predictions were generated as above, but using only data obtained at 29°C , the temperature for which N dependences were determined. Measured CO_2 assimilation and stomatal conductance are plotted versus predictions based on leaf N in Fig (3.11).

3.3.4 Discussion of cotton results

In several studies, cotton has responded very strongly to elevated CO_2 levels during growth. In a survey of a large number of crops, Kimball (1983) found that a doubling of CO_2 produced an average 33% increase in crop yield, but cotton has consistently shown a much stronger response. In a glasshouse study, Mauney *et al.* (1978) found that an approximate doubling of CO_2 increased lint and seed yields by 179% and 140%, respectively. Field studies (Kimball *et al.* 1983) showed a 92% increase in seedcotton yield. Cure and Acock (1986), based on a literature survey, report an average increase in biomass accumulation for cotton of 84% (± 126). Wong (1979) grew cotton at 330 and 640 μbar CO_2 and four levels of nitrogen. After forty days, dry weight in elevated CO_2 was approx. twice that in ambient CO_2 , regardless of nitrogen treatment. Wong (1990) makes the valid point that much of the reported dry weight increase in plants grown in 640 μbar consists of non-structural carbohydrate, primarily

starch. If non-structural carbohydrates are eliminated from the growth analysis, however, the increase in total structural biomass remains substantial in elevated CO_2 , averaging over 80% across nitrogen treatments. Thomas and Strain (1991) measured 30% more biomass in plants grown in 650 μbar CO_2 than in plants grown in 350 μbar after 36 days. What attributes of cotton confer this ability to respond more strongly to elevated CO_2 than many other plants? Although a number of factors, including allocation patterns, must be considered, we focus here on net photosynthesis.

Long-term growth at elevated CO_2 often results in a decline in photosynthetic capacity, associated with starch accumulation, anatomical changes and reduced enzyme activity and chlorophyll content (e.g., Aoki and Yabuki 1977; Sage *et al.* 1989; von Caemmerer and Farquhar 1984; Wulff and Strain 1982; summarized for crops by Cure and Acock 1986). This reduction in assimilation capacity has been demonstrated for many species and may occasionally result in assimilation rates of acclimated plants grown and measured at 650 μbar CO_2 which are less than those of plants grown and measured at 350 μbar (von Caemmerer and Farquhar 1984; Larigauderie *et al.* 1988).

Previous studies to determine the effect of growth at elevated CO_2 on photosynthetic capacity in cotton plants have yielded conflicting results. Based on four studies, Cure and Acock (1986) report an average increase of 60% (± 14) in net photosynthesis in cotton during short-term exposure to doubled CO_2 , but only an average 13% (± 19) increase after plants had acclimated for several weeks to elevated CO_2 . Sasek *et al.* (1985) found that net photosynthesis in cotton plants grown at 350 μbar CO_2 increased by 50% when exposed to 1000 μbar CO_2 . However, plants grown continuously at 1000 μbar had rates only 15% higher at 1000 μbar than those grown and measured at 350. They attributed this decline to changes in leaf biochemistry associated with accumulation of starch in the leaves of plants grown at high CO_2 .

Radin *et al.* (1987), on the other hand, grew cotton in the field in open-top chambers, and found that photosynthetic

Figure 3.9: Measured stomatal conductance to water vapor plotted against the product of Assimilation $\times$ relative humidity divided by external $p(\text{CO}_2)$ for leaves of plants grown in 350 and 650 $\mu\text{bar CO}_2$. Data for which $C_a < 300 \mu\text{bar}$ were excluded. Lines are fits to Eqn (3.14). (Adapted from Harley et al. 1991b)

Figure 3.10: Comparison of measured values of net photosynthesis, stomatal conductance and C_i with values predicted by the fully parameterized model, using parameter values in Table (3.1) for leaves of plants grown in 350 and 650 $\mu\text{bar CO}_2$. Data for which $C_a < 300 \mu\text{bar}$ were excluded. (Adapted from Harley et al. 1991b)

capacity in leaves of plants grown at 350, 500 and 650 μbar CO_2 remained essentially the same, despite the accumulation of starch to high levels in leaves of plants grown in high CO_2 , such that photosynthesis of leaves in CO_2 -enriched chambers was 58% (500 μbar CO_2) and 76% (650 μbar CO_2) higher than in ambient chambers.

These contradictory results are at least partially explained by Thomas and Strain (1991) who demonstrate conclusively that a decline in photosynthetic capacity is induced in potted cotton plants as the root system becomes too large for the pot, and that the photosynthetic decline is rapidly reversible if plants are transplanted to larger pots. Thus, the results of Sasek *et al.* (1985) may be an artifact resulting from inadequate pot size, a consideration which must be born in mind when interpreting all CO_2 growth experiments in which plants are grown in relatively small pots. Plants grown under elevated CO_2 typically grow faster and exhibit higher root:shoot ratios, and so would be expected to outgrow their pots sooner than those grown at ambient CO_2 .

In this study, in which plants were grown in pots previously shown to be large enough to avoid pot size artifacts (Thomas and Strain 1991), there is only a slight indication that the photosynthetic properties of leaves changed as a result of CO_2 level during growth. Neither J_{max} nor TPU differed significantly between treatments; estimates of V_{cmax} were about 10% lower for plants grown at high CO_2 , but these differences were not significant at the 5% probability level ($P=0.064$). Stomatal conductance was reduced by about 23% when measured at 650 versus 350 μbar , regardless of CO_2 concentration during growth. This reduction is less than the 40% average reduction in conductance reported by Morison (1985) who summarized data from 16 C_3 and 9 C_4 species. The slope of the relationship between stomatal conductance and $A \cdot \text{RH}/C_a$ (Eqn 3.14) was slightly lower in plants grown in high CO_2 , but this difference was also not significant at the 5% level ($P=0.069$).

If we adopt the parameter set for 350 μbar grown plants (Table 3.1) we can employ the model to predict assimilation and

stomatal conductance at both $C_a=350$ and $C_a=650$ μbar (Fig 3.12). Given a leaf temperature of 29°C , PFD of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 50% relative humidity, $A_{350}=21.2$ ($C_i=261$) and $A_{650}=27.4$ ($C_i=499$) (Fig 3.12A). Thus, despite a 23% decline in stomatal conductance, short-term exposure to 650 μbar CO_2 results in a 30% increase in assimilation. If we use the parameter set for plants grown at 650 μbar CO_2 (Fig 3.12B), predicted assimilation at C_a of 650 μbar drops only slightly ($A_{650}=26.3$; $C_i=488$). Thus, declines in leaf photosynthetic capacity due to growth at 650 μbar CO_2 result in less than a 5% decrease in assimilation compared to non-acclimated plants.

Relationship between model parameters and leaf N. We parameterized our model for a limited set of leaves, i.e., recently fully expanded leaves of a given age (25-33 days). Model parameters obtained on fully expanded leaves declined over time and parameters also declined as leaves aged beyond full expansion. If the model is to be a useful tool for simulating whole canopy gas exchange over time, the nature of changes in model parameters will have to be addressed. However, parameterizing the model for even a limited subset of leaves is cumbersome, and we sought to determine the feasibility of predicting leaf parameters based on leaf N, which is easily measured.

For a given species, net photosynthesis, measured at ambient CO_2 , light saturation and in the normal temperature range, correlates strongly with measured leaf N, unless a large proportion of N has been invested in non-photosynthetic function, such as defense (Field and Mooney 1986), although Evans (1989) has shown that the relationship becomes more complex when plants are grown under widely different light regimes. That model parameters, based on allocation of proteins and other N-containing molecules, also correlate with N is not surprising, but we know of only one other study (Field 1983) which quantified the relationship.

The parameters V_{cmax} , J_{max} and TPU were linearly related with N (r^2 values >0.9 ; Fig 3.8) when leaf N content

Figure 3.11: Comparison of measured values of CO_2 assimilation and stomatal conductance with values predicted by the model, using parameter values based on regression equations of parameters against leaf N shown in Figure 3.8. All data obtained at 29°C ; data for which $C_a < 300 \mu\text{bar}$ were excluded. (Adapted from Harley et al. 1991b)

Figure 3.12: Model simulations of net photosynthesis as a function of ambient CO_2 , under growth PFD and temperature conditions, using fully parameterized model for plants grown at 350 (Panel A) and 650 $\mu\text{bar CO}_2$ (Panel B). Parameters are from Table (3.1). Shown are model predictions of CO_2 assimilation (A), stomatal conductance (g_s) and C_i , assuming ambient CO_2 of 350 or 650 μbar (Panel A) or 650 μbar (Panel B). (Adapted from Harley et al. 1991b)

varied with leaf age. The fact that these three parameters, related to the three potential biochemical limitations to assimilation, varied in parallel suggests that leaf N exerts a major controlling role in each process, and that the allocation of N is highly regulated such that these limitations remain similarly balanced as total leaf N varies.

The V_{cmax} vs. N relationship was reduced by 12% ($P=0.033$) in leaves grown at high versus low CO_2 . Thus, for a given amount of leaf N, leaves of plants grown in high CO_2 attain slightly less Rubisco activity than those of plants grown in ambient CO_2 . This could result from a decline in either the amount or activation state of the enzyme, both of which have been shown to occur at high CO_2 (Sage *et al.* 1989), but we are unable to distinguish between the two.

Model strengths and weaknesses.

The Farquhar photosynthesis model has been widely used to interpret measured photosynthetic data and to analyze the potential limitations to CO_2 uptake under differing environmental conditions. We have shown that, in the case of cotton, it is important to include a potential limitation due to Pi, which may become limiting if the rate of Pi release during triose phosphate utilization (sucrose and starch synthesis) fails to keep pace with the rate of triose phosphate production in the Calvin cycle.

Estimates of model parameters were obtained relatively easily from gas exchange data alone, although estimates of R_d were quite variable and did not exhibit the expected relationship with either leaf temperature or leaf N, forcing us to use an average value of 0.82 for all leaves. Any error in predicting assimilation introduced by doing so (maximum error of $\approx 1.0 \mu mol m^{-2} s^{-1}$) is small relative to net assimilation in cotton under most conditions, although at low PFD the error may become significant. R_d has been determined effectively from gas exchange data previously (Brooks and Farquhar 1985) but the determination is difficult and sensitive to small errors in measurement.

The Ball *et al.* (1987) model of stomatal conductance, modified slightly

here, remains empirical, and in our data set the linear relationship suggested by the model breaks down at $C_a < 300 \mu bar$. Leuning (1990) excluded data with $C_s < 150 \mu bar$ when calculating model parameters, and Ball and Berry (1991) did similarly. The exclusion of data with low C_s or C_a seems justifiable if the model is only used to predict assimilation and conductance at ambient CO_2 or above. Leuning (1990) successfully employed the stomatal model of Ball *et al.* (1987) in attempting to model simultaneously photosynthesis and conductance in *Eucalyptus grandis*, although he suggested that model performance was improved by replacing C_s (Eqn 3.13) with $C_s - \Gamma$, where Γ is the CO_2 compensation point. In our study, if only data for which $C_a > 300 \mu bar$ are used, the interaction between the biochemical model and the empirical stomatal model is sufficiently robust to provide reasonable estimates of C_i values and associated assimilation rates whether parameter values are estimated from temperature (Fig 3.10) or on the basis of leaf N (Fig 3.11).

3.3.5 Summary

We have shown that the integrated models of Farquhar *et al.* (1980) and Ball *et al.* (1987) are equally applicable to plants grown at ambient and elevated CO_2 , and that changes in photosynthetic characteristics resulting from growth treatment can be incorporated via changes in model parameters. In this study, however, and despite the accumulation of starch levels exceeding $50 g/m^2$ (Thomas and Strain 1991), the photosynthetic properties of cotton were only slightly different in plants grown at $650 \mu bar$ CO_2 than in plants grown at $350 \mu bar$. The parameter V_{cmax} declined by approx. 10% but this had little impact on assimilation since leaves generally operated at sufficiently high values of C_i that W_c was not limiting. Stomatal conductance measured at $650 \mu bar$ CO_2 was reduced by approx. 23% compared with that measured at $350 \mu bar$, regardless of the CO_2 level during growth; i.e., there was no acclimation of stomatal behavior. Despite this reduction in leaf conductance, C_i remained over $200 \mu bar$

higher at 650 μ bar CO₂ than at ambient CO₂. Because the biochemistry of photosynthesis in cotton undergoes very little change when plants are grown at elevated CO₂, leaves can take considerable advantage of the extra CO₂ made available, resulting in approx. a 25% increase in net assimilation rate, measured at the conditions experienced during growth.

3.4.0 An Improvement to the Model of C₃ Photosynthesis under Phosphate-limited Conditions.

Material in this section has been previously published (Harley and Sharkey 1991).

Introduction. One of the functions of modeling is to summarize existing knowledge, often employing simplifying assumptions; a second function is to generate new hypotheses. The C₃ leaf model originally proposed by Farquhar *et al.* (1980) has performed well in both areas, generating considerable research which has enhanced our understanding of factors limiting assimilation and their interactions. When data obtained at high CO₂, high light and low temperature proved inconsistent with the model, it was modified to include limitations arising from inadequate utilization of triose phosphate (Sharkey 1985a). The formulation presented by Sharkey establishes a Pi-limited ceiling for assimilation but does not lead to reversed sensitivity of assimilation to either CO₂ or O₂, as has been frequently observed. We propose a simple modification which explains the reversed sensitivity of net photosynthesis to both CO₂ and O₂ under conditions where Pi limits assimilation.

Sharkey (1985a) suggested that if C_i and light are high enough, the rate of release of inorganic phosphate via triose phosphate utilization (i.e., starch and sucrose synthesis) may become inadequate to recycle the Pi sequestered in the production of triose phosphates, in which case Pi may become limiting to photosynthesis.

Based on the stoichiometry of Pi consumption and release in the integrated photosynthetic carbon reduction (PCR) and photorespiratory carbon oxidation (PCO)

cycles, and assuming that C is maximally conserved (i.e, three-fourths of the carbon lost to the chloroplast as glycolate is recycled as glycerate), the rate at which Pi is consumed is equal to $(V_c/3 - V_o/6)$ (Sharkey 1985a). If Pi is limiting, net Pi consumption must equal the rate of Pi release via triose phosphate utilization. Thus,

$$TPU = \frac{V_c}{3} - \frac{V_o}{6} \quad (3.16)$$

where TPU is the rate of triose phosphate utilization or starch and sucrose synthesis, and

$$V_c = W_p = 3 \cdot TPU + 0.5V_o \quad (3.17)$$

This formulation for carboxylation under Pi-limited conditions, identical to Eqn (3.9) places a ceiling on net photosynthesis such that when Pi limits carboxylation, net assimilation becomes totally insensitive to both CO₂ and O₂. Indeed, the presence of O₂ insensitivity has been used as an indication that assimilation is phosphate-limited (Sharkey 1985b). On the other hand, data in which A vs. C_i curves measured at ambient O₂ (210 mbar) and low O₂ (10 or 20 mbar) cross over, such that low O₂ becomes inhibitory, have been reported repeatedly (Jolliffe and Tregunna 1973; Viil *et al.* 1977; McVetty and Canvin 1981; Sharkey 1985a; Brown *et al.* 1986; Leegood and Furbank 1986; Sharkey and Vasey 1989). This phenomenon is generally associated with high irradiance and superambient CO₂, although at low temperatures, the cross-over of A vs. C_i curves measured at 20 and 210 mbar O₂ may occur at ambient CO₂ or below (Leegood and Furbank 1986; Sage and Sharkey 1987). In these cases, leaves do not become insensitive to O₂ (except at the crossover point) but rather, sensitivity to O₂ is reversed. Furthermore, reversed sensitivity to O₂ is frequently accompanied by reversed sensitivity to CO₂, such that net assimilation declines slowly with increasing CO₂, particularly at low O₂ but also at ambient O₂ (von Caemmerer and Farquhar 1981; Woo and Wong 1983; Sharkey 1985a; Brown *et al.* 1986). We propose a modification of the existing model of carboxylation under Pi-limiting conditions, in which some additional fraction of the C lost to the chloroplast as glycolate fails to return to the chloroplast as glycerate, resulting in a

Figure 3.13: Model fits to A vs. C_i response curves measured on a cotton leaf (left panels) or a soybean leaf (right panels) at 20 (open symbols) and 200 mbar O_2 (closed symbols). In A and D, the model was fit assuming that 3/4 of the C lost as glycolate returns to the chloroplast as glycinate; in B and E, it is assumed that none of the C returns, and in C and F, it is assumed that 1/2 of the C returns. Best least-squares estimates of parameter values are shown. (Adapted from Harley and Sharkey 1991)

net increase in stromal Pi. It will be shown that such a modification induces reversed sensitivity to both CO₂ and O₂ when Pi limits carboxylation.

3.4.1 Experimental Methods

Experiments were performed on leaves of cotton plants used in the experiments described in Section 3.3 above and the same photosynthesis measurement system was used. Leaf temperature during measurement was maintained at 29±0.2°C, with PFD at leaf level of approx. 1500 µmol m⁻² s⁻¹. Curves relating net photosynthesis to C_i were obtained in the following way. The initial measurement was made at the highest pCO₂ (≈1000 µbar) and 200 mbar O₂. After the measurement, O₂ was reduced to 20 mbar for the second measurement. CO₂ was then reduced to the next desired level, another measurement taken and O₂ returned to 200 mbars. Thus, during the curve, the partial pressure of O₂ was switched back and forth between 20 and 200 mbar as CO₂ was reduced.

3.4.2 Results

Gas Exchange Data. Fifteen pairs of A vs. C_i curves measured at 20 and 200 mbar O₂ were obtained, and all exhibited "O₂-insensitive photosynthesis" (sensu Sharkey 1985a), as indicated by a reduced sensitivity to O₂ with increasing C_i, in excess of that predicted by current models of C₃ photosynthesis which fail to incorporate a phosphate limitation. Photosynthesis measured at 20 mbar O₂ reached a maximum in all leaves at C_i values between 300 and 500 µbar and then declined slowly with increasing CO₂. Ten of the pairs of curves crossed over slightly, such that increasing O₂ stimulated net assimilation at values of C_i greater than approx. 500 µbar (Fig. 3.13; left panels); the remaining 5 pairs converged but failed to cross over.

For purposes of comparison, we re-analyzed previously published data of Sharkey (1985a), in which photosynthesis measured on soybean exhibited pronounced

reversed sensitivity to O₂ at values of C_i above 400 µbar, as well as reversed sensitivity to CO₂ at both 20 and 210 mbar O₂ (Fig 3.13; right panels).

Modeling. Harley *et al.* (1985,1986) successfully fit the photosynthesis model of Farquhar *et al.* (1980) to A vs. C_i curves measured on soybean and the Mediterranean sclerophyll *Arbutus unedo* at 2 and 21% O₂, by assuming that assimilation was limited either by the amount and activity of Rubisco or by the rate of regeneration of RuBP. Attempts to do so with either the soybean or cotton data presented here were unsuccessful (not shown), resulting either in large underestimates of photosynthesis throughout the curvature portion of the A vs. C_i response or large overestimates at high C_i. The response of assimilation to C_i saturated too abruptly to be fit according to those assumptions, and it was apparent that a third limitation was operating at high values of C_i.

We assumed that this third limitation was associated with inadequate triose phosphate utilization and adopted the modifications to the model proposed by Sharkey (1985a), which are embodied in Eqn (3.17) above. The model was fit to measured data on cotton (Fig 3.13; left panels) and soybean (Fig 3.13; right panels) using non-linear least squares regression techniques to iterate for the best fit values of V_{max}, J_{max}, TPU and R_d. Imposing a phosphate limitation allowed us to fit the model to the data quite well. In 20 mbar O₂, assimilation in cotton became TPU-limited at very low C_i (≈200 µbar), while at ambient O₂ such limitations arose only at C_i greater than 500 µbar. The more severely Pi-limited soybean leaf became phosphate-limited at approx. 150 µbar CO₂ at 20 mbar O₂ and 300 µbar at 210 mbar O₂.

Although imposing a phosphate limitation led to much-improved model performance, differences between measured responses and model behavior remain apparent, particularly in the case of soybean. The Pi limitation in Eqn (3.17) leads to complete CO₂ insensitivity at 20 mbar O₂ above the C_i at which Pi becomes limiting

and both CO₂ and O₂ insensitivity at 200 mbar O₂ once Pi is limiting. At 20 mbar O₂, however, the measured data does not become totally insensitive to CO₂, but exhibits an optimum, above which assimilation declines slowly with increasing C_i. This behavior may result in a crossover of 20 and 200 mbar O₂ curves. Furthermore, the maximum measured rate of assimilation is higher at 20 than at 200 mbar O₂ while the model imposes the same maximum Pi-limited rate, independent of O₂.

Sharkey and Vassey (1989) found that in potato leaves exhibiting reversed sensitivity to O₂, starch synthesis was inhibited upon switching from 210 to 20 mbar O₂. They argued that phosphoglucisomerase was inhibited in 20 mbar O₂ by increased PGA concentration as described by Dietz (1985). Reduced Pi release in starch synthesis could then lead to the observed reversed sensitivity to O₂. However, an increase in PGA and decrease in Pi also stimulate ADPglucose pyrophosphorylase activity (Preiss *et al.* 1985). The ultimate effect is difficult to predict without knowing the control coefficient for stromal phosphoglucisomerase. The inhibition of the overall rate of photosynthesis will likely occur under a limited range of conditions (Neuhaus *et al.* 1989; Kruckeberg *et al.* 1989). The effects of O₂ on starch production warrant further study, but we believe that the reduction in phosphoglucisomerase activity caused by PGA is unlikely to be a general effect. Viil *et al.* (1977), for instance, report that twice as much C is incorporated into starch in *Phaseolus* at 0.5% O₂ than at 21%.

Harris *et al.* (1983), Sharkey (1985a,b) and Walker *et al.* (1986) have suggested that the observed stimulation of assimilation by O₂ under Pi-limited conditions might involve the contribution of Pi released in the PCO cycle. Usuda and Edwards (1982) showed that the Pi optimum for photosynthesis in wheat chloroplasts was increased by lowering the O₂ concentration from 21 to 6%, and proposed that conditions which favored glycollate synthesis (i.e., oxygenation of RuBP and de-phosphorylation of phosphoglycollate) might alleviate the

potential for Pi limitations to occur. Phosphoglycollate produced by the oxygenation of RuBP is de-phosphorylated in the chloroplast by glycollate-P phosphatase and the glycollate transported to the cytosol where it participates in a series of reactions in both the peroxisome and the mitochondria, the site of photorespiratory CO₂ release during the conversion of glycine to serine. Glycerate, produced from serine in the peroxisome, is transported back to the stroma where it is phosphorylated by glycerate kinase and joins the PGA pool. Given the stoichiometry of these reactions, a maximum of three-fourths of the C lost to the chloroplast as glycollate (a 2-carbon molecule) is recycled as glycerate (a 3-carbon molecule) and one-fourth is released as CO₂. In addition, the re-esterification of glycerate in the glycerate kinase reaction consumes Pi at a rate equal to one-half that at which Pi is released in the glycollate-P phosphatase reaction. In isolated chloroplasts, in which glycerate does not return to the chloroplasts, oxygenation of RuBP and de-phosphorylation of P-glycollate result in a net gain in stromal Pi (at a rate equal to V_O) with the potential to enhance CO₂ assimilation when Pi levels in the medium are suboptimal, as shown by Usuda and Edwards (1982). In intact leaves, however, the re-esterification of Pi in the glycerate kinase reaction in the chloroplast negates any beneficial effects of increased photorespiration. Under our initial assumptions, $V_c = 3 \cdot \text{TPU} + 0.5V_o$ (Eqn 3.17); increasing V_O by the amount ΔV_o thus stimulates V_c by the amount $0.5\Delta V_o$; however, this is exactly balanced by an equivalent increase in photorespiratory CO₂ release (Eqn 3.3).

Thus, if carbon is recycled conservatively in the photorespiratory pathway, i.e., if 3/4 of the C lost as glycollate returns as glycerate, any beneficial effect of increased rates of photorespiration is precluded. However, it is apparent from the above discussion that when photosynthesis is Pi-limited rather than C-limited, the net rate of Pi-release inside the chloroplast (and therefore Pi-dependent carboxylation) would be enhanced if less than three-fourths of the glycollate C returned to the stroma for re-phosphorylation. We

have investigated how such a diversion of C would affect the behavior of the photosynthesis model at high CO₂.

In the extreme case in which none of the C lost as glycollate were returned to the chloroplast, all of the Pi normally sequestered in the glycerate kinase reaction at a rate of $V_O/2$ would be available for photophosphorylation and regeneration of RuBP. The net sequestration of Pi thus becomes $V_C/3 - V_O/6 - V_O/2 = V_C/3 - 2V_O/3$. If this is just balanced by Pi release from starch and sucrose production, as it should be if Pi is limiting, then

$$\frac{V_C}{3} - \frac{2V_O}{3} = \text{TPU} \quad (3.18)$$

and

$$W_p = V_C = 3 \cdot \text{TPU} + 2V_O \quad (3.19)$$

We incorporated the potential effects of Pi release in the PCO cycle by substituting Eqn (3.19) for (3.17) in the model. Using this formulation, when Pi is limiting, assimilation becomes sensitive to both CO₂ and O₂, but in a reversed sense. That is, increasing CO₂ inhibits photosynthesis while increasing O₂ stimulates photosynthesis, as demonstrated below. It should be noted that when Eqn (3.19) is used to describe Pi-limited carboxylation, W_p becomes dependent on V_O , but V_O , as well as V_C , is simultaneously dependent on W_p . This interdependence requires that an iterative solution be performed to find that value of V_O which simultaneously satisfies both Eqns (3.3) and (3.19). We determined best-fit parameter values using both cotton and soybean data, with results shown in Figs (3.13B) and (3.13E). As written, Eqn (3.19) assumes that none of the C which leaves the chloroplast as glycollate returns as glycerate. The additional Pi thus made available in the PCO cycle stimulates carboxylation under Pi-limited conditions and leads to reversed sensitivity to both CO₂ and O₂. Although qualitatively reasonable for both species, in the case of soybean the reversed sensitivity to O₂ produced by this model far exceeds that observed in the measured data. Thus, in order to reduce the amount of Pi made available in the PCO cycle, we assume that some fraction of the C lost as glycollate returns to the chloroplast as glycerate where it is then re-

phosphorylated. By varying the fraction of glycollate C returning to the chloroplast between 0 (Fig 3.13B,E) and 3/4 (Fig 3.13A,D), it is possible to adjust the degree of reversed O₂ sensitivity. For example, if one-half of the glycollate C (i.e., two-thirds the potential amount) returns to the chloroplast as glycerate, the rate of Pi sequestration in the glycerate kinase reaction is reduced by $0.5V_O/3$ and the net sequestration of Pi becomes $V_C/3 - V_O/6 - 0.5V_O/3 = V_C/3 - V_O/3$. Thus,

$$\text{TPU} = \frac{V_C}{3} - \frac{V_O}{3} \quad (3.20)$$

and

$$V_C = 3 \cdot \text{TPU} + V_O \quad (3.21)$$

Fig 3.13C shows the simulated model response compared with measured cotton data using Eqn (3.21). Fig 3.13F shows a model fit to soybean data under the same set of assumptions. Incorporating Eqn 3.21 greatly improved the soybean fit; however, because Pi limitations arose at much higher C_i in cotton, the fit to the cotton data was only slightly affected.

This version of the model successfully simulates the qualitative effects of O₂ frequently observed when Pi regeneration limits photosynthesis. At 20 mbar O₂, simulated A declines slowly with increasing C_i above the C_i at which Pi becomes limiting (approx. 100 μbar in soybean and 200 μbar in cotton). In soybean at 210 mbar O₂, A reaches a maximum at C_i ≈ 375 μbar in simulation, above which Pi is limiting and A declines. In cotton, photosynthesis at 200 mbar O₂ continues to be limited by electron transport mediated RuBP regeneration and increases as expected with increasing C_i to above 800 μbar. The 20 and 200 mbar O₂ curves intersect at C_i equal to approx. 600 μbar, above which increased O₂ stimulates net assimilation. For this model parameterization for cotton, Pi becomes limiting at 200 mbar O₂ only at C_i > 950 μbar, above which A declines slowly in simulation. In both species, therefore, the 20 and 200 mbar O₂ curves cross over in simulation at a C_i value below that at which Pi becomes limiting at ambient O₂; i.e., the fact that increased O₂ stimulates assimilation does not necessarily mean that Pi is limiting at ambient O₂.

Figure 3.14: A vs. C_i response curves simulated at 210 mbar O_2 , depicting the effect of decreasing rates of triose phosphate utilization (TPU). Simulations based on parameterization for soybean shown in Fig (3.13F), assuming that 1/2 of the C lost as glycolate returns to the chloroplast as glycerate. Leaf temperature=25°C and PFD=1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. (Adapted from Harley and Sharkey 1991)

As we've seen, above the C_i at which Pi becomes limiting, assimilation declines at both 20 and 210 mbar O_2 . This results from the fact that photorespiration and thus the proposed release of Pi in the PCO cycle decline with increasing C_i . The slope of the decline in assimilation is strongly dependent on C_i . As the TPU capacity of the leaf declines (perhaps due to stress) relative to the capacity for triose phosphate production, Pi becomes limiting at lower and lower C_i . As a result, the slope of the decline in assimilation with increasing C_i can become quite steep when the point of transition falls to 300 μ bar CO_2 and below, as seen in the model simulations in Fig (3.14). Qualitatively similar results were reported for water stressed leaves of *Xanthium strumarium* by Sharkey (1985a, Fig 1, although the accompanying decline in the initial slope of the A vs. C_i response suggests a concomitant reduction in the Rubisco-limited rate of assimilation.)

3.4.3 Discussion

Early attempts to explain reversed sensitivity to O_2 focused on the role of oxygen as a potential electron acceptor. Vill *et al.* (1977) suggested that O_2 might enhance ATP production and RuBP regeneration via pseudocyclic phosphorylation, but the Mehler reaction is nearly saturated at 4.5% O_2 (Heber and French 1968) and is unlikely to lead to significant stimulation of assimilation. Alternatively, McVetty and Calvin (1981) proposed that O_2 might promote cyclic phosphorylation by maintaining the redox state of electron carriers. Each of these hypotheses fails to explain the observed reversed sensitivity to CO_2 which frequently accompanies reversed sensitivity to O_2 .

More recent explanations for inhibition of assimilation by low O_2 have centered on phosphate metabolism. Several lines of evidence on chloroplasts (Usuda and Edwards 1982) and intact leaves (Leegood and Furbank 1986; Sharkey *et al.* 1986; Walker *et al.* 1986; Sharkey and Vanderveer 1989) demonstrate that Pi can limit assimilation. Under the assumptions of

previous models, however, Pi limitations lead to O_2 insensitivity, but not to reversed sensitivity. Sharkey *et al.* (1988) suggest that if assimilation is limited by the capacity of TPU during feedback-limited photosynthesis, then reversed sensitivity to O_2 can only occur by a reduction in the capacity of either starch or sucrose synthesis as O_2 is reduced. Sharkey *et al.* (1988) found a reduction in the capacity for sucrose synthesis due to reduced cytosolic Fru-1,6-bisphosphatase activity in a mutant of *Flaveria linearis* which exhibited reversed sensitivity to O_2 , but reduced enzyme activity alone is an inadequate explanation unless it can be demonstrated that sucrose synthesis in the mutant is also inhibited by 2% O_2 .

Leegood and Furbank (1986) found that reversed sensitivity to O_2 in leaf discs of spinach at 12°C was eliminated by the addition of phosphate to the medium. They propose that reversed O_2 sensitivity results from sub-optimal concentrations of Pi in the cytosol which restricts the export of triose phosphate from the stroma, restricting sucrose synthesis as well as lowering stromal Pi. Addition of phosphate accelerates the exchange of triose phosphate for Pi across the chloroplast membrane, eliminating the inhibitory effect of low O_2 . The initial effect of reducing O_2 , however, and the event which sets these processes in motion, is theorized to be the inhibition of Pi release in the stroma by the de-phosphorylation of glycolate 2-phosphate, one of the initial products of the oxygenation of RuBP. Reversed sensitivity to CO_2 remains unexplained by these proposals.

Experimental data in which leaves assumed to be Pi-limited exhibit reversed sensitivity to both O_2 and CO_2 could be explained if increased photorespiration resulted in a net increase in stromal Pi. Given the accepted stoichiometry of the integrated PCO and PCR pathways however, increased photorespiration cannot affect stromal Pi levels as long as C is recycled conservatively in the PCO cycle, i.e., three-fourths of the C lost as glycolate returns as glycerate. The modeling exercise presented above, however, indicates that if C is not recycled conservatively, there is necessarily a concomitant increase in stromal Pi. Under Pi-limited conditions therefore, increased

oxygenation of RuBP and production of P-glycollate would result in increased stromal Pi and increased net assimilation, which would thus exhibit reversed sensitivity to both CO₂ and O₂. What evidence exists to support the idea that C is not re-cycled conservatively in the PCR pathway?

It has long been recognized that amino acids such as serine and glutamate, generated during the recycling of C and N during photorespiration, are significant components of phloem exudates (Ziegler 1974), challenging the notion that C is cycled conservatively. Furthermore, during photorespiration, there is an increased incorporation of ¹⁴C into glycine and serine, apparently at the expense of starch (Wardlaw 1983). Using ¹⁴C, Madore and Grodzinski (1984) showed that during photorespiration, glycine, serine and other amino acids are labelled in significant quantities and may be transported from the leaf. Indeed, after a 1-min labelling with ¹⁴CO₂ followed by a 15-min chase, over 10% of total label in both leaf and petiole was in amino acids. Furthermore, they report a strong increase in amino acid labelling, particularly that of glycine and serine, with increasing O₂, thereby correlating increased amino acid synthesis and transport with increased photorespiration.

We have investigated the effect which this diversion of C to amino acids would have on the behavior of the photosynthesis model at high CO₂. If significant amounts of C remained in glycine, the assumption, implicit in Eqn (3.3), that photorespiratory CO₂ release is equal to 0.5V_O would be invalidated since CO₂ is released in the glycine to serine conversion. The only quantitative data on amino acid labelling during photorespiration of which we are aware (Madore and Grodzinski 1984) indicate that at 20 mbar O₂, approx. 5 times as much serine is labelled as glycine (on a molar basis), while at ambient O₂, 2-4 times as much serine is produced. In terms of C, therefore, it appears that at least 2/3 of the C is in serine. Model simulations (not shown) for the extreme case in which it was assumed that 2 glycine left the photorespiratory pathway for each serine produced only very slight changes in model behavior. Thus, loss

of glycollate C to amino acids during photorespiration would result in the model behavior described above.

3.5.0 Reassessment of the Assumption that Mesophyll Conductance to CO₂ is Infinite

Material presented in this section has been submitted for publication (Harley *et al.* 1991a; Loreto *et al.* 1991).

Introduction. The photosynthetic fixation of CO₂ occurs at the enzyme RuBP carboxylase-oxygenase (Rubisco) which sits at the end of a complex diffusion path. In diffusing from the air outside the leaf boundary layer to the site of fixation in the chloroplast stroma, CO₂ encounters a number of resistances, across which the pCO₂ necessarily drops, following Fick's first law of diffusion, i.e.,

$$A = \frac{C_a - C_s}{R_b} = \frac{C_s - C_i}{R_s} = \frac{C_i - C_c}{R_m} \quad (3.22)$$

where A is net CO₂ assimilation, C_a, C_s, C_i and C_c are the pCO₂ in the air outside the boundary layer, at the leaf surface, in the leaf intercellular air space, and at the site of fixation in the chloroplast stroma, respectively, and R_b, R_s and R_m are the resistances to CO₂ flux across the leaf boundary layer, through the stomata, and across the leaf mesophyll (i.e., between the intercellular air space and the site of fixation) respectively. Mesophyll resistance has sometimes been defined in such a way that it includes biochemical factors, but we use it here in the more restricted sense of a diffusion resistance. These resistances may be broken down further or lumped together in various ways (Nobel 1991) but this relatively simple formulation serves our purpose. The pCO₂ falls across each resistance, each of which thus poses an additional limitation to photosynthesis whenever CO₂ is not saturating.

Because CO₂ and water vapor share a common diffusion path from the outside air to the intercellular air spaces, accurate estimates of R_b and R_s may be made from analysis of water vapor fluxes. The resistance to CO₂ flux across the mesophyll is much more difficult to assess, and has often

been assumed to be negligibly small (e.g. Farquhar *et al.* 1980). The plant species used to verify models of photosynthesis typically had high rates of photosynthesis which facilitated measurements but probably inadvertently selected for plants with low R_m . In such plants, indirect evidence based on stable isotope fractionation and the response of photosynthesis to CO_2 indicated that R_m was small (Evans *et al.* 1986). However, this may not hold for plants with thick leaves and/or low rates of photosynthesis. To evaluate this question, additional methods are needed for the estimation of R_m .

Nobel (1991) estimated R_m by considering each step in the CO_2 diffusion path (cell wall, plasmalemma, cytosol, chloroplast envelope, stroma) and estimating the diffusion path length, area available for diffusion and the diffusion coefficient for each step. This method is not practical however for measurements on a large number of species.

From Eqn (3.22), it is apparent that, given accurate measurement of A and C_i , estimates of R_m may be obtained if C_c can be estimated. Techniques for directly measuring C_c do not exist, but two methods for indirectly estimating C_c and thus determining R_m have recently been published. The first relies on the fractionation of stable carbon isotopes during photosynthesis. The extent to which Rubisco discriminates against CO_2 containing the heavier ^{13}C isotope depends in a fairly simple way on the resistances encountered by CO_2 as it diffuses from the air to the site of fixation (Farquhar *et al.* 1982). Since the leaf discriminates against $^{13}CO_2$, air which passes over a leaf will be enriched in $^{13}CO_2$. By trapping the CO_2 from an airstream passing over a leaf, Evans *et al.* (1986) were able to determine the discrimination expressed by the leaf and thus the total diffusion resistance to CO_2 of the leaf. Subtracting from the total resistance the resistances associated with the boundary layer and the stomata, accurately determined from analysis of water vapor fluxes, gave an estimate of the resistance associated with the mesophyll. This technique is robust, but requires a ratio mass spectrometer and a vacuum line in close

proximity to an open gas exchange system for trapping CO_2 .

A second method described by Bongli and Loreto (1989) exploits the fact that when RuBP regeneration (i.e., photosynthetic electron transport) limits photosynthesis, photosynthetic CO_2 assimilation continues to respond to increasing pCO_2 due to the suppression of photorespiration. The CO_2 response of photosynthesis under these conditions depends upon the specificity of Rubisco and the pCO_2 at the enzyme. Since the specificity of Rubisco is quite similar across C_3 species, whether estimated *in vitro* (Jordan and Ogren 1984) or *in vivo* using gas exchange analysis (Brooks and Farquhar 1985), the response of photosynthesis to pCO_2 under RuBP-limited conditions provides an indirect estimate of C_c . For this method, chlorophyll fluorescence quenching analysis is used to ensure that the rate of electron transport is constant over the range of intercellular pCO_2 evaluated, as is required for this method.

The modeling method for the estimation of C_c requires only a gas exchange system and a steady-state fluorometer, both of which are more accessible than ratio mass spectrometers.

In this report we develop the theory behind the modeling method, investigate the sensitivity of the analysis to errors in the estimation of critical parameters such as the rate of mitochondrial respiration occurring during photosynthesis and the specificity of Rubisco for CO_2 and compare results obtained using the two methods.

3.5.1 Experimental Methods.

Plant material and growth conditions. The following species were used in this study: *Arbutus unedo*, *Cucurbita pepo*, *Gossypium hirsutum*, *Nicotiana glauca*, *Quercus ilex*, *Q. rubra*, *Simmondsia chinensis* and *Xanthium strumarium*. Plants were grown in pots in a greenhouse under temperatures ranging from 20 to 30°C, were watered daily and fertilized weekly with full strength Hoagland's solution. Experiments were carried out during July and September 1990, at the University of Wisconsin.

Figure 3.15: Simulated response of photosynthetic electron transport (panel a) and net photosynthesis (panel b), generated by the photosynthesis model, assuming PFD=1000, temperature=25°C, $V_{cmax}=50$, $J_{max}=120$, TPU=6.5 and $R_d=1.0$. Actual photosynthesis (bold line) is the minimum of the Rubisco-limited (open circles), RuBP-limited (closed circles) and phosphate-limited (triangles) rates of CO₂ assimilation. Arrows mark transitions between limitations. (Adapted from Harley *et al.* 1991)

Gas-exchange measurements. Leaves were enclosed in a temperature-controlled aluminum cuvette in an open gas-exchange system. CO₂ was measured before and after the cuvette using a LiCor 6251 infrared gas analyzer, and humidity was monitored using a General Eastern Dew-10 hygrometer. Leaf temperatures were maintained at 25°C and incident PFD was 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Calculations of photosynthetic parameters were made using equations of von Caemmerer and Farquhar (1981).

Carbon isotope discrimination. After a steady-state photosynthesis rate was obtained, air leaving the cuvette was passed through a vacuum line where CO₂ was collected in a liquid nitrogen trap. The ¹³C/¹²C ratio of CO₂ from samples of air entering and leaving the cuvette was analyzed using a Finnigan Delta E mass spectrometer. Leaf discrimination against ¹³C, and subsequently C_c and g_m were calculated using equations of Evans *et al.* (1986).

Chlorophyll fluorescence. Measurements of steady-state fluorescence were made using a Walz PAM 101 modulated fluorometer, following the protocol of Loreto and Sharkey (1990).

3.5.2 Results

Modeling method for estimating g_m

Theory. In the discussion above, the term diffusion resistance was convenient because resistances are additive. Photosynthesis, however, is directly related to the inverse of resistance, or conductance, and we shall use the term mesophyll conductance, designated g_m, hereafter. Thus,

$$A = (C_i - C_c) \cdot g_m \quad (3.23)$$

Model behavior at 25°C and PFD=1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ is illustrated in Fig (3.15B), assuming a given parameter set (V_{cmax}=50; J_{max}=120; TPU=6.5; R_d=1.0), with net photosynthesis described as the minimum of the Rubisco, electron transport and phosphate limited rates (W_c, W_j, W_p, respectively) at any given value of C_c.

Although for the purposes of modeling it is convenient to assume that net photosynthesis is entirely limited by one of the three factors discussed above, this is clearly not strictly correct. The overall process of CO₂ assimilation is highly regulated, such that if any one factor becomes limiting, other processes are down-regulated to maintain a more or less balanced photosynthetic metabolism. Sage (1990) modeled the regulation of Rubisco activity, electron transport and TPU, based on the assumption that non-limiting processes are regulated downwards to balance the capacity of limiting processes. Employing such a model, given J_{max}, we can estimate the actual rate of regulated electron transport expected for a given value of C_c, as in Fig (3.15A). Note particularly that when W_j is limiting, electron transport rates remain constant.

Fig (3.15) depicts model simulations based on C_c, the pCO₂ in the stroma, which is independent of g_m. If photosynthesis is related to C_i however, estimates of g_m markedly affect the shape of the response, as C_i in Eqns (3.4)-(3.9) is replaced by the term C_i-A/g_m. Since A is dependent on C_c and C_c is simultaneously dependent on A, an iterative solution is required. Fig (3.16) shows the effect of varying g_m on the photosynthetic response to C_i using the same parameter set as in Fig (3.15), but lowering PFD from 1000 to 750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to remove limitations arising from inadequate TPU. As g_m is decreased, the value of C_c associated with a given value of C_i decreases, lowering assimilation in both the Rubisco-limited and electron transport-limited portions of the response. Thus, in principle, one can analyze measured A vs. C_i response curves in order to estimate the value of g_m, assuming the remaining model parameters can be accurately estimated. (For the purposes of estimating mesophyll conductance to CO₂ flux, limitations due to inadequate triose phosphate utilization are inadequately understood, and will no longer be considered in this context.)

We develop here a technique for estimating g_m from analysis of measured A vs. C_i response curves which requires only that J remain constant, and thus employs only

Figure 3.16: A family of curves, generated using the model, parameterized as in Fig (3.15), but with $PFD=750$ to eliminate the phosphate limitation on photosynthesis. The assumed value of mesophyll resistance was varied from $0.05 \text{ mol m}^{-2} \text{ s}^{-1}$ to infinite, as indicated in the figure legend. (Adapted from Harley *et al.* 1991)

Figure 3.17: A family of curves depicting how the variance in the estimate of J changes as different values of mesophyll conductance (g_m) are used, for each of the curves in Fig (3.16). Variance reaches zero when the value of g_m used to generate each curve is assumed. (Adapted from Harley *et al.* 1991)

that region of the curve over which J is limiting (Fig 3.15).

Estimation of g_m assuming constant rates of electron transport. In the nearly linear initial portion of an A vs. C_i response curve, assimilation is Rubisco-limited and the slope of the curve is proportional to V_{cmax} . However, V_{cmax} cannot be estimated independently of g_m ; as g_m decreases, C_c decreases and the estimate of V_{cmax} increases to compensate. No one pair of values provides a unique fit to the data, and since we have no independent estimate of the "true" V_{cmax} , g_m cannot be estimated in this fashion.

The specificity factor, τ , is equal to $O/2\Gamma_*$, where Γ_* is the CO_2 compensation concentration in the absence of R_d (Farquhar and von Caemmerer 1982). Substituting for τ in Eqn (3.6) and (3.8),

$$A = J \cdot \frac{C_i - \Gamma_*}{4(C_i + 2\Gamma_*)} - R_d \quad (3.24)$$

Rearranging, and substituting $C_i - A/g_m$ for C_i ,

$$J = (A + R_d) \cdot \frac{4(C_i - A/g_m + 2\Gamma_*)}{C_i - A/g_m - \Gamma_*} \quad (3.25)$$

We have assigned Γ_* a value of $43.1 \mu\text{bar } CO_2$ at 25°C and $200 \text{ mbar } O_2$. The value of R_d is equal to A at $C_i = \Gamma_*$ and may be estimated by extrapolating the initial portion of an A vs. C_i response curve to Γ_* , or more accurately by adopting a procedure developed by Brooks and Farquhar (1985). If R_d and Γ_* are assigned values and A and C_i are determined from gas exchange measurements, we are left with two unknowns, J and g_m . If it can be demonstrated that the rate of electron transport remains constant over a range of C_i values, as it should if electron transport is limiting, it is possible to determine that value of g_m which minimizes the variance in the estimates of J , calculated using Eqn (3.25); i.e., to determine that value of g_m which provides the best fit to the data, assuming only that electron transport rate is constant.

Using steady-state chlorophyll fluorescence to determine the range over which electron transport is constant. This analysis can only be applied over a range of C_i values for which the rate of electron transport remains constant. Chlorophyll fluorescence, determined concurrently with each gas exchange measurement, may be used to obtain an independent estimate of the appropriate range of C_i values to be used in estimating g_m .

Genty *et al.* (1989) demonstrated that the quantum yield of electron transport is proportional to $\Delta F/F_m$, where F_m is maximal fluorescence yield and ΔF is the difference between F_m and F_s , the steady-state fluorescence yield. Thus, if $\Delta F/F_m$ remains constant, assuming constant PFD, electron transport rate may be assumed to remain constant, and the technique described above for estimating g_m is valid.

Sensitivity of the method to different value of g_m . In order to analyze the sensitivity of the technique, we utilized the family of A vs. C_i curves illustrated in Fig (3.16), in which the g_m was varied from 0.05 to $0.80 \text{ mol m}^{-2} \text{ s}^{-1}$. For each curve, using only those data points for which electron transport was limiting, we assumed a range of values for g_m . For each g_m , we calculated a value of J for each pair of A and C_i values using Eqn (3.25), and then determined the resulting variance from the mean, as

$$\text{Variance in } J = \frac{\sum_{i=1}^n (J_i - \hat{J})^2}{n-1} \quad (3.26)$$

where n is the number of paired values of A and C_i , J_i is the calculated value of J for cases 1 through n and $\hat{J}$ is the mean of all the calculated values of J . We then examined the relationship between the variance in the estimates of J and the estimate of g_m (Fig 3.17). Naturally, for these ideal data sets, the variance in the estimates of J reached zero when the value of g_m used to generate the data was used in the analysis. However, this point of minimum variance became less and less distinct as the g_m value used to

Figure 3.19: Demonstration of the Modeling method of estimating mesophyll conductance, g_m , using experimental data from a leaf of *Quercus rubra*. In Panel A, net photosynthesis and $\Delta F/F_m$ are both shown as a function of C_i . The best model fit to the data in Panel A, assuming infinite g_m , is shown in Panel B, with parameter estimates. The variance in the estimates of J , calculated using Eqn. (3.25) for the six data points for which $\Delta F/F_m$ is constant, over a range of estimates of g_m is shown in panel C, with variance reaching a minimum at $g_m=0.083 \text{ mol m}^{-2} \text{s}^{-1}$. Finally, Panel D, shows the best model fit to the data, given $g_m=0.083$, with new parameter estimates.

Table 3.2: Values of mesophyll conductance estimated for four leaves of red oak (*Quercus rubra* L.). Estimates using the carbon isotopic discrimination method were made under varying conditions of CO₂ and O₂. All estimates using the modeling method were made from curves obtained at ambient (210 mbar) O₂. (Adapted from Loreto *et al.* 1991b)

Experimental Conditions	Four Replications				Mean (n=4)
	Mesophyll Conductance (mol m ⁻² s ⁻¹)				
<i>Isotopic Method</i>					
350 μbar CO ₂ 200 mbar O ₂	0.17	0.10	0.18	0.15	0.15
750 μbar CO ₂ 200 mbar O ₂	0.12	0.14	0.11	0.08	0.11
350 μbar CO ₂ 20 mbar O ₂	0.12	0.18	0.15	0.11	0.14
350 μbar CO ₂ 380 mbar O ₂	0.16	0.19	0.10	0.10	0.14
<i>Modeling Method</i>					
350 μbar CO ₂ 200 mbar O ₂	0.20	0.11	0.14	0.12	0.14

generate the data increased, indicating that the proposed technique becomes less robust the higher the value of g_m .

Sensitivity of g_m estimate to errors in R_d and Γ_ .* Given the validity of Eqn (3.24), this analysis rests on three assumptions: 1) electron transport is constant over the range of C_i values analyzed, 2) R_d is accurately estimated, and 3) Γ_* at 25°C and 200 mbar O_2 is 43.1 $\mu\text{bar CO}_2$. The assumption of constant electron transport is buttressed by the independent estimates of $\Delta F/F_m$ provided by fluorescence analysis. To determine the effect of error in our estimates of Γ_* and R_d on the resulting estimate of g_m , we estimated g_m for each curve in Fig (3.16), while allowing either Γ_* or R_d to vary over a range of $\pm 10\%$. The results of this sensitivity analysis are shown in Fig (3.18). The error introduced by varying either Γ_* or R_d becomes increasingly significant as g_m increases. Nevertheless, for $g_m < 0.4 \text{ mol m}^{-2} \text{ s}^{-1}$, the error introduced by a $\pm 10\%$ error in the estimation of R_d is less than 3%. The estimate of g_m is more strongly affected by errors in Γ_* ; when $g_m = 0.4$, a 10% underestimate in Γ_* results in a 32% underestimate of g_m , and a 10% overestimate of Γ_* results in a 92% overestimate of g_m .

Application of Modeling Method to Measured Data. The procedure for utilizing this technique is illustrated in Fig (3.19). Fig (3.19A) depicts net photosynthesis and the associated value of $\Delta F/F_m$ as a function of C_i for a leaf of red oak (*Quercus rubra*). We assume, based on fluorescence data ($\Delta F/F_m$ constant), that electron transport is effectively constant for the six data points above 350 $\mu\text{bar CO}_2$, and that these points may be used in estimating g_m . In Fig (3.19B), we fit the model to the data, assuming infinite g_m (i.e., $C_c = C_i$), obtaining the model parameters shown. It is clear that the slope of the modeled response in the region of constant J has a lower slope than the measured data, implying that g_m is less than infinite. For each of a range of assumed

values of g_m , we determine the variance from the mean of the values of J calculated using Eqn (3.25). Fig (3.19C) shows the variance in the estimates of J as g_m is varied, with the variance reaching a minimum at that value of g_m which generates the best fit to the data ($g_m = 0.083 \text{ mol m}^{-2} \text{ s}^{-1}$). Finally, Fig. (3.19D) illustrates a new model fit to the data, with g_m fixed at 0.083, resulting in a much improved fit over the region of interest. Since the lower g_m results in lower values of C_c , the estimates of both $V_{c\text{max}}$ and J are necessarily higher than in Fig (3.19B).

Using these techniques, estimates of g_m were obtained from leaves of a variety of species exhibiting a wide range of photosynthetic capacities. These estimates are plotted against measured CO_2 assimilation (A) in Fig (3.20) and against measured stomatal conductance, g_s , in Fig (3.21) (open symbols in both figures).

Isotopic method for estimating g_m .

We also obtained estimates of g_m using mass spectrometry to determine discrimination against ^{13}C for a variety of species. Estimates obtained by the modeling method and the isotopic method for leaves of *Quercus rubra* are compared in Table (3.2). Estimates from several species are also plotted against A and g_s in Figs (3.20) and (3.21) respectively (closed symbols).

3.5.4 Discussion

We have discussed two methods of estimating g_m , based on quite different assumptions and techniques. Both are sensitive to measurement errors, particularly as g_m increases. The value of g_m is inversely proportional to $(C_i - C_c)$ (Eqn 3.23). As g_m increases, C_c also increases relative to C_i and thus the quantity $(C_i - C_c)$ decreases. As $(C_i - C_c)$ decreases, any error introduced into the estimate of C_c exerts an increasingly large effect on the estimate of g_m . If one examines Fig (3.16), it is apparent that the difference between the curves generated by repeated doubling of g_m is reduced as g_m increases, until the difference between $g_m = 0.4$ and

Figure 3.20: Relationship between mesophyll conductance, g_m , and CO_2 assimilation for leaves of eight different species with different photosynthetic capacities. Estimates of g_m were made using either the carbon isotope method (closed circles) or the modeling method (open squares). Slope is that of a regression forced through the origin. (Adapted from Loreto *et al.* 1991)

Figure 3.21: Relationship between mesophyll conductance, g_m , and stomatal conductance, g_s , for leaves of eight species with different photosynthetic capacities. Estimates of g_m were made using the carbon isotope method (closed circles) or the modeling method (open squares). Slope is that of a regression forced through the origin. (Adapted from Loreto *et al.* 1991)

$g_m = 0.8 \text{ mol m}^{-2} \text{ s}^{-1}$ is very slight. Using ideal data sets, generated by the model, these slight differences can be resolved, but applying the technique to measured gas exchange data will become increasingly problematic for g_m above approx. $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$. For high values of g_m , the isotopic method is preferable.

Despite the sensitivity of the methods, when applied to leaves of the same plant, both techniques arrived at similar estimates (Table 3.2). The data in Figs (3.20) and (3.21) were arrived at using both techniques. Linear regressions relating g_m , estimated using both methods, to g_s and A were statistically indistinguishable, and the data were pooled for subsequent analysis. Linear regressions of g_m versus g_s and g_m versus A , both forced through the origin, indicate that, on average, g_m is approx. 50% greater than g_s and that g_m ($\text{mol m}^{-2} \text{ s}^{-1}$) is approx. 2.1% of A ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). From Eqn. (3.23) it is apparent that the drop in CO_2 between C_i and C_c is equal to A/g_m . Thus, across a variety of species with widely differing rates of photosynthesis, the average CO_2 drop across the mesophyll is $1/0.021$ or approx. $48 \mu\text{bar}$, a result in general agreement with data obtained by von Caemmerer and Evans (1991) using the isotopic method.

Since C_c is substantially less than C_i , estimates of photosynthetic model parameters which are made under the assumption that $C_c = C_i$ will necessarily be underestimates (Fig. 3.19, compare B and D). For those interested in obtaining parameter estimates based on C_c , the two techniques discussed here will be of considerable use. Both techniques are quite time consuming and/or expensive, however. From Figs (3.20) and (3.21), it is clear that somewhat cruder, but quite useful, estimates of g_m and therefore C_c may be made by relating g_m to measured values of either g_s or A .

3.6.0 Summary

There is a virtual consensus among modelers of C_3 photosynthesis that the model first proposed by Farquhar *et al.* (1980) is an extremely valuable tool for analyzing leaf photosynthetic behavior. Since its inception, it has been modified repeatedly, most significantly by the inclusion of a potential limitation arising from inadequate phosphate (Sharkey 1985b). We have developed here a further modification of the model under Pi-limited conditions, which better simulates measured data, and raises important questions concerning the flow of C during photorespiration. In addition, we have investigated methods of estimating the magnitude of the mesophyll conductance to CO_2 flux, which inevitably leads to a reduction in C_c , requiring a re-evaluation of model parameters.

We have shown that it is practical to parameterize the model from easily obtained gas-exchange data, for leaves of plants grown under any environmental conditions, including varying levels of CO_2 . Comparison of model parameters is perhaps the best way in which to obtain a quantitative comparison between leaves, and the model also allows one to make confident predictions of leaf behavior over a range of light intensities and temperatures.

The remaining challenge at the leaf level is to build up a substantial data base which characterizes the changes in photosynthetic characteristics (i.e., model parameters) for a wide range of species, and ultimately to begin elucidating the controls which determine how different leaves respond to environmental change. Changes in leaf behavior result primarily from changes in the allocation of critical nutrients, particularly N. Thus, in order to understand leaf response to environmental change, leaf level processes must be integrated into a whole plant context, in which canopy structure and resource allocation play a critical role.

4.0.0 MODELING THE PLANT CANOPY (CANDO)

The module CANDO simulates canopy photosynthesis and transpiration in response to a changing environment, especially elevated CO₂. Since a generic leaf module has been developed to simulate leaf photosynthesis and transpiration (see Chapter 3), CANDO is in fact a scaling up from leaf level to canopy level. A canopy can be treated as a collection of leaves with different physiological properties exposed to different microenvironments, so the major task of CANDO is to determine the profiles of each environmental factor and the profiles of leaf physiological properties.

In this chapter a brief description of the structure of module CANDO and its application to estimate the effect of elevated CO₂ on canopy photosynthetic rates is presented, followed by a detailed discussion about how to model radiation transfer in a canopy and a coordination theory of leaf nitrogen allocation within a canopy. Much of the material presented in this chapter has been submitted for publication (Reynolds *et al.* 1991).

4.1.0 Extrapolating Leaf Response to a Canopy

While several models can mimic single leaf behavior quite well under a wide range of conditions (Reynolds and Acock 1985), exposure of plants to elevated CO₂ will most likely complicate our ability to extrapolate individual leaf behavior to the level of a canopy. These effects of elevated CO₂ can be considered either 1) short-term, i.e., responses of plants grown at ambient concentrations and subjected to "pulse" exposures of elevated CO₂, or 2) long-term, i.e., responses of plants that have been continuously grown at elevated CO₂ atmospheres. Examples of short-term effects are the altered light and temperature responses of leaf photosynthesis and increased leaf temperature due to reduced leaf transpiration (Percy and Bjorkman 1983, Morison and Gifford 1984). Long-term effects include altered canopy light and temperature profiles that may result from increased leaf area and above-ground biomass

typically associated with continuous exposure to elevated CO₂ (Kramer 1981; Kimball and Idso 1983; Strain 1985) and potential changes in leaf photosynthetic characteristics (Kramer 1981, Acock *et al.* 1985).

Acock *et al.* (1985) noted several reasons why short-term studies of single leaf photosynthesis are inadequate for making predictions of canopy photosynthesis during long-term exposures to higher CO₂: leaf photosynthetic characteristics vary with position in the canopy, brief exposures to high CO₂ ignore potential long-term adaptive responses, and short-term measurements mask changes in sink-strengths that may occur during canopy development. The physiological status of leaves varies within a canopy chiefly due to non-homogeneous light and temperature environments during ontogeny (Bunce 1983).

We estimate the effects of short-term exposure to doubled CO₂ concentrations on whole plant gas exchange in the mediterranean sclerophyll, *Quercus coccifera* by taking detailed information on leaf level responses to increased CO₂ and incorporating this information into a plant canopy model. We employ a detailed canopy model, parameterized and validated for *Q. coccifera* (Caldwell *et al.* 1986; Meister *et al.* 1987), a species for which considerable physiological data also exist (Tenhunen *et al.* 1985). We use computer simulations to examine some potential short-term effects of canopy response to elevated CO₂ by accounting for key interactions between structural and functional components of a canopy. The simulation model utilizes modules based on readily-made gas exchange measurements of individual leaves, simulates several classes of leaves in multiple layers, and includes a leaf energy balance. Simplifications will be required since this complex canopy model is an integral part of a whole-plant growth model that we are developing to study long-term response of ecological systems to elevated CO₂ (Reynolds *et al.* 1987). Since the leaf submodel required the most computer time (due to iterative solutions of leaf energy balance and internal

CO₂ concentration), we investigated the effects on model behavior of 1) eliminating the leaf energy budget subroutine (in which case leaf temperatures were set equal to air temperature) and 2) aggregating leaf classes in several different ways. Using predictions of daily net photosynthesis and transpiration from the most detailed version of the canopy model as a basis for comparison, we introduced various simplification schemes to investigate 1) the magnitude of errors incurred and 2) the sources of such errors.

4.1.1 Methods

Leaf submodel. The leaf submodel is composed of two parts, leaf gas exchange and leaf energy balance. The leaf gas exchange model used here is described in Chapter 3. The advantage of this degree of physiological detail is that the complex interactions of CO₂ concentration, light, temperature, and air humidity can be accounted for in a realistic fashion.

Leaf temperature, an important input to the leaf gas exchange model, is an outcome of leaf energy balance considerations rather than an independent environmental variable. While the energy balance could be omitted by assuming leaf temperature is equal to ambient air temperature, this would make it impossible to assess the contribution of leaf temperature change induced by changes in other environmental variables, which could potentially be significant with elevated CO₂ concentrations. The importance of incorporating a leaf energy budget in the model is assessed below.

The environmental variables that drive the complete leaf submodel are: shortwave radiation (including photosynthetically active radiation (PAR) and near-infrared radiation), ambient air temperature, relative humidity, CO₂ concentration, wind speed and longwave radiation from the sky, soil surface and neighboring leaves in the canopy.

Canopy model. The canopy model is based on Caldwell *et al.* (1986). This model was modularized to be readily expandable and to facilitate testing the effects of introducing varying degrees of detail in

canopy structure and function. Necessary canopy structure parameters have been estimated for *Quercus coccifera*, a Mediterranean shrub for which a large body of data on leaf function is also available (Caldwell *et al.* 1986; Meister *et al.* 1987; Tenhunen *et al.* 1985). The primary task of the canopy model is to calculate the environmental variables for each leaf within the canopy, and to use these variables as inputs to the leaf submodel to calculate assimilation and transpiration of these leaves. Total canopy assimilation and transpiration is simply the sum of those from all the leaves. Leaves in a similar environment can be grouped for simplification. A brief summary of the model is given below.

Leaf aggregation. The plant canopy is treated as horizontally homogeneous and vertically-layered. In each layer, eight structural parameters (*i.e.*, leaf and stem area indices, leaf and stem mean tip angles, leaf and stem clumping factors, leaf width and proportion of leaves that are alive) and five physical and physiological parameters (*i.e.*, reflectance and transmittance of leaves to PAR and near-IR, and leaf nitrogen content) are independently specified. From the mean leaf tip angle in each layer, fractions of leaves in three inclination classes of 15, 45 and 75 degrees are determined by using an ellipsoidal leaf angle distribution (Campbell and Norman 1989). Leaf azimuthal orientation is assumed to be random. Within each layer, total leaf area is partitioned into sunlit and shaded area. Both sunlit and shaded leaf area is separated into three classes according to average leaf inclinations, and the sunlit leaf area of each inclination group is further divided into six classes according to azimuthal orientations relative to the sun azimuth. Therefore there is a total of 210 leaf classes (21 in each of 10 layers). This large number of leaf classes is intended to minimize errors resulting from nonlinearities in the responses of both leaf CO₂ assimilation and transpiration to environmental variables, particularly PAR.

Shortwave and longwave radiation. Light absorption by leaves is the sum of light intercepted from three sources: direct solar beam, diffuse skylight, and diffuse light received after reflection from and transmission through other leaves. The model also accounts for the shading effect of stem material. Several approximations in the calculation of direct beam, sky diffuse and leaf diffuse light environments in the original Caldwell *et al.* (1986) model were removed. The relatively poor conservation of shortwave flux in the original model was corrected by implementing more exact forms of the equations, resulting in more closely balanced fluxes. For example, sky diffuse light incident on leaves in a layer was originally calculated as the product of flux density entering the layer and the skylight view factors (Duncan *et al.* 1967). As noted by Gutschick and Wiegel (1988), this overestimated the sky diffuse flux. A nearly balanced diffuse flux was obtained by using average flux density integrated within a layer. Also in the original formulation, average direct beam irradiance for sunlit leaves in a canopy layer was calculated by averaging the irradiation incident on leaves displayed at 12 azimuth angles (15°, 45°, . . . 345° from the sun) (Duncan *et al.* 1967).

Incident longwave radiation from the sky is calculated from air temperature and humidity (Brutsaert 1975). Both the sky and soil surface longwave radiation are attenuated as they pass through the canopy.

Ambient air temperature, humidity and CO₂ concentration. The model does not include mass balances with turbulent transfer of water vapor, warm air or CO₂. Simulation of these mechanisms requires estimates of soil fluxes and parameter estimation, and validation requires measurements of aerodynamic properties and scalar profiles (Nobel 1983). This information was not available for the *Quercus coccifera* stands simulated in this study. We assume that the importance of these profiles for simulating effects of increased CO₂ on canopy gas exchange is small at the wind speeds typical for this site. Air temperature profiles are calculated by linear interpolation between temperature measured in the top canopy

layer and at the soil surface. Absolute humidity and CO₂ concentration are assumed to be constant throughout the canopy.

Wind speed. Wind speed in each canopy layer enters into calculations of boundary layer conductance in the leaf energy balances. A vertical profile of wind speed is based on hourly measurements at the top of the canopy and a simple logarithmic attenuation within the canopy.

4.1.2 Model Implementation

Caldwell *et al.* (1986) and Meister *et al.* (1987) measured in detail the physical structure of an extensive *Quercus coccifera* canopy growing in a natural macchia at the Research Station Quinta de São Pedro, south of Lisbon, Portugal in Spring and Summer 1983. In addition, they obtained information on how leaf physiological properties varied with depth in the canopy. Caldwell *et al.* (1986) used this information to parameterize and validate a detailed shrub canopy model. We use here a slightly modified version, into which we have incorporated a detailed model of leaf photosynthesis and conductance (Harley and Tenhunen 1991; Ball *et al.* 1987), in order to investigate the potential effects of short term exposure to doubled CO₂.

In order to compare simulated total daily CO₂ uptake and water loss of *Q. coccifera* under doubled CO₂, the canopy model was run for *Q. coccifera* using canopy structure parameters similar to those measured by Caldwell *et al.* (1986) and Meister *et al.* (1987), assuming an ambient CO₂ concentration of either 340 or 680 ppm, and utilizing hourly weather data measured at the site in Portugal on May 7, when air temperature reached 28°C, and on June 10, 1983 when air temperatures exceeded 32°C. Parameters for the new leaf submodel were derived by fitting to the same data sets that were used to parameterize the original model (Otto Lange, unpubl. data).

Attempts were made to simplify the overall model by reducing the number of leaf classes, and the model was used to investigate the consequences of aggregating leaf classes in various ways. Regardless of the way in which leaf classes were

aggregated, the most complex version of the model was used to determine the vertical profile of environmental factors which drive the leaf model, particularly PAR and near infrared radiation. These inputs were then used to drive the leaf model for each leaf class, which ranged in number from 210 in the most complex version to 2 in the simplest. The six aggregation schemes, in order of decreasing complexity, are given in Table (4.1).

Schemes 1-4 represent multilayer models and Schemes 5 and 6 represent single layer models. The single layer models were realized in our program by treating all layers as an averaged layer. Schemes 1 and 2 are similar to models of high complexity and Scheme 3 to those of intermediate complexity described by Norman (1980), with the exception that all three include a leaf energy balance and attenuate sunlit leaf area using information about the leaf angle distribution. Scheme 3 describes the canopy model of Caldwell *et al.* (1986). Scheme 4 corresponds to models that calculate average irradiance at various canopy depths, including the simplest of the three models compared by Norman (1980), and the models of Monsi and Saeki (1953), and Hirose and Werger (1987). Scheme 6 is similar to the simple model of Norman (1982) for sunlit and shaded foliage of a vertically homogeneous canopy.

Although our methods of computing irradiances differ from these published models, the identification of leaf classes for solving photosynthesis models is very similar. To facilitate comparison of results, all schemes used the same calculations of irradiance, which considered 21 leaf classes in each of 10 layers; they differ only in the degree to which these classes were aggregated for calculation of gas exchange. Daily total assimilation and transpiration resulting from the implementation of these schemes were compared using input data from May 7 and June 10, 1983.

Simulations were also conducted to investigate effects of changing vertical profiles of canopy structure and physiological properties. Each of the six vertical profiles (leaf and stem area index, leaf and stem inclination, leaf width and leaf nitrogen content) was replaced by a uniform profile in which the single value was the leaf area

weighted average value for the parameter in question, and the results compared with those obtained using the actual measured profiles.

4.1.3 Results

Performance of the six aggregation schemes. Table (4.2) gives estimates of daily total CO₂ assimilation using input data for May 7 and June 10, 1983 obtained using the six leaf aggregation schemes outlined above. Leaf nitrogen is assumed to decrease linearly with canopy depth from 2.6 g N/m² in the top layer to 1.0 in the bottom layer. Since canopy structure and physiological characteristics were assumed to be unchanged, differences between the two dates reflect only the effect of the change in weather conditions. Air temperatures on June 10 were much higher than those on May 7, resulting in substantially lower photosynthetic rates. Despite reduced stomatal conductance on June 10, rates of transpiration were similar on the two dates as a result of much higher VPD on the latter. The daily total assimilation (mmol CO₂ m⁻² d⁻¹) of the canopy are given for Scheme 1 (bold face), which contains the greatest amount of structural detail (Table 4.1) and thus serves as a basis for comparison. The results of simulations using increasingly simplified schemes (Table 4.1;) are given as relative differences from Scheme 1 (referred to as "errors" below). The contributions of sunlit and shaded leaves are listed separately to facilitate understanding the nature of these differences. Results are given for both current ambient and doubled CO₂.

Scheme 2, which adopted a Gaussian integration for sunlit leaves in each layer gave excellent results though not as good as those of Goudriaan (1986), since the included leaf submodel was more complex and realistic. Replacing three shaded leaf classes (Scheme 1) by a single shaded class (Scheme 2) introduced negligible error. Scheme 3 also gave satisfactory results, though using a single sunlit leaf class in each layer led to overestimates of >13% on May 7, as predicted above. The fact that using a single sunlit leaf class on June 10 resulted in only 1% error (and in fact lead to an underestimate of photosynthesis for sunlit

Table 4.1: Summary of the six schemes by which leaf classes were aggregated in order to test the effects of various model simplifications on model results (From Reynolds *et al.* 1991).

Scheme Number	Total No. of Leaf Classes	Scheme Description
1	210	18 classes of sunlit leaves, representing the various irradiances resulting from leaves being arrayed in 6 azimuthal classes and 3 inclination angle classes, and 3 classes of shaded leaf, representing the average irradiance on 3 inclination angle classes in each of 10 layers.
2	40	3 sunlit leaf classes for Gaussian integration (Coudriaan 1984) and one shaded leaf class in each of 10 layers.
3	20	One sunlit and one shaded leaf class in each of 10 layers.
4	10	One average leaf class in each of 10 layers.
5	21	18 classes of sunlit leaves and 3 classes of shaded leaves for the entire canopy.
6	2	One sunlit and one shaded leaf class for the whole canopy.

Table 4.2: Comparison of daily whole canopy assimilation and water use efficiency, calculated using each of six different leaf aggregation schemes (Table 4.1). Daily totals were obtained using hourly input data measured on both May 7 and June 10, 1983. Results using Schemes 2-6 are presented as relative errors vis-a-vis Scheme 1, for which absolute values are given. Results are given separately for sunlit and shaded leaves, and for total canopy (From Reynolds *et al.* 1991).

		CO ₂ ASSIMILATION (mmol m ⁻² ground day ⁻¹)						WUE (mmol/mol)	
		SUNLIT		SHADED		TOTAL		TOTAL	
		340	680	340	680	340	680	340	680
Scheme									
May 7	1	392	608	178	232	570	840	4.9	9.8
	2	-2%	-1%	0%	0%	-1%	-1%	0%	0%
	3	+13%	+18%	0%	0%	+9%	+13%	-1%	0%
	4					+93%	106%	+2%	+1%
	5	-19%	-17%	0%	0%	-13%	-12%	-3%	0%
	6	-11%	-5%	+1%	0%	-7%	-4%	-5%	-2%
June 10	1	134	241	234	348	369	589	3.5	6.5
	2	0.4%	0.0%	0.1%	0.1%	0.2%	0.1%	-0.1%	-0.3%
	3	-2.1%	2.0%	0.1%	0.1%	-0.7%	0.9%	0.9%	1.6%
	4					78%	79%	-6.1%	-4.6%
	5	-30%	-24%	0.1%	3.4%	-11%	-8.0%	2.4%	4.2%
	6	-36%	-27%	0.0%	4.4%	-13%	-8.4%	5.1%	8.2%

leaves in one case) was fortuitous, a result of the predominance of supraoptimal temperatures. Scheme 4, which used a single averaged leaf class for each layer, overestimated both assimilation and transpiration by over 100%, a large error that was expected based on our analysis of the leaf submodel. Both Schemes 5 and 6, which aggregated leaf classes vertically, underestimated total assimilation and transpiration by a substantial amount, due primarily to errors in estimates for sunlit leaves. The fact that increasing the number of sunlit leaf classes, based on incident PAR (Scheme 5), failed to eliminate the large errors incurred for sunlit leaves (Scheme 6) confirmed the conclusion (based on analysis of the leaf submodel) that these errors were a result of vertical gradients of environmental variables other than PAR. Simulated water use efficiency (WUE), calculated as daily CO_2 assimilation divided by daily water use ($\text{mmol CO}_2/\text{mol H}_2\text{O}$) was quite conservative, indicating that errors introduced into estimates of CO_2 assimilation and transpiration by the various schemes tended to move in parallel.

Table (4.3) shows the relative response of assimilation to doubled CO_2 using the six aggregation schemes for May 7 (A) and June 10 (B). Differences in the relative response to doubled CO_2 between the six Schemes were not as large as expected, even for Scheme 4, which performed very poorly in terms of absolute responses of assimilation and transpiration (Table 4.2). All aggregation schemes indicated that assimilation would increase by about 47-57%, and that transpiration would decrease by 20-27% on May 7, with an improvement in WUE of about 100%. On the warmer day, June 10, doubled CO_2 lead to an increase in daily C gain of 60-68%, a decrease in water loss of 13-16%, and in improvement of WUE of 88-94%. In contrast to the difficulty of predicting plant photosynthetic response to increasing CO_2 from single leaf measurements, these estimations of canopy CO_2 assimilation integrate spatial and temporal variation in irradiance and leaf temperature, as well as vertical variation in leaf N, to provide a

much more robust prediction of whole plant response.

Effect of vertical structural and physiological gradients. Table (4.4) depicts the relative errors caused by replacing each of the six vertical structural or physiological gradients in turn by an averaged constant value, for May 7 and June 10, respectively. Note that these simulations were performed using the most complex version of the model (210 leaf classes), testing the effect of simplifying the description of vertical canopy structure one factor at a time. The results suggest that errors caused by assuming an averaged constant profile of leaf width (LW) and both leaf and stem inclination angles (LIA and SIA) are negligible. Assuming an averaged constant stem area index (SAI) increased the stem area in the upper layers of the canopy and thus reduced the light intercepted by leaves lower in the canopy, causing an underestimate of up to 6% for both assimilation and transpiration. Using a constant leaf area index (LAI) profile underestimates assimilation by up to 5%.

When a constant leaf nitrogen content was assumed, N was in effect reallocated from upper to lower canopy layers; thus, additional N was allocated to leaves for which PAR was the primary limiting factor, and too little N was allocated to the upper layers where additional N in the photosynthetic machinery would be beneficial. This resulted in approx. a 10% underestimate of assimilation; since stomatal conductance is proportional to assimilation (Ball *et al.* 1987), transpiration was also underestimated (Table 4.4). This result is consistent with the work of Hirose and Werger (1987), Field (1983), and Gutschick and Wiegel (1988), all of whom showed that commonly observed gradients in leaf nitrogen and photosynthetic capacity, both of which decrease with canopy depth, are associated with increased whole canopy photosynthetic performance.

Table (4.5) illustrates the effect of each of these vertical profile simplifications on the the relative response of canopy assimilation and transpiration to doubled CO_2 . As in the case of the leaf aggregation

Table 4.3: Simulated relative responses of daily assimilation, transpiration and water use efficiency of the canopy to doubled CO₂ using six different leaf aggregation schemes, calculated using hourly input data measured on May 7, and June 10, 1983. Results are given separately for sunlit and shaded leaves, and for total canopy (From Reynolds *et al.* 1991).

		CO ₂ ASSIMILATION (mmol m ⁻² ground day ⁻¹)			TRANSPIRATION (mol m ⁻² ground day ⁻¹)			WUE (mmol/mol)
		SUNLIT	SHADED	TOTAL	SUNLIT	SHADED	TOTAL	TOTAL
May 7	Scheme 1	+55%	+30%	+47%	-22%	-33%	-26%	+98%
	2	+56%	+30%	+48%	-22%	-33%	-25%	+98%
	3	+62%	+30%	+53%	-20%	-33%	-23%	+99%
	4			+57%			-20%	+96%
	5	+59%	+30%	+49%	-22%	-38%	-27%	+104%
	6	+55%	+30%	+53%	-20%	-39%	-25%	+105%
June 10	1	+80%	+49%	+60%	-13%	-16%	-15%	+88%
	2	+79%	+49%	+60%	-13%	-17%	-15%	+88%
	3	+87%	+49%	+62%	-11%	-17%	-14%	+89%
	4			+61%		-17%	-16%	+91%
	5	+94%	+54%	+65%	-8%	-18%	-14%	+92%
	6	+105%	+55%	+68%	-5%	-18%	-13%	+94%

Table 4.4.: Relative errors in predicted canopy photosynthesis and water use efficiency for May 7 and June 10, 1983 which result from assuming an averaged constant profile for each of several canopy structural properties. LAI denotes the leaf area index, LIA the leaf inclination angle, LW the leaf width, SAI the stem area index, SIA the stem inclination angle, LNC the leaf nitrogen content. Results are given separately for sunlit and shaded leaves, and for total canopy (From Reynolds *et al.* 1991).

		CO ₂ ASSIMILATION (mmol m ⁻² ground day ⁻¹)						WUE (mmol/mol)	
		SUNLIT		SHADED		TOTAL		TOTAL	
		340	680	340	680	340	680	340	680
May 7	Profile								
	LAI	-4%	-4%	-4%	-4%	-4%	-4%	-2%	-2%
	LIA	+1%	0%	0%	-1%	0%	0%	+1%	+1%
	LW	0%	0%	0%	0%	0%	0%	0%	0%
	SAI	-6%	-6%	-3%	-3%	-5%	-5%	-2%	-2%
	SIA	0%	-1%	0%	0%	0%	0%	0%	0%
	LNC	-18%	-16%	-2%	-2%	-13%	-12%	-2%	-1%
June 10	LAI	-3%	-3%	-7%	-5%	-5%	-4%	-4%	-5%
	LIA	+2%	+2%	0%	0%	+1%	+1%	+1%	+1%
	LW	0%	0%	0%	0%	0%	0%	+0%	0%
	SAI	-9%	-8%	-4%	-3%	-6%	-5%	-2%	-3%
	SIA	0%	0%	0%	0%	0%	0%	0%	0%
	LNC	-22%	-17%	-4%	-3%	-11%	-9%	-4%	-4%

Table 4.5: Relative response of daily assimilation, transpiration and water use efficiency of the canopy to doubled CO₂ on May 7 and June 10, 1983 which result from assuming an averaged constant profile for each of several canopy structural properties. LAI denotes the leaf area index, LIA the leaf inclination angle, LW the leaf width, SAI the stem area index, SIA the stem inclination angle, LNC the leaf nitrogen content. Results are given separately for sunlit and shaded leaves, and for total canopy (From Reynolds *et al.* 1991).

		CO ₂ ASSIMILATION (mmol m ⁻² ground day ⁻¹)			TRANSPIRATION (mol m ⁻² ground day ⁻¹)			WUE (mmol/mol)
		SUNLIT	SHADED	TOTAL	SUNLIT	SHADED	TOTAL	TOTAL
Profile								
May 7	LAI	+56%	+31%	+48%	-22%	-33%	-25%	+97%
	LIA	+55%	+30%	+47%	-23%	-33%	-26%	+97%
	LW	+55%	+30%	+47%	-22%	-33%	-25%	+97%
	SAI	+55%	+31%	+48%	-23%	-33%	-25%	+98%
	SIA	+55%	+30%	+47%	-23%	-33%	-25%	+97%
	LNC	+58%	+31%	+48%	-22%	-33%	-26%	+99%
June 10	LAI	+78%	+51%	+61%	-13%	-14%	-14%	+87%
	LIA	+79%	+49%	+60%	-13%	-16%	-15%	+88%
	LW	+79%	+49%	+60%	-13%	-16%	-15%	+88%
	SAI	+81%	+50%	+61%	-13%	-15%	-14%	+87%
	SIA	+79%	+49%	+60%	-14%	-16%	-15%	+88%
	LNC	+90%	+51%	+63%	-9%	-16%	-13%	+88%

schemes (Table 4.3), the relative effects of doubling CO₂ were similar for all vertical aggregation schemes.

4.1.4 Conclusions

The leaf submodel, including gas exchange and energy balance, is the basic unit from which extrapolation to the level of the plant canopy can be made. This extrapolation requires a detailed description of the micro-environmental variables, the inputs to the leaf submodel, for each leaf within the canopy. Our multi-layer model with independent structural and physiological parameters and 21 leaf classes in each of 10 layers, together with a well-tested mechanistic leaf gas exchange submodel, ensures a reliable exploration of the canopy response to short term exposure to elevated CO₂. By integrating temporal and spatial variability of environmental inputs to the leaf model, the use of the canopy model provides a much more robust estimation of the effects of short-term

doubling of CO₂ than is possible from single leaf measurements.

In order to incorporate the canopy model into a whole plant growth model to simulate effects over time, simplifications will become necessary. Hence, the most detailed version of the canopy model provides a solid reference against which to compare the performance of various simplification schemes. Based on our analysis, we draw the following conclusions.

1) The daily total assimilation of *Quercus coccifera* canopy would be expected to increase by approx. 50-60% and transpiration to decline by 15-25% under short-term exposure to doubled CO₂. This would result in approximately a doubling of whole canopy water use efficiency.

2) The leaf energy balance is an essential part of the leaf submodel. Ignoring it will lead to potentially large errors in leaf temperature, and result in unacceptably large errors in estimation of canopy gas exchange.

3) Multi-layer canopy models with Gaussian integration for sunlit leaves and a single

averaged class of shaded leaves give excellent results. Multi-layer models with a single average sunlit and a single average shaded leaf class can satisfactorily describe canopy responses if errors of as much as 15% are acceptable.

4) If a level of 15% relative error is acceptable, a single-layer canopy model with vertical aggregation of leaf classes may be adopted, i.e., incorporating a single average sunlit and a single average shaded leaf class.

5) Canopy models that do not distinguish between sunlit and shaded leaves severely overestimate both assimilation and transpiration and should be avoided.

6) Use of a constant profile of stem inclination, leaf inclination and leaf width leads to minimal errors. A constant profile of leaf area index and stem area index result in errors of about 5%. When quantitative data for these profiles are lacking, qualitative agreement can be achieved by assuming a linearly increasing stem area index profile and a parabolic leaf area index profile. A constant profile of leaf nitrogen content underestimates daily assimilation and transpiration by more than 10%, particularly for a dense canopy with considerable self-shading. It is preferable to adopt a linearly or exponentially decreasing leaf nitrogen content (and/or photosynthetic capacity) with depth.

8) If only the relative response of canopy assimilation, transpiration and water use efficiency to elevated CO₂ is of interest, each of the various simplification schemes presented above is adequate.

It should be emphasized that these conclusions are based on a canopy of moderate LAI (4.4), composed of relatively small leaves (2.5 cm). It should also be stressed that our conclusions about canopy response to elevated CO₂ are predictions for short-term exposure to CO₂ only. While we anticipate that generalizations relating to extrapolating from leaf level models to the level of the whole canopy models should apply generally, several additional factors become important at longer time scales. Whereas we have assumed a constant canopy structure, changes in above ground biomass, leaf size and total leaf area have frequently been reported in experimental studies of

longer-term exposure (weeks, months) to elevated CO₂ (Cure and Acock 1986), all of which would significantly affect vertical profiles of leaf model input variables. And while we assume constant leaf physiology, numerous studies indicate that changes in leaf N and photosynthetic capacity frequently occur in plants grown at elevated CO₂ (Sage *et al.* 1989; Larigauderie *et al.* 1988; Wulff and Strain, 1982; Cure and Acock, 1986). Changes in both canopy structure and leaf physiology will have to be considered in analyzing long term effects of growth in high CO₂ on whole plant CO₂ assimilation and water relations.

4.2.0 A Comparison of Three Models of Radiation Transfer in a Canopy

Models of radiation transfer in canopies are applied mainly in two fields. For the applications in plant micrometeorology and productivity, simplified versions of radiation transfer are often required. Remote sensing of vegetation that basically depends on patterns of bidirectional reflection from canopies, however, demands sophisticated models of bidirectional transfer of radiation in canopies. Since radiation sources usually come from all directions in the sky, and leaves scatter radiation in all directions, radiation transfer is in fact always a bidirectional transfer. Any radiation transfer models neglecting the bidirectional nature are simplified models. The models of Kubelka and Munk (1931), Monsi and Saeki (1953), de Wit (1965), and many others, are such kinds of models. Goudriaan's model (1977) was a bidirectional model but due to the iteration method used to solve the equations, radiation variation in different azimuths was ignored.

Three models of bidirectional transfer of radiation in canopies, CUPID, developed by Norman (1978, 1980, 1982), Caldwell's (Caldwell *et al.* 1986) and KMC, developed by Chen (1985), are investigated here and their performances are compared. Norman dealt with the bidirectional transfer by separating direct radiation from the sun from diffuse radiation from the sky and assuming diffuse radiation at any levels in a canopy is uniform. Caldwell *et al.* (1986) also

treated direct and diffuse radiation separately, and in addition, he distinguished diffuse radiation directly from sky from that scattered by leaves. Chen (1985) derived two differential equations in vector-matrix form to describe bidirectional transfer of radiation in canopies. Both Norman's and Caldwell's models avoided complete treatment of bidirectional transfer by making simplifying assumptions. Although these assumptions are physically acceptable, consequences of these assumptions have never been fully studied. Simplifications are inevitable for developing a model, but it is important to understand the consequences of the simplifications, since it helps us to understand the usefulness and limitations of the models. It is by no means easy, however, to examine the consequences of a simplifying assumption. Comparison of results from models with real measured data cannot reveal the consequence of a specific simplifying assumption, since there are many other simplifications in the model compared with a real canopy. The only way to examine the consequences of a specific simplifying assumption is to compare the results from the models with the simplification with the results from a model without the simplification. To make the comparison meaningful, the remaining parts of the models must be consistent with each other. This is not a trivial requirement, since individual modelers always have their own preference in choosing model structure and functions, and the communication between modelers is usually poor. Although the ultimate validation of a model is to compare model outputs with measured data, comparison between models is important as well. It improves communication between modelers, that has been proven so difficult to do. It enhances confidence of the modelers, because it is hard to make a large program bug-free. Moreover, although Chen's model KMC is conceptually simple and can provide analytical solutions to bidirectional transfer of radiation in canopies, the mathematics employed is more complicated and requires longer computer time. Norman's and Caldwell's models are more practical to use.

Radiation profiles in a canopy and bidirectional reflectance from a canopy are examined here. Since CUPID and KMC deal with profiles, bidirectional reflectance and

interceptions, while Caldwell's model in its current version only deals with interception, in this section only Norman's model CUPID and Chen's model KMC are examined.

4.2.1 Norman's Approach

Radiation transfer in a canopy. Two radiation sources, sky diffuse and sun direct, were clearly distinguished. The sky diffuse radiation was assumed uniform. The radiation in a canopy was assumed to be composed of three components: direct beam from the sun, diffuse radiation of both directly from the sky and that generated by multiple scattering by leaves. Extinction of the sun beam into the canopy was straightforward based on Beer's law, although the extinction coefficient was determined according to the sun zenith and azimuth angles. The diffuse radiation, however, comes from all directions. To avoid solving bidirectional transfer of radiation in the canopy, Norman made a simplifying assumption: diffuse radiation at each level in the canopy, either downward or upward, was uniform. This was true in fact only for a canopy with horizontal, Lambertian leaves. Deviation from this condition will cause error in calculation of radiation profile in a canopy. To examine the magnitude of this error is one of the main purposes of this section.

Once the uniformity of the diffuse radiation was assumed, diffuse radiation at each level in a canopy could be fully described by two variables, the total amount of downward and the total amount of upward diffuse radiation, and the transfer of the sky diffuse radiation in a canopy could be represented by Kubelka-Munk equations and solved analytically. Norman used the discrete form of Kubelka-Munk equations and solutions were given for total amounts of downward and upward radiation at the bottom (or top) of each canopy layer. The diffuse radiation scattered by leaves to the direct sun beam was included in the transfer equations as additional sources. But once the source terms were added, analytical solutions to Kubelka-Munk equations were no longer possible. Norman solved the equations by a few iterations starting from the analytical solutions without sources.

The solutions of Kubelka-Munk equations in discrete form are accurate only for a thin canopy layer. The term thin means multiple scattering within the layer is negligible. For a canopy with a total leaf area index of 4 divided into 10 layers, each layer has a leaf area index of 0.4, which cannot be treated as a thin layer. To solve this problem Norman developed a 'thick' layer approach. He divided a 'thick' layer into a number of thin sublayers, and calculated the reflectance from the top and transmittance through the bottom of this layer by solving Kubelka-Munk equations for this thick layer. The reflectance and transmittance thus obtained included the multiple scattering within this layer. When they were used in the whole canopy model with thick layers, accuracy is greatly improved without a substantial increase of computer time.

Bidirectional reflectance of the entire canopy. As a matter of fact, once the diffuse upward radiation at the top of the canopy is obtained, it contains information of bidirectional reflectance. But due to the assumption of uniformity, this information was lost. Norman then developed a method to calculate the bidirectional reflectance directly.

When one looks into a canopy from a direction specified by a view zenith and a view azimuth angle, a fraction of the whole viewing field occupied by a certain layer (including the soil surface) can be easily calculated by using the extinction coefficient of a direct beam incident from the same direction as the view direction. The leaves in each layer that can be seen are either sunlit or shaded. For an inclined shaded leaf with a zenith angle of leaf normal q , the fraction of the upper hemisphere seen by the upper and lower faces of the leaf are $(1+\cos q)/2$ and $(1-\cos q)/2$, respectively. Alternatively, the fraction of the lower hemisphere seen by the upper and lower faces of the leaf are $(1-\cos q)/2$ and $(1+\cos q)/2$, respectively (Norman, 1980). Based on the assumption that the downward and upward diffuse radiation is always uniform, the intercepted diffuse radiation by an inclined leaf can be calculated from these fractions multiplied by the intensity of the diffuse radiation at the

level where this leaf is located. Thus, the bidirectional reflectance and transmittance of the shaded leaves can be obtained when the leaf scattering characteristics are known. For a sunlit leaf, the irradiance from the sun beam should be added. This can be obtained from the beam flux density and the incident angle of the sun beam relative to the leaf normal, which is a function of beam and leaf normal directions. All leaf angle classes must be included and weighted by their areas in the layer. Then scattered radiance from each layer are added together weighted by the fraction of the viewing field occupied by each layer.

4.2.2 Chen's Model

The Kubelka-Munk equations consider only the total amounts of downward and upward radiation, so they cannot be used to solve bidirectional transfer of radiation in a canopy. If a whole hemisphere is divided into a number of contiguous sectors, and radiation from each sector is arranged orderly into an one-dimensional array, the radiation from different directions of a hemisphere can be represented by a radiation vector. Under this notation, radiation from a uniform sky is represented by such a radiation vector with all the elements having the same values, if the radiation intensities refer to those at the planes perpendicular to the radiation directions. Any non-uniform sky can be easily described by assigning appropriate values of radiation intensities to the corresponding sectors. Even the direct radiation from the sun can be included, which enormously increases the value of radiation intensity in the sector where the sun is located. Therefore, there is no need to treat direct and diffuse radiation separately. The radiation condition of the sky, with the sun and clouds at any position in the sky can be fully described by a downward radiation vector. Moreover, reflected or transmitted radiation in different directions in the upper and lower hemisphere can also be arranged into an array of the same order to form a scattered upward radiation vector and a scattered downward radiation vector.

Lambertian reflection or transmission are only an idealized situation. Generally, reflection and transmission coefficients of a

leaf depend on viewing direction as well as incident direction. Using the notion of radiation vector, a bidirectional reflection coefficient r_{ij} represents the ratio of the value of the reflected radiation vector in sector j , over the value of the incident radiation vector in sector i . If all reflection coefficients for each viewing direction i and incident direction j are arranged into rows and columns, respectively, in the same order as defined in the radiation vector, they form a two-dimensional array, called the reflection matrix of the leaf, which fully describes the characteristics of bidirectional reflection of the leaf. The transmission matrix of a leaf can be formed in the same way. The scattering characteristics of any horizontal canopy layers containing a number of leaves in various inclinations and orientations can also be completely specified by a bidirectional reflection and transmission matrix.

Using the notion of radiation vectors, the bidirectional transfer of radiation through a canopy can be specified to find the upward and downward radiation vectors at any level in a canopy when an incoming downward radiation vector from the sky is given. Using the notion of a scattering matrix, the bidirectional reflection from the top of a canopy can be specified to find the bidirectional reflection matrix at the top of a given canopy with a known structure, leaf reflection, and transmission matrices. Using vector and matrix notation, Chen (1985) derived two differential equations where the two variables are downward and upward radiation vectors, and coefficients are bidirectional backward-scattering and forward-scattering matrices. The equations are similar to the Kubelka-Munk equations in the appearance, but the essential difference is that Chen's equations deal with bidirectional transfer of radiation in canopies. Analytical solutions to the profiles of downward and upward radiation vectors as well as the bidirectional reflectance matrix of the whole canopy have been found. The solutions to Chen's equations are much more complex than those to Kubelka-Munk equations, since multiplication of two matrices is not permutable, division of scalar variables must be replaced by matrix inversion, and the square root operation of

variable must be replaced by solving for eigen values and similarity transformation of a matrix. Chen's equations and the analytical solutions are presented as follows.

$$dx/dl = -(M-F)x + By \quad (4.1)$$

$$dy/dl = -Bx + (M-F)y \quad (4.2)$$

with boundary conditions:

$$x(l=0) = d \quad (4.3)$$

$$y(l=L) = R_s x(l=L) \quad (4.4)$$

where x and y are downward and upward radiation vectors, respectively, M the penetration matrix, F the forward-scattering and B the backward-scattering matrices of the canopy layers, l the cumulative leaf area index downward, L the total leaf area index of the canopy, d the given incoming radiation vector, R_s the bidirectional reflectance matrix of soil surface.

Summing Eqs(4.1) and (4.2) gives

$$d(x+y)/dl = -(M-F+B)(x-y) \quad (4.5)$$

and subtracting (4.2) from (4.1) yields

$$d(x-y)/dl = -(M-F-R)(x+y) \quad (4.6)$$

Differentiating (4.6) with respect to l and using (4.5) gives

$$d(x-y)^2/dl = (M-F+R)(M-F-R)(x-y)^2 \quad (4.7)$$

Eq (4.7) can be solved as

$$x-y = V \exp(Kl) V^{-1} c_1 + V \exp(-Kl) V^{-1} c_2 \quad (4.8)$$

where K is a diagonal matrix that can be obtained by similarity transformation, $V K^2 V^{-1} = (M-F+R)(M-F-R)$, and c_1 and c_2 are two constant vectors. From (4.6), $x+y$ can be obtained as

$$x+y = -(M-F+B) V K^{-1} V^{-1} [V \exp(Kl) V^{-1} c_1 - V \exp(-Kl) V^{-1} c_2] \quad (4.9)$$

From (4.8) and (4.9) x and y can be found

$$x = -H V \exp(Kl) V^{-1} c_1 + J V \exp(-Kl) V^{-1} c_2 \quad (4.10)$$

$$y = -J V \exp(Kl) V^{-1} c_1 + H V \exp(-Kl) V^{-1} c_2 \quad (4.11)$$

where $H = (M-F+B) V K^{-1} V^{-1} - I$, $J = (M-F+B) V K^{-1} V^{-1} + I$, in which I is the identity matrix. The two constant vectors c_1 and c_2 can be fixed based on boundary conditions (4.3) and (4.4):

$$c_1 = -0.5 J^{-1} F d \quad (4.12)$$

$$c_2 = 0.5 J^{-1} (I - R_s F) d \quad (4.13)$$

where $R_i = H J^{-1}$ is the bidirectional reflectance matrix of a canopy with an

infinite L , $F=(1+CR_i)^{-1}C$, in which $C=E(-L)GE(-L)$, where $G=(R_sR_i-1)^{-1}(R_i-R_s)$, and $E(-L)=V\exp(-KL)V^{-1}$. Substituting (4.12) and (4.13) into (4.10) and (4.11), the downward and upward radiation vectors at level of the cumulative leaf area index l can be obtained:

$$x(l) = [R_i E(l) F - E(-l) (R_i F - I)] d \quad (4.14)$$

$$y(l) = [E(l) F - R_i E(-l) (R_i F - I)] d \quad (4.15)$$

where $E(l)=V\exp(Kl)V^{-1}$, $E(-l)=V\exp(-Kl)V^{-1}$. The bidirectional reflectance matrix of the whole canopy R_{cp} can be obtained as:

$$R_{cp} = R_i + (I - R_i^2) F \quad (4.16)$$

When L tends to infinity, $\exp(-kL)$ and thus C and F tend to zero, R_{cp} becomes R_i .

4.2.3 Results

Variations of downward diffuse radiation in zenith directions. When radiation penetrates through a canopy with non-horizontal leaves, it extinguishes more quickly as the zenith angle of the radiation source increases. Therefore, even for the case when the diffuse radiation incident on the top of a canopy is uniform in all zenith directions, the diffuse radiation in a canopy, both downward and upward, is non-uniform.

Fig (4.1) shows the dependence on zenith angle of the downward diffuse radiance at the bottom of a canopy with a spherical leaf angle distribution obtained from Chen's model (KMC) and Norman's model (CUPID). It can be seen that the downward diffuse radiances from KMC are not uniform. At the bottom of the canopy, only radiation from low zeniths remains. CUPID gives much lower values of radiance for visible radiation. For near-infrared radiation, the reduction of the radiation at the bottom of the canopy is partly compensated by the strong multiple scattering between the leaves due to the much higher scattering coefficients of the leaves to the near-infrared radiation.

Profiles of the downward and upward diffuse radiation. Profiles of the downward and upward diffuse visible or near-infrared radiation in canopies are shown in Fig (4.2) and Fig (4.3). The letters in each panels are abbreviations: L stands for Lambertian, N for non-Lambertian, and the

word non-Lambertian here means the scattering characteristics of the leaves are described by Norman's parabolic functions, O for ideally overcast sky, C for clear sky and the figure following C stand for the sun zenith angle. The solid lines represent the results from KMC, and the broken lines for CUPID.

It can be seen from Fig (4.2) that the intensities of the downward diffuse visible radiation within a canopy obtained from CUPID are always smaller than those from KMC. This is because of the overestimated interception of the diffuse radiation as a result of assuming the diffuse radiation being always uniform in each direction. For near-infrared radiation, the scattering coefficients of the leaves are very high, a large part of the intercepted radiation are re-scattered rather than directly absorbed by leaves. Since the overestimated interception also overestimates the diffuse radiation resulted from the multiple scattering, it is hard to say how CUPID deviate from KMC. Fig (4.2) shows that, under overcast sky, these two factors are compensating each other, while under clear sky, CUPID overestimates the intensities of the diffuse near-infrared radiation within the canopy. Fig (4.3) shows that the upward diffuse radiation obtained from CUPID is always larger than that from KMC due to the overestimated interception of the diffuse radiation by CUPID. Comparing with the drastic differences in the downward diffuse radiance obtained from the two models shown in Fig (4.1), however, the deviation of the downward and upward diffuse radiation profiles obtained from the two models are surprisingly small.

Bidirectional reflectance from the entire canopy. Bidirectional reflected radiance in the principal plane under a clear sky with the sun at zenith of 65 degrees from the entire canopy (which has a spherical leaf angle distribution) are shown in Fig (4.4). For visible radiation, the facing-sun reflected radiances are much larger than the back-sun ones. For near-infrared radiation, however, they are more symmetrical due to the very high scattering coefficients. The differences between the results from the two models are negligible when the sun is

Figure 4.1: Comparison of the variation in zenith direction of the downward diffuse radiation obtained from Chen's model KMC and Norman's model CUPID.

Figure 4.2: Comparison of profiles of downward diffuse radiation obtained from models of KMC and CUPID.

Figure 4.3: Comparison of profiles of upward diffuse radiation obtained from models of KMC and CUPID.

Figure 4.4: Comparison of bidirectional reflectance obtained from models of KMC and CUPID.

high, and increase as the sun approaches the horizon. But it can be seen that the differences are quite small compared with those of radiation profiles shown in Fig (4.3). This can be expected, however, since in CUPID the bidirectional reflectance from the entire canopy is calculated directly from the leaves in each layers. As shown in Fig (4.3), the downward diffuse radiation from the two models become more different as one moves down into the canopy, but the leaves deep in the canopy contribute little to the bidirectional reflectance of the entire canopy.

4.2.4 Conclusions

Norman's assumption that diffuse radiation within a canopy remains uniform affects the accuracy of the calculated profiles of diffuse radiation in a canopy, but the errors incurred are small. The effect of this approximation on the bidirectional reflectance from the entire canopy, is quite small. Therefore, Norman's model can be satisfactorily used for modeling radiation transfer in a canopy.

4.3.0 Coordination Theory of Leaf Nitrogen Allocation in a Canopy

In spite of the complexity of plant response to environmental factors revealed by laboratory and field studies, theoretical biologists try to find simple rules which govern plant behavior. Optimization theory is one such attempt. The basic assumption is that after millions of years of strong selection, those plants which have optimized responses to their environment have survived and are successful. Optimization theory has been utilized to examine stomatal behavior (Cowan and Farquhar, 1977), dry matter partition between shoot and root (Schulze *et al.* 1983; Hilbert 1990; Hilbert *et al.* 1991), adjustment of length of the periods of vegetative and reproductive growth, and nitrogen distribution within a canopy (Field, 1983; Hirose and Werger, 1987). The patterns of control variables that are potentially obtained based on optimization theory do indeed resemble the actual ones, suggesting that plants may exhibit tendencies to optimize.

Optimization theory, however, has encountered some difficulties. Optimization is often made over a definite period of time, either twenty-four hours or a whole growing season, and the optimal control strategy obtained is specific to the patterns exhibited by driving variables over this time period. It is hard to imagine that plants can foresee such patterns. It might be argued that plants have 'learned' to respond to an 'average' environment in which they survived through long period of evolution, but it does not help to answer the question how plants respond to actual environmental conditions that always deviate from the 'average'. Secondly, oversimplifications have to be made in order to obtain an analytical solution to the optimal control strategy, *i.e.* the rule governing the response of the plant to the environment, which is the most important thing to be known. When the model becomes more realistic and complex, only numerical solutions to the optimal strategy can be obtained, and no simple rules governing the response of the plant to the environment can be derived from those numerical solutions. Finally, biologists remain unconvinced about optimization due to the lack of realistic mechanisms that will permit optimal control.

On the other hand, coordination of growth in the whole plant, whereby a proper balance is maintained between shoot and root, between nitrogen content and carbon content, between vegetative growth and fruiting, *etc.*, is well known (Wareing 1970; Reynolds and Thornley 1981). In this section, which considers nitrogen distribution within a plant canopy, an alternative to optimization theory (Field, 1983; Hirose and Werger, 1987); the "coordination theory" is proposed. We hypothesize that the basis of plant response to the environment is related to internal coordination of two processes limiting leaf photosynthesis. We will show that the daily carbon assimilation of a canopy with a nitrogen distribution resulting from internal coordination is close to that obtained by optimization theory.

4.3.1 Method

Leaf gas exchange model. Among a variety of models of leaf photosynthesis, we

have chosen to investigate canopy nitrogen distribution which explicitly describes two processes that may be limiting for photosynthesis. The model was developed for whole leaf gas exchange by Harley and Tenhunen (1991), and is based on Farquhar and von Caemmerer (1983) (for a summary description see Chapter 3).

The effect of leaf nitrogen content on photosynthetic capacity. It has long been observed that for a wide variety of plants, leaf nitrogen content and photosynthetic capacity are highly correlated (Natr 1975; Field 1983; Hirose and Werger 1987). In the photosynthesis model of cotton leaves (Harley *et al.* 1991), the maximum rate of W_c and W_j at the optimum leaf temperature, V_{cmax} and J_{max} , respectively, are found to be linearly related to the leaf nitrogen content:

$$V_{cmax} = a_v \cdot N + b_v \quad (4.17)$$

$$J_{max} = a_j \cdot N + b_j \quad (4.18)$$

where a_v , b_v , a_j and b_j are parameters determined through linear regression. For cotton leaves, $a_v = -9.6$, $b_v = 60.0$, $a_j = -4.6$, $b_j = 98.1$ (Harley *et al.* 1991). Since V_{cmax} and J_{max} are two important parameters determining the potential Rubisco-limited rate of carboxylation W_c , and the potential RubP-limited rate of carboxylation, W_j , W_c and W_j are regulated by the leaf nitrogen content. Fig (4.5A) shows the dependence of W_c and W_j on leaf nitrogen content for the leaf temperature of 25C, the intercellular CO_2 concentration of 200 ppm, and the photosynthetically active radiation (PAR) of 100, 500, 900, and 1300 $\mu mol s^{-1} m^{-2}$. It can be seen that the response of W_c to nitrogen does not change with PAR, while W_j depends strongly on PAR.

The coordination theory. It can be seen from Fig (4.5A) that the leaf nitrogen content required to balance W_c and W_j depends strongly on the PAR level if the leaf temperature and intercellular CO_2 concentration is fixed. Fig (4.5B) shows explicitly the dependence of the imbalance between W_c and W_j on the leaf nitrogen

content ($W_c - W_j$) at different leaves of PAR. It can be seen that the amount of leaf nitrogen which is required to bring a balance between W_c and W_j increases with the PAR level. Within a canopy, particularly a dense one, PAR level changes more strongly than other micrometeorological factors. It can be expected that the imbalance between W_c and W_j of the leaves in the top layers would be quite different with those of the leaves in the bottom layers if the leaf nitrogen contents in each layer are the same. Our coordination theory assumes that plants would try to reduce the imbalance between W_c and W_j . There might be several possible ways the plants can do, in this section however, it is assumed that the plants would coordinate the leaf nitrogen contents in different layers. From Fig (4.5B) it can be seen that in order to keep balance between W_c and W_j the leaves at a higher PAR level demands a higher nitrogen content than the leaves at a lower PAR level. This analysis is only based, however, on the assumption of a fixed leaf temperature and fixed intercellular CO_2 concentration. In a canopy, leaf temperature and intercellular CO_2 concentration are strongly affected by stomatal conductance, which depends on various environmental factors such as wind speed, air temperature, air humidity, and radiation (short wave radiation as well as long wave radiation). The actual imbalance of a leaf in a given layer would be determined by the combination of all these environmental factors. Therefore, a canopy model which allows one to simulate canopy micrometeorology and daily canopy photosynthesis is required to test the coordination theory and to see if this theory would give a realistic distribution of leaf nitrogen contents. The canopy model used here is the module CANDO described in section 4.1.0.

Since no plant growth and root activity is considered in this section, the total amount of leaf nitrogen is assumed to be fixed. The simulation is run hourly for a typical summer day from sunrise to sunset for a cotton canopy, with an arbitrarily

Figure 4.5: (A) W_c and W_j as a function of leaf nitrogen content at the PAR leaves of 100, 500, 900 and 1300 $\mu\text{mol s}^{-1} \text{m}^{-2}$, and (B) corresponding imbalance ($W_c - W_j$). The leaf temperature is 25C, and the intercellular CO_2 concentration is 200 ppm.

determined vertical profile of leaf nitrogen content first (a uniform one, for instance). In each hour, vertical profiles of radiation, wind speed, air temperature and humidity are calculated. Every hour the difference between W_c and W_j of each leaf group in each layer is calculated and then added up, weighted by the leaf area of the group to obtain the imbalance between W_c and W_j averaged over the whole layer. These hourly imbalances are accumulated to obtain daily imbalances. Our coordination theory assume that these daily imbalances act as a measure of 'sink strength' for nitrogen, and the nitrogen is reallocated between layers according to the relative value of the daily imbalances, under the constraint of a fixed total amount of nitrogen. The leaf nitrogen contents are also restricted by a maximum and a minimum leaf nitrogen content. The nitrogen reallocation rate is determined by a parameter that reflects the time needed for coordination taking place. After a new leaf nitrogen profile is obtained, the daily simulation is run again under the same weather condition. This procedure is repeated for 10 days to obtain the final distribution of leaf nitrogen.

4.3.2 Results

In many plant communities, nitrogen availability limits canopy assimilation. A decreasing leaf nitrogen with depth in the canopy has been observed (Friedrich and Huffaker 1980; Field 1983; Field and Mooney 1983). Hirose and Werger (1987) proposed that the decreasing leaf nitrogen with depth reflects the optimization of daily canopy assimilation. They assumed an exponentially decreasing nitrogen distribution within a canopy:

$$N(l) = N_0 \exp(-kl) \quad (4.19)$$

where l is the cumulative leaf area index from the top downward, N_0 the leaf nitrogen content at the top of the canopy, and k the attenuation coefficient. They found an optimal attenuation coefficient which maximized the daily canopy assimilation.

Fig (4.6) shows three different leaf nitrogen distributions within a canopy (uniform, optimal exponential and coordinated) and the corresponding daily

time courses of canopy photosynthetic rate at the total amount of nitrogen of 5 and 7 gm^{-2} . It can be seen that at both nitrogen levels, the uniform distribution gives the lowest canopy photosynthetic rate, and the coordinated distribution gives the highest one.

Fig (4.7) shows the daily total canopy assimilation obtained from these three distributions at four levels of total canopy nitrogen (4, 5, 6 and 7 gN/m^{-2}). It can be seen that the daily total canopy assimilation obtained from either distribution increases with the total amount of nitrogen, and that obtained from the coordinated theory at any level of total canopy nitrogen is consistently higher than that obtained from the optimal exponential leaf nitrogen distribution.

4.3.3 Conclusions and Discussion

Although both optimization theory and coordination theory try to explain plant behavior, they are quite different theories. Optimization theory starts with an assumed objective function which must be optimized, (daily carbon assimilation of a canopy in this case), then selects from all feasible control functions (leaf nitrogen distribution functions within the canopy in this case) the one which gives an optimized value for the objective function. The critical point of applying coordination theory is to determine which processes are to be coordinated, (the two processes possibly limiting leaf photosynthesis in this case), but with no *a priori* consideration of optimization.

The results of this study that the coordination of leaf photosynthesis through nitrogen distribution realizes optimization of daily canopy assimilation suggests that the coordination is a more fundamental concept than optimization. The coordination theory also brings together other two important concepts, balance and feedback. The goal of the coordination is internal balance, and the means of coordination is based on feedback. Although coordination is closely linked to balance, but they are different. Plants are never in a balance, facing an ever-changing environment, plants are involved in an endless balance seeking process.

Figure 4.6: Profiles of leaf nitrogen contents (uniform, optimal exponential and coordinated) and the corresponding daily time courses of canopy photosynthetic rate.

Figure 4.7: Comparison of daily canopy assimilation obtained from three different nitrogen distribution in the canopy at four levels of canopy nitrogen.

5.0.0 MODELING GROWTH AND ALLOCATION

The most important aspect of GePSI is its prediction of allocation of carbon (C) and nitrogen (N) for growth of the various plant organs (i.e., the interaction of component parts). Our ability to predict growth of plants at elevated CO₂ under a wide range of environmental conditions, including variable soil nutrient status, is critically dependent on the modeling of allocation. Consequently, much of our effort in this part of the program focuses on understanding and state-of-the-art modeling of resource allocation and biomass partitioning. Material in this chapter is taken from Hilbert (1990), Hilbert and Reynolds (1991), and Hilbert *et al.* (1991).

5.0.1 Objectives

The general objective is to understand and simulate the growth of whole plants in response to CO₂, temperature, light, and nitrogen. This work integrates results at the organ level (canopy and root) to predict root:shoot ratios, tissue carbon and N concentrations, and whole-plant growth rates. Specific objectives include:

- 1) To simulate the dynamic allocation of resources (C and N) to biomass growth, both above and belowground. This module will predict root:shoot ratio and growth rate based on inputs from the canopy module and root activity routines and must respond realistically to elevated CO₂ as well as water and N availability.
- 2) To understand and predict the allocation of N in leaves which controls the photosynthetic properties of a plant in response to light and CO₂. This involves understanding the response of photosynthetic properties to resource availability and simulating the dynamic allocation of N to photosynthetic enzymes in leaves.

5.1.0 Introduction: the Importance of Allocation in Plant Modeling

During the past two decades plant ecophysiology has been very successful in describing the controls on leaf level processes such as photosynthesis and transpiration (Mooney and Chiariello 1984, Pearcy *et al.*

1987) and progress has been made on the physiological behavior of roots (e.g., Schrader 1978, Weatherley 1982, Clarkson 1985). Thus, we now have a reasonably good understanding of how plants acquire carbon, nitrogen, and water and the environmental controls on rates of assimilation of these basic resources. This understanding has been applied in theoretical analysis as well as in a large number of simulation models of leaf and whole plant dynamics. Given this success, many ecophysiolgists are now stressing the importance of whole plant studies that integrate physiological knowledge at the organ level with the controls on resource allocation (Mooney and Chiariello 1984) and the effects of multiple resource limitation (Chapin *et al.* 1987, Mooney *et al.* 1987). The basic difficulty at this time is that while we are often able to predict the rates of resource acquisition (given information about the environment of the roots or shoots), we have much less ability to predict the allocation of these resources to plant parts or processes. Consequently, plant growth in response to patterns of resource availability, including elevated carbon dioxide, is poorly understood and difficult to predict. An understanding of allocation and an ability to model it are an essential part of developing models which predict response to elevated atmospheric CO₂ and global change.

Much productive effort has been expended to describe and understand the controls on photosynthesis with the often implicit assumption that this knowledge helps to explain whole plant behaviors. Yet, while understanding of organ level processes is necessary for prediction of whole plant behavior, it is not sufficient. This is why understanding allocation is critical. Photosynthetic rates are often not well-correlated with growth rates because of the importance of C allocation to subsequent C gain (see discussions by Monsi 1968, Charles-Edwards 1982, Mooney 1987). The comparison of growth rates of commercial and wild radishes is a good illustration (Mooney and Chiariello 1984) -- both radishes have the same photosynthetic rates per unit leaf area

but different carbon allocation patterns (the wild form accumulates about twice the dry weight of the commercial form after five weeks of growth as a result of greater allocation of C to leaves). Many species of *Gossypium* studied by El-Sharkawy *et al.* (1965) had similar photosynthetic rates but differed significantly in their production of dry matter. Similarly, when estimated over a season or more, differences in maintenance respiration or C loss from roots can cause differences in productivity, even when long term photosynthetic C fixation and water use are the same.

Patterns of resource allocation to roots and shoots, therefore, are critical in determining the physiological efficiency, relative growth rate, ultimate size, and reproductive effort of plants. In fact, changing allocation patterns may be one of the most effective means by which plants deal with environmental stresses (Chapin *et al.* 1987) and one of the main challenges in understanding growth of plants is the quantitative description of this partitioning of growth between roots and shoots (Johnson 1985). A comprehensive understanding of allocation and its controls will significantly increase our basic understanding of whole plant growth and the mechanisms by which plants maximize their resource acquisition.

Our modeling related to allocation (biomass partitioning) includes a theoretical approach which predicts the optimal allocation of N to the photosynthetic process in leaves and the partitioning of biomass between roots and shoots (Section 5.2.0). We are also developing simulation techniques which will predict the dynamic allocation patterns of C and N in response to growth at elevated levels of carbon dioxide (Section 5.3.0). These approaches are based on the well established principle of balanced root and shoot activity but extend it by considering the variable allocation of N to photosynthetic enzymes.

5.2.0 Optimal Leaf Nitrogen Concentration and Root:Shoot Ratio in Response to Light, Nutrition, and Carbon Dioxide

5.2.1 Background

Morphological and physiological characteristics of plants vary considerably in response to resource availability. The regulation of leaf nitrogen, for example, is an important means by which plants can adjust their physiological status to the prevailing environment. Root:shoot ratios also vary with resource availability and can directly affect leaf nitrogen concentrations. These interdependent responses, occurring both temporally and spatially, must be understood to interpret plant adaptations to various environments, responses to resource availability, and temporal variations in plant characteristics related to seasonal changes in resource levels. Phenotypic plasticity of this kind complicates the task of predicting plant growth since knowledge about a plant growing in one environment may not apply in another. A good example is the attempt to predict plant growth following the expected doubling of atmospheric carbon dioxide by the middle of the next century (Bacastow and Keeling 1973, Woodwell *et al.* 1983). Studies of plants grown for long periods at high carbon dioxide concentrations often indicate that photosynthetic rates are lower than would be expected from brief exposure to elevated carbon dioxide concentrations, that significant changes in root:shoot ratio occur, and that growth is less stimulated than would have been predicted from short term experiments (Wong 1979, Larigauderie *et al.* 1988). A fuller understanding of coupled changes in photosynthetic efficiency and root:shoot partitioning in response to resource availability is necessary to extend our ability to predict growth under a wide range of conditions.

Here, we present a quantitative analysis of the leaf nitrogen concentration and root:shoot ratio that maximize whole-plant relative growth rate depending on the availability of light, carbon dioxide, and nitrogen. We implicitly assume that knowledge of the optimal response to resource availability can be used to predict the actual response. Of course, not all plants will behave optimally in all environments and not all responses to resource availability are adaptive. Obligate shade plants, for example, are often unable to adjust to growth in high light (Björkman 1981). Thus our

analysis of optimal leaf nitrogen and root:shoot ratio does not necessarily predict the precise response that a specific plant species will display when exposed to an altered environment. It is nonetheless very important to know what optimal behavior is in a given environment and to understand the interacting costs and benefits associated with this behavior. While plants differ in the degree of plasticity that they can display, we still expect them to operate optimally within the environmental conditions that they typically experience (e.g. Gadgil and Gadgil 1979).

Two general approaches have been used to investigate responses to resource availability. One, focusing on biomass allocation, is exemplified by the balanced root and shoot activity theory (Brouwer 1962, Davidson 1969, Thornley 1972), the other by cost/benefit analysis of resource allocation within organs (Givnish 1986a), especially nitrogen concentration in leaves.

The balanced activity theory states that the assimilation of carbon by the shoot is kept in balance with the uptake of nitrogen by the roots. It was quantified by Davidson (1969) as

$$\sigma_s W_s = \lambda \sigma_r W_r \quad (5.1)$$

where σ_s is the shoot specific activity (carbon uptake rate per unit shoot weight), σ_r is the root specific activity (usually defined as nitrogen uptake rate per unit root weight), W_s and W_r are the weight of shoots and roots respectively, and λ is a proportionality constant equaling the C:N ratio in dry matter. This balance of activity is assumed to be maintained through changes in allocation to shoot and root biomass. So, for example, when plants become carbon limited due to shading or aboveground herbivory, they compensate by allocating more resources to shoot growth and less to roots (Jameson 1963, Chapin 1980, Painter and Detling 1981, Archer and Tieszen 1986). Changing specific activities can also balance root and shoot activity but, unfortunately, the theory can not precisely predict the degree to which specific activity changes simultaneously with altered biomass allocation. Another deficiency of this approach is the assumption of a constant C:N ratio in the biomass.

The plasticity of physiological processes has been studied through the analysis of optimal strategies, especially of leaves (e.g. Mooney and Gulmon 1979, Givnish 1986b). One approach relies on analysis of the costs and benefits of particular strategies (Givnish 1986a) and an important axiom, borrowed from microeconomics, that production is maximized when marginal revenue equals marginal cost. Revenue is the gross resource gain and is a function of the allocation of some resource. Marginal revenue is the derivative of the relationship describing revenue as a function of allocation. Cost is the expense associated with each level of resource allocation and marginal cost is again defined as the derivative of this function. Occasionally, similar analysis have been made for the costs and revenue of producing roots and shoots (Oriens and Solbrig 1977, Gadgil and Gadgil 1979) although these have been mostly qualitative and empirical.

A particularly important problem is the determination of optimal leaf nitrogen concentration. The primary motivation for the study of leaf nitrogen concentration is the strong correlation between it and photosynthetic capacity (Mooney *et al.* 1978, Gulmon and Chu 1981, Evans 1983, Field *et al.* 1983, Field and Mooney 1986) and ultimately plant growth rates. The reason for this relationship is that a large proportion of leaf nitrogen is contained in photosynthetic enzymes, including ribulose 1,5-bisphosphate (RuBP) carboxylase-oxygenase (Huffaker 1982, Evans 1983, Yamashita and Fujino 1987), carbonic anhydrase (Cowan 1986), and enzymes involved in electron transport and the regeneration of RuBP (Kirk and Tilney-Bassett 1978, Field and Mooney 1986, Evans and Terashima 1987).

Mooney and Gulmon (1979) present a qualitative argument for the increase in leaf nitrogen which is generally observed in plants growing in high light conditions. They recognize that the marginal revenue (net gain in their terminology) of investment in leaf enzymes declines to zero as the photosynthesis versus leaf nitrogen curve saturates. Since this curve is observed to saturate earlier for plants grown at low light, they infer that marginal revenue declines to zero at lower leaf nitrogen concentrations

when plants are grown in low light. They also hypothesize that the cost of investment in leaf enzymes is at least a linear and probably an upward bending function of leaf nitrogen concentration so that the optimal investment in leaf nitrogen must be lower for shade plants. While qualitatively useful, this argument lacks a precise statement of costs and does not consider changes in root and shoot fraction, which we will show to be important in determining both revenue and cost at the whole-plant level.

A number of mathematical analyses have investigated the optimal spatial allocation pattern of a fixed amount of shoot nitrogen (Field 1983, Cowan 1986, Charles-Edwards *et al.* 1987, and Hirose and Werger 1987). While very useful, none of these studies ask the broader question of optimal allocation in terms of whole plant carbon balance or relative growth rate.

Here we simultaneously consider both morphological and physiological responses and predict the optimal leaf nitrogen concentration and root:shoot ratio that maximize whole-plant relative growth rate. The optimal leaf nitrogen concentration for different levels of resource available to the root and shoot (light, carbon dioxide, and nitrogen availability) is determined as is the optimal root:shoot ratio that is necessary to produce that leaf nitrogen concentration. This synthesis of the balanced activity and optimal allocation approaches is made possible by a simple analysis of costs and benefits of nitrogen allocation in terms of biomass partitioning to the roots and shoots. We provide an analysis of the factors that influence optimal leaf nitrogen concentrations and demonstrate that the generally observed responses of leaf nitrogen concentrations to nutrition, light, and carbon dioxide concentration are adaptive in that they tend to maximize relative growth rate. At the same time we determine the optimal root:shoot ratio in response to resource availability. The value of this approach is the recognition that morphological and physiological responses to resource availability are interrelated and that changes in one are coupled with changes in the other. By considering both simultaneously, a more comprehensive

understanding of plant response to multiple resources is possible.

5.2.2 Derivation of the Optimization Criterion

We assume that the whole-plant growth rate is proportional to the rate of carbon gain,

$$dW/dt = kh\sigma_s W_s', \quad (5.2)$$

where W is the total plant dry weight (g), W_s is the dry weight of shoots (g), k is the proportionality constant between carbon and biomass (g biomass g⁻¹ C fixed), h is specific leaf area (m² leaf g⁻¹ shoot), and σ_s is the shoot specific activity on an area basis (g C m⁻² d⁻¹). Shoot specific activity is a complex variable that will be shown to depend on leaf nitrogen concentration (N), photon flux density (PFD), and internal CO₂ concentration (C). A list of variables used in section 5.2 and their dimensions is given in Table 5.1.

Dividing both sides of Eqn (5.2) by total plant weight (W) gives the expression for relative growth rate (RGR, d⁻¹),

$$(1/W) dW/dt = kh\sigma_s f_s \quad (5.3)$$

where f_s is the fraction of biomass in the shoot. Thus, RGR is directly proportional to both the fractional allocation of biomass to the shoots and to the photosynthetic rate of those shoots. However, there is a trade-off between shoot mass and photosynthetic capacity since allocation to roots is necessary to acquire the nitrogen that is used in photosynthetic enzymes. All else being equal, an increased shoot fraction must reduce the leaf nitrogen concentration and, consequently, the photosynthetic capacity. This linking between photosynthetic rates and root:shoot ratio is central to our approach and is analyzed by considering the costs and benefits (revenue) of investment in leaf nitrogen. We define the costs and revenue of leaf nitrogen in terms of the plants relative growth rate by assume that s_s and f_s are, in part, functions of leaf nitrogen concentration.

Using the identity $f_s = 1 - f_r$ where f_r is the fraction of biomass in the roots, Eqn (5.3) can be re-written as

$$(1/W) dW/dt = kh\sigma_s - kh\sigma_s f_r. \quad (5.4)$$

This approach is described in Hilbert (1990) and Hilbert *et al.* (1991). The terms on the right-hand-side of Eqn (5.4) represent the revenue ($kh\sigma_S$) and cost ($kh\sigma_S f_r$) associated with the investment in leaf nitrogen. Revenue is the RGR (d^{-1}) that would be possible if there was no need to invest in roots while cost is the decrease in RGR due to allocation to roots.

Marginal revenue (MR) and marginal cost (MC) (units: $g \text{ biomass } g^{-1} N d^{-1}$) are obtained from the derivative of the cost and revenue functions with respect to leaf nitrogen concentration (N) ($g \text{ nitrogen } m^{-2} \text{ leaf}$). Implicit differentiation of Eqn (5.4) yields

$$MR = d(\text{revenue})/dN = kh d\sigma_S/dN \quad (5.5)$$

and, recalling that both σ_S and f_r are functions of N ,

$$MC = kh(f_r d\sigma_S/dN + \sigma_S df_r/dN). \quad (5.6)$$

Thus, marginal revenue is primarily dependent on the slope of the photosynthesis versus N curve while marginal cost has two components, $f_r d\sigma_S/dN$ and $\sigma_S df_r/dN$. The leaf nitrogen concentration that maximizes RGR is considered optimal (N_{opt}) and occurs where $MC = MR$. Setting Eqn (5.5) equal to Eqn (5.6) and simplifying, the optimization criterion is given as

$$f_s d\sigma_S/dN = \sigma_S df_r/dN \quad (5.7)$$

Solving this equation for N provides the optimal leaf nitrogen concentration. As will be seen later, for a given set of environmental conditions, there is a unique root:shoot ratio that corresponds with this N_{opt} . Thus, by finding N_{opt} , we also find the optimal root:shoot ratio.

Alternatively, the optimal root:shoot ratio can be obtained by differentiating RGR by root fraction and setting the result equal to zero. Solving this equation for f_r gives the optimal root fraction and root:shoot ratio. We can then calculate a unique leaf nitrogen concentration associated with the predicted optimal root:shoot ratio. Since the optimization criterion found in this way is identical to Eqn. (5.7), the predicted optimal root:shoot ratios and N_{opt} are the same using either method. Thus, the optimization criterion provides both the physiological and morphological

characteristics that are optimal for any combination of light, carbon dioxide, and nitrogen uptake rate. Derivation of Eqn (5.7) was possible without specifying the functional relationships between σ_S , f_r , f_s , and N . In order to complete the analysis and determine the effects of CO_2 and light, we now specify these functions.

Shoot and root fractions as functions of leaf nitrogen concentration. To find f_s and f_r as functions of leaf nitrogen concentration (N), we assume balanced exponential growth (e.g., Thornley 1976); that is, a plant that is growing exponentially with constant shoot and root specific activities, root:shoot ratio, and carbon and nitrogen concentrations in its tissues. Nitrogen concentration in the plant ($g N g \text{ biomass}^{-1}$) is then determined by the rate of nitrogen uptake ($\sigma_r W_r$ in $g N d^{-1}$) divided by the growth rate of biomass ($g \text{ biomass } d^{-1}$) given by Eqn (5.2) (see Hilbert 1990). Nitrogen uptake rate is the product of root specific activity for nitrogen (σ_r , measured in $g N g^{-1} \text{ root } d^{-1}$) and root biomass (W_r). Assuming that all tissues have the same nitrogen concentration, dividing the tissue nitrogen concentration on a weight basis by the specific leaf area (h) gives the leaf nitrogen concentration on a leaf area basis ($g N m^{-2}$)

$$N = \sigma_r W_r / kh^2 \sigma_S W_s \quad (5.8)$$

Solving for $f_s = W_s/W$ gives

$$f_s = \sigma_r / (kh^2 \sigma_S N + \sigma_r). \quad (5.9)$$

Recalling that σ_S is a function of N , the derivative of f_s [Eqn (5.9)] with respect to leaf nitrogen is

$$df_s/dN = - \sigma_r kh^2 (\sigma_S + N d\sigma_S/dN) / (kh^2 \sigma_S N + \sigma_r)^2 \quad (5.10)$$

The shoot fraction f_s is, by definition, $(1 - f_r)$ so

$$df_r/dN = - df_s/dN \quad (5.11)$$

Shape of the photosynthesis vs. leaf nitrogen curve

Rectangular hyperbola. Several possible functions could be used for the relation between σ_S and N . The hyperbolic

Table 5.1: List of symbols used in the analysis of optimal allocation.

Symbol	Definition	Units
A_1	RuBP carboxylase limited photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
A_2	RuBP limited photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
C	intercellular concentration of CO_2	$\mu\text{l/l}$
f_r	fraction of biomass in the root	dimensionless
f_s	fraction of biomass in the shoot	dimensionless
h	specific leaf area	$\text{m}^2 \text{ g}^{-1}$
I	photosynthetically active radiation	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$
I_0	photon flux density at noon	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$
I_{max}	maximum rate of electron transport	$\mu\text{Eq m}^{-2} \text{ s}^{-1}$
k	proportionality constant	$\text{g biomass g C}^{-1} \text{ fixed}$
MC	Marginal cost	$\text{g d.wt. g N}^{-1} \text{ d}^{-1}$
MR	Marginal revenue	$\text{g d.wt. g N}^{-1} \text{ d}^{-1}$
N	leaf nitrogen concentration	g N m^{-2}
N_{opt}	optimal leaf nitrogen concentration	g N m^{-2}
R_d	dark respiration in leaves	$\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$
RGR	whole-plant relative growth rate	d^{-1}
V_{cmax}	maximum carboxylation velocity	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
W	total dry weight of plant	g d.wt.
W_r	dry weight of roots	g d. wt.
W_s	dry weight of shoots	g d. wt.
σ_s	shoot specific activity	$\text{g C m}^{-2} \text{ d}^{-1}$
σ_r	root specific activity	$\text{gN g root}^{-1} \text{ d}^{-1}$

Figure 5.1: Empirical photosynthetic model given by Eqn (5.12). (Figure from Hilbert 1990)

function presented by Ågren & Ingstedt (1987),

$$\sigma_s = P_m (N - n_1) / (N + n_2), \quad (5.12)$$

can be used to investigate the responses to nitrogen nutrition and is plotted in Fig 5.1. The derivative of photosynthesis with respect to nitrogen content is then

$$d\sigma_s/dN = P_m(n_1 + n_2) / (N + n_2)^2 \quad (5.13)$$

Since this model describes the photosynthetic rate per unit weight of leaves, the specific leaf weight parameter (h) is not necessary in the analysis.

Mechanistic Photosynthesis Model.

We have also used a mechanistic model of instantaneous photosynthesis developed by Farquhar, Von Caemmerer, and Berry (1980) to investigate the responses to light and CO₂. While this model ignores some factors that can limit photosynthesis in certain circumstances (e.g., limited chloroplast inorganic phosphate supply and the light activation requirement of RuBPCarboxylase), it is widely considered to be a highly useful and effective model (Pearcy *et al.* 1987).

The Farquhar *et al.* model is primarily intended to describe the rate of C₃ photosynthesis as a function of light and carbon dioxide. It assumes that photosynthesis is either ribulose biphosphate (RuBP) saturated or limited by the light-driven regeneration of RuBP. When photosynthesis is RuBP saturated, assimilation of CO₂ is given by

$$A_1 = V_{cmax} (C - k_1) / (C + k_2) - R_d \quad (5.14)$$

where V_{cmax} is the maximum RuBP carboxylase activity and R_d is the dark respiration rate (see Table 5.2 for the definitions of k_1 and k_2). When RuBP is limiting, assimilation depends on the instantaneous PFD (I), C , and the activity of photosynthetic enzymes involved in the electron transport chain,

$$A_2 = J (C - k_1) / (4.5 C + 10.5 k_1) - R_d \quad (5.15)$$

where

$$J = J_{max} I / (I + 2.1 J_{max}) \quad (5.16)$$

and J_{max} is the light saturated rate of whole chain electron transport. The actual photosynthetic rate is given by the minimum of A_1 and A_2 .

Introducing the dependency of photosynthesis on N is straightforward since

the three most important parameters in this model (V_{cmax} , J_{max} , and R_d) are expected to be proportional to the concentration of leaf proteins (Evans 1983, Field 1983, Evans and Terashima 1987). Following Field (1983) we make V_{cmax} , J_{max} , and R_d linear functions of (N)

$$V_{cmax} = k_3 N + k_4 \quad (5.17)$$

$$J_{max} = k_5 N + k_6 \quad (5.18)$$

$$R_d = k_7 N + k_8 \quad (5.19)$$

where k_3 through k_8 are constants. These constants were determined empirically for a chaparral shrub, *Lepechinia calycina* (Field 1983), and are used throughout (see Table 5.2).

Using Eqns (5.14) - (5.19), photosynthesis can be calculated as a function of leaf nitrogen concentration. The effects of light (Fig 5.2A) and internal carbon dioxide concentration (Fig 5.2B) on this function can also be examined. Whether assimilation is RuBP-saturated (A_1) or RuBP regeneration-limited (A_2) at any particular N depends on the specific levels of light and internal CO₂ concentration. At high light intensities the relationship between photosynthesis and N is linear over a large range. The model predicts this since, at high light, the photosynthetic rate is given by A_1 at most or all values of N and A_1 is proportional to V_{cmax} , which is itself a linear function of N (Farquhar *et al.* 1980, Field 1983, Seemann, Sharkey, Wang, and Osmund 1987). At lower light levels, however, and over a broad enough range of N , this relationship is predicted to be nonlinear. Note that RuBP regeneration-limited photosynthesis is a hyperbolic function of J_{max} and consequently of N . A linear relation at high light and a nonlinear one at low light were described experimentally by Gulmon and Chu (1981) and our predictions (Fig 5.2A) correspond well with photosynthesis versus nitrogen curves measured at six light levels by Hirose and Werger (1987). Unfortunately, analogous studies of photosynthesis as a function of leaf nitrogen concentration where CO₂ is varied have not been reported.

Optimal leaf nitrogen concentration depends on the daily carbon assimilation (σ_s) and, thus, on integrated daily PFD. Experiments have shown that the daily

Growth and Allocation

Table 5.2: Parameters used for the numerical calculation of photosynthesis and N_{opt} in all figures. No specific plant is represented but estimated parameters were chosen to fall within the expected range. (From Hilbert *et al.* 1991)

Parameter	Definition	Units	Value	Source
k1	CO ₂ compensation point without dark respiration	$\mu\text{l/l}$	31.0	Farquhar <i>et al.</i> , 1980
k2	*		827	"
k3	linear regression coefficients		35.7	Field 1983
k4	"		12.4	"
k5	"		92.55	"
k6	"		13.85	"
k7	"		0.775	"
k8	"		-238	"
h	specific leaf area	$\text{m}^2 \text{g}^{-1}$	0.02	estimate
K	growth efficiency	$\text{g biomass g}^{-1} \text{C}$	1.54	estimate

* $k_2 = k_c (1 + O/k_O)$ where k_c and k_O are the Michaelis-Menten constants for CO₂ and oxygen. O is the partial pressure of oxygen at the site of carboxylation.

Figure 5.2: Net instantaneous photosynthetic carbon exchange rate (CER) as a function of leaf nitrogen concentration calculated from a mechanistic photosynthesis model using the parameters in Table 5.2. A) Effect of varying irradiance ($C=240 \text{ ml/l}$). B) Effect of varying internal CO₂ concentration ($I_0=1500$). (Figure from Hilbert *et al.* 1991)

light integral is often more important than instantaneous or average PFD in determining leaf characteristics (Chabot 1979, Bunce 1983) so shoot specific activity is calculated by integrating the instantaneous photosynthetic rate, given by the Farquhar *et al.* (1980) model, over a day. The internal CO₂ is assumed to remain constant while the daily light course is given by a sine square curve (Hirose and Werger 1987). The instantaneous PFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is given by

$$I = \begin{cases} I_0 \sin^2 (\pi(t-6)/12) & (6 \leq t < 18) \\ 0 & (0 \leq t < 6, 18 \leq t < 24) \end{cases} \quad (5.20)$$

where t is solar time (hours) and I_0 is the maximum PFD occurring at noon ($t=12$).

Examples of integrating the photosynthesis model with the PFD given by Eqn (5.20) are presented in Fig (5.3). When the daily light integral is large (e.g. $34.56 \text{ mol m}^{-2} \text{d}^{-1}$, which corresponds to a peak PFD of $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$), σ_S is a nearly linear function of N (Fig 5.3A); at low light levels, σ_S is strongly nonlinear and declines at intermediate and high levels of leaf nitrogen. This decline is due to the high rates of respiration associated with large N and the very low rates of photosynthesis (see also: Hirose and Werger 1987).

Since A1 (RuBP-saturated photosynthesis) is a function of CO₂ but not of light [see Eqn (5.14)], the initial slope of the σ_S vs. N function is relatively unaffected by light, while increasing internal CO₂ concentrations increases the initial slope (Figs 5.2 and 5.3). This characteristic of the the photosynthesis versus N curve is not due to a change in the relative allocation of nitrogen between RuBP carboxylase (V_{cmax}) and enzymes involved in the light reactions (J_{max}). Such changes might occur and also be subject to optimization (von Caemmerer and Farquhar 1981, Cowan 1986, Evans 1989) but they are not responsible for the different effects of light and CO₂ on the σ_S vs. N function. In our model, changes in the relative allocation to V_{cmax} and J_{max} as N increases would be caused by differing slopes of the V_{cmax} and J_{max} vs. N functions - here determined empirically by Field (1983). Given his parameters, the ratio of J_{max} and V_{cmax} changes only slightly for N greater

than 1.0. Further empirical work to determine the relationships between N and J_{max} , V_{cmax} , and R_d is necessary, especially looking for generalities among species.

The photosynthesis versus leaf nitrogen curves presented in Figs 5.2 and 5.3 are calculated with a constant C because we implicitly assume that conductance is generally proportional to photosynthetic capacity (see Sims and Pearcy 1989). Consequently, C should remain relatively constant despite changes in leaf nitrogen. For simplicity, we also assume that C remains constant diurnally - again reflecting the coupling of conductance and assimilation. This relative constancy of C , excluding the early morning and evening hours, has been observed in a number of studies (e.g., Ehleringer 1988, Roessler and Monson 1985).

Analytic solution using the rectangular hyperbola. The optimization criterion [Eqn (5.7)] can be written as

$$(1/f_S) df_r/dN = (1/\sigma_S) d\sigma_S/dN. \quad (5.21)$$

The shoot fraction [Eqn (5.9)] is

$$f_S = \sigma_r / (\sigma_r + k\sigma_S N) \quad (5.22)$$

and from Eqns (5.10) and (5.11),

$$df_r/dN = \sigma_r (k\sigma_S + kN d\sigma_S/dN) / (\sigma_r + k\sigma_S N)^2 \quad (5.23)$$

so

$$(1/f_S) df_r/dN = k\sigma_S / (\sigma_r + k\sigma_S N) + kN d\sigma_S/dN / (\sigma_r + k\sigma_S N). \quad (5.24)$$

Substituting (5.24) into (5.21) and multiplying both sides by σ_S gives

$$k\sigma_S^2 / (\sigma_r + k\sigma_S N) + k\sigma_S N d\sigma_S/dN / (\sigma_r + k\sigma_S N) = d\sigma_S/dN. \quad (5.25)$$

Grouping the two terms containing $d\sigma_S/dN$ and simplifying gives

$$k\sigma_S^2 / (\sigma_r + k\sigma_S N) = [\sigma_r / (\sigma_r + k\sigma_S N)] d\sigma_S/dN. \quad (5.26)$$

Further simplification yields

$$k\sigma_S^2 / \sigma_r = d\sigma_S/dN. \quad (5.27)$$

Substituting Eqns (5.12) and (5.13) into Eqn (5.27) gives

$$kP_m^2 (N-n_1)^2 / \sigma_r (N+n_2)^2 = P_m (n_1+n_2) / (N+n_2)^2 \quad (5.28)$$

which, after re-arranging and simplifying becomes

$$(N-n_1)^2 = \sigma_r (n_1+n_2) / kP_m. \quad (5.29)$$

Solving for N gives

$$N_{opt} = [\sigma_r (n_1+n_2) / kP_m]^{1/2} + n_1. \quad (5.30)$$

Figure 5.3: Net daily photosynthetic carbon exchange rate (CER) as a function of leaf nitrogen concentration calculated from a mechanistic photosynthesis model with the parameters in Table 5.2 and a daily light course given by Eqn (5.20). A) Effect of varying integrated daily irradiance ($C=240 \text{ ml/l}$). B) Effect of varying internal CO_2 concentration ($I_0=1500$). (Figure taken from Hilbert *et al.* 1991)

This simple equation predicts the optimal tissue nitrogen concentration of a plant as a function of its photosynthetic characteristics (P_m , n_1 , and n_2) and its capacity to take up nitrogen from the environment (σ_r).

Numerical solution using the mechanistic photosynthesis model. By substituting Eqns (5.9), (5.10), and (5.11) into the optimization criterion [Eqn (5.7)], along with the numerically estimated derivative of σ_s with respect to N , we obtain a complete specification of the requirements for N_{opt} . Any combination of carbon dioxide concentration, light, and root specific activity can be chosen and N_{opt} calculated. The corresponding optimal root:shoot ratio can be found from N_{opt} using Eqn (5.9).

Figs 5.4A and B illustrate revenue, cost, MR, and MC for a plant growing at ambient CO_2 ($C=240 \mu\text{l/l}$), a daily light integral of $25.92 \text{ mol m}^{-2} \text{ d}^{-1}$, and a root specific activity of $.04 \text{ gN g root}^{-1} \text{ d}^{-1}$. Revenue is proportional to the daily photosynthetic rate and reaches its maximum at an N slightly greater than 6.0. MR declines almost linearly over the range of feasible leaf nitrogen concentrations. Cost, on the other hand, is a roughly sigmoidal function of N so MC is approximately quadratic. This reflects the fact that tissue nitrogen concentration is determined by the balance of carbon and nitrogen assimilation. MC decreases beyond a certain N because of the continuing decline of $d\sigma_s/dN$. At large N , carbon acquisition is only slightly affected by increased nitrogen concentration ($d\sigma_s/dN$ is small or negative) so a small increase in root fraction can have a relatively large impact on tissue nitrogen concentration - as a consequence, marginal cost declines. At low values of N , a small increase in leaf nitrogen increases the plant carbon balance considerably so a relatively large increase in root fraction is necessary in order to raise the nitrogen concentration. MR and MC are equal where RGR (e.g. revenue-cost) is maximized, in this case, at about 4.0 gN m^{-2} (N_{opt}).

5.2.3 Results and Discussion

Shoot fraction and nitrogen concentration when nutrition is varied. By varying root specific activity in Eqn (5.30), the optimal plant nitrogen concentration can be predicted for a range of nitrogen availabilities (assuming that σ_r is some function of soil nitrogen availability). Eqn (5.12) gives the shoot specific activities for any value of N_{opt} . By substituting these values (N_{opt} and σ_s) along with σ_r into Eqn (5.22) the appropriate shoot fraction and root:shoot ratio can be calculated. Figure 5.5 presents the general relationship between plant nitrogen concentration and root:shoot ratio and root specific activity (a function of soil nitrogen availability). Root:shoot ratio declines monotonically and leaf nitrogen concentration increases monotonically with increasing σ_r . This is qualitatively similar to the predictions made by Ågren and Ingestad (1987) and Levin *et al.* (1989) whose analyses follow from the assumption that growth rate is proportional to total nitrogen content. Here it is similarly assumed that the terms σ_s and f_s in the relative growth rate equation are functions of nitrogen concentration but a simple proportionality is not assumed. Consequently, the predicted relationship between relative growth rate and optimal nitrogen concentration (Fig 5.5A) is nonlinear, although not strongly so. A linear equation fits the data generated for Fig 5.5A with an r^2 of 0.995. Thus this result is consistent with empirical observations of a near-linear relation between plant nitrogen concentration and relative growth rate as described by Ågren and Ingestad (1987). On the other hand, relative growth rate is a strongly nonlinear function of nitrogen content when optimal concentrations are not considered (Fig 3C). The high cost (large root allocation) of concentrating nitrogen eventually leads to a decreased relative growth rate at tissue nitrogen concentrations above the optimum. When one considers plants with optimal nitrogen concentrations and root:shoot ratios, however, the relation between nitrogen concentration and relative growth rate (Fig 5.6A) conforms with what is generally observed. This suggests that plants tend to respond to nitrogen nutrition in a more or less optimal fashion.

Figure 5.4: Examples of cost, revenue, relative growth rate (revenue - cost), marginal revenue and marginal cost when $C=240 \mu\text{l/l}$, daily $\text{PFD}=25.92 \text{ mol m}^{-2} \text{ d}^{-1}$, and root specific activity is $.04 \text{ gN g root}^{-1} \text{ d}^{-1}$. A) Revenue and cost curves as a function of leaf nitrogen concentration. Relative growth rate (RGR) is revenue minus cost. B) Marginal revenue (MR) and marginal cost (MC) as functions of leaf nitrogen concentration. Net carbon balance and relative growth rate are maximized at the leaf nitrogen concentration where the MR and MC curves intersect (c. 4.0 g m^{-2} leaf N). (Figure from Hilbert *et al.* 1991)

Figure 5.5: Optimal plant nitrogen concentration and root shoot ratio found from Eqns (10) and (5) as they change with root specific activity which is itself some increasing function of soil nitrogen availability. Plant nitrogen concentration increases and root:shoot ratio decreases monotonically with increasing nitrogen availability. Parameters set at $k=1.54$, $P_m=0.5$, $n_1=0.005$, and $n_2=0.03$. (Figure from Hilbert 1990).

Figure 5.6: Shoot fraction and relative growth rate as functions of optimal nitrogen concentration when nutrition is varied as in Fig 5.5. (A) Relative growth rate is a nonlinear function of optimal plant nitrogen concentration. The nonlinearity, however, is slight over a reasonable range of nitrogen concentrations. (B) Shoot fraction increases monotonically with increasing plant nitrogen concentration. Parameters chosen as in Fig 5.5. (Figure from Hilbert 1990).

As in Levin *et al.* (1989), the relation between shoot fraction and tissue nitrogen (Fig 5.6B) is monotonically increasing, with a relatively linear portion at higher nitrogen concentrations. Also similar to their work, there is a threshold tissue nitrogen concentration below which relative growth rate becomes negative. Here, that threshold is equal to the photosynthetic leaf nitrogen threshold (n_1) and N_{opt} will always be greater than n_1 .

The optimization approach presented here and the theory based on the nitrogen productivity concept result in generally consistent predictions despite using quite different methods. The analysis used here may be more general because it predicts the relation between relative growth rate and tissue nitrogen rather than assuming it as a phenomenological starting point.

Light acclimation. In order to test the ability of our approach to predict trends in leaf nitrogen and analyze their adaptive significance we used Eqn (5.7) to predict N_{opt} and root:shoot ratio for plants growing in low, medium, and high light environments (using Eqn. 5.20 with peak PFD of $I_0=300$, 500, and $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$). The predicted N_{opt} were, respectively, 1.13, 1.85, and 4.13 g N m^{-2} . The integrated daily PFD for the low light environment is approximately equal to the low light treatment in the classic light acclimation experiment with *Atriplex triangularis* (Björkman *et al.* 1972) but much higher than would be experienced by a rainforest shade plant. Using the predicted N_{opt} in the photosynthesis model, we generated instantaneous photosynthetic light response curves and RGR for plants acclimated to each of the three light levels (Fig 5.7A). The results for photosynthesis are qualitatively similar to light response curves observed in experiments where plants are grown at several different light levels (e.g., Björkman *et al.* 1972, Björkman 1981). The high light adapted plants have the highest instantaneous photosynthetic rates at most light levels (Fig 5.7A). However, the low light adapted plants have a lower light compensation point and a slightly greater photosynthetic rate at very low light levels. Thus, as described by Givnish (1988), the

adaptive significance of low leaf N at low and intermediate light is not clearly indicated by the instantaneous photosynthetic rates.

Givnish (1988) argues that a better assessment of adaptation to light level is possible by considering photosynthesis as a function of leaf mass or protein content. In this way the costs of leaf construction can be indirectly incorporated and Givnish demonstrates that the photosynthetic advantage of lower leaf nitrogen at intermediate and low light levels is apparent. Our cost-benefit analysis can take this argument a step farther by explicitly considering root costs and determining relative growth rates.

Plots of RGR versus light calculated by our model (Fig 5.7B) clearly indicate the advantage of decreased N in response to growth at low irradiance level and compare well with the results of Givnish (1988). Plants acclimated to any particular light level have higher RGR at this light level compared to plants grown at other levels of irradiance. The reason for this is that the low light adapted plants have a much higher fraction of their biomass in productive shoots than plants with high N which are acclimated to high light. Plants adapted to intermediate and high light, for example, have approximately equal σ_s at intermediate light but since the intermediate light grown plants have a larger shoot fraction (lower root:shoot ratio), they fix more carbon per gram of total plant weight than the high light adapted plants. This illustrates the importance of determining the costs of a physiological trait on a whole-plant basis. The cost of growing leaves with high photosynthetic capacity mostly relates to the root biomass allocation which is necessary to produce a given leaf nitrogen concentration. Plants with the highest rates of photosynthesis per unit leaf area or weight are not necessarily the best adapted in a given environment.

General responses to light and carbon dioxide. The effect of light level on leaf nitrogen has been well established in a number of empirical studies. Leaf nitrogen concentration on an area basis is generally

Figure 5.7: A comparison of instantaneous photosynthesis and relative growth rate for plants adapted to three light environments. Optimal leaf nitrogen concentrations and root:shoot ratios were calculated for plants growing in low light (peak photon flux rate of 300 mmol m⁻² s⁻¹), intermediate light (500 mmol m⁻² s⁻¹), and high light (1500 mmol m⁻² s⁻¹). Internal CO₂ concentration held constant at 240 ml/l and a nitrogen uptake rate of .04 g N g⁻¹ d⁻¹. A) Instantaneous photosynthetic light response curves for plants acclimated to low, intermediate, and high light - calculated using the leaf nitrogen concentration which is optimal for plants growing at each of the three light levels. B) Relative growth rates as a function of daily light integral, given the optimal leaf nitrogen and root:shoot ratio for plants adapted to three light levels. In all figures the arrows show the predicted rate at the light level to which the plants are acclimated. (From Hilbert *et al.* 1991)

lower for species occurring in shaded versus open habitats (Björkman 1968, Goodchild, Björkman, and Pylotis 1972) and most species increase leaf nitrogen concentration when grown in full versus low light (Björkman 1968, 1981; Björkman *et al.* 1972, Langenheim *et al.* 1984). A similar trend occurs for leaves within a canopy (Field 1983, Hirose and Werger 1987).

Numerous studies on a variety of plants grown at high levels of CO₂, on the other hand, show decreased photosynthetic capacity compared with plants grown at ambient levels (Madsen 1975, Wong 1979, Peet and Willits 1984, Hocking and Meyers 1985, Norby, O'Neill, and Luxmoore 1986, Larigauderie *et al.* 1988) and this response is correlated with decreased *N*. Lower *N* can decrease photosynthetic capacity and might be expected to limit the growth response of plants exposed to high CO₂ (Porter and Grodzinski 1984, Peet, Huber, and Patterson 1986, Mortensen 1987). Percy and Björkman (1983) argue that this is an adaptive redistribution of resources since less RuBP carboxylase is needed at high CO₂ for an equal amount of carbon fixation. Interestingly, however, this response is opposite to that observed for light which also increases the carbon fixed per unit of leaf nitrogen.

Figures 5.7 and 5.8 illustrate the predicted response of *N*_{opt}, root:shoot ratio, and maximal relative growth rate to light and internal carbon dioxide concentration. As is generally observed empirically, *N*_{opt} increases with increasing light (Fig 5.5A). A major reason for this is that, at high irradiances, the slope of the photosynthesis versus *N* curve remains high over a large range of leaf nitrogen concentrations (Fig 5.2). Consequently, marginal revenue declines more slowly at high than at low light. *N*_{opt} approaches a constant with increasing light that depends on the internal CO₂ concentration (*C*). While this response was qualitatively predicted by Mooney and Gulmon (1979), they were not able to define costs precisely and they did not predict simultaneous changes in root:shoot ratio. Our analysis predicts increased optimal root:shoot ratios (Fig 5.5B) in conjunction with increased *N* at high light, a general

trend often observed empirically (Clough, Randall, and Terri 1979, Björkman 1981, Mahall, Parker, Fonteyn 1981, Fetcher, Strain, and Oberbauer 1983, Popma and Bongers 1988). CO₂ has little effect on root:shoot ratios (Fig 5C). As expected, RGR increase hyperbolically with increasing daily light reception (Fig 5.5C) and the response to increased CO₂ is greatest at high light levels.

Our cost-benefit analysis predicts that *N*_{opt} should decrease at elevated CO₂ levels (Fig 5.6A). The primary reason for this is that CO₂ increases the initial slope of the σ_S versus *N* curve, causing a decline in slope (i.e., shift to A₂) to occur at lower *N* (Fig 5.2B). This response is the direct result of the strong dependency of the rate of RuBP saturated carboxylation on CO₂ [Eqn (11)]. Thus, the marginal revenue and marginal costs intersect at lower *N* when plants are grown at elevated CO₂ levels. This response does appear to be adaptive since the RGR that the plant maintains under these circumstances is greater than that which would occur if high *N* and high photosynthetic capacity were maintained (Fig 5.6C). Photosynthetic capacity is reduced but this is preferable to paying the higher cost of increased root:shoot ratios necessary to maintain a higher *N*.

The root:shoot ratio is relatively unaffected by CO₂ (Fig 5.6B), but strongly affected by light and specific root uptake of nitrogen (σ_r) (data not shown, see Hilbert 1990). While it is difficult to generalize from the available data, the predicted lack of root:shoot response to CO₂ seems consistent with empirical results when plants are grown at low levels of nitrogen nutrition (Oechel and Strain 1985). On the other hand, root:shoot ratios are generally observed to increase when plants are grown at high CO₂ with non-limiting nitrogen (Larigauderie *et al.* 1988). Finally, the responses to growth at elevated CO₂ (both *N*_{opt} and RGR) are predicted to be largest when light levels are high.

The opposite responses to light and CO₂ are due to their different role in photosynthesis and consequently their

Figure 5.8: Predicted responses to daily PFD at three levels of internal CO₂ when root specific activity is 0.01 gN g root⁻¹ d⁻¹. The three CO₂ levels are typical for plants growing at high elevation (170 μl/l), plants at sea level and current atmospheric CO₂ levels (240 μl/l), and a future high atmospheric CO₂ environment (400 μl/l). A) Predicted optimal leaf nitrogen concentrations calculated by solving Eqn (6) numerically. B) Predicted optimal root:shoot ratios found from Eqn. (8). C) Resulting relative growth rates given the optimal leaf nitrogen concentration and root:shoot ratios. (From Hilbert *et al.* 1991)

Figure 5.9: Predicted responses to internal CO₂ concentration at three daily PFD (mol m⁻² d⁻¹) and a specific root activity of 0.01 gN g root⁻¹ d⁻¹. A) Predicted optimal leaf nitrogen concentrations. B) Predicted root:shoot ratios. C) Resulting maximal relative growth rates. (From Hilbert *et al.* 1991).

different effects on the A1 and A2 curves in the photosynthesis model. This can best be illustrated by considering plots of A1 and A2 versus N when CO₂ is increased compared with A1 and A2 following an increase in PFD. In Fig 5.7A we plot A1 and A2 when I is 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and C is 240 $\mu\text{l/l}$. The optimal leaf nitrogen predicted for a plant growing in this environment ($I_0=500$, $C=240$) occurs at approximately the point where A1 equals A2. If C is increased (Fig 5.7B) then the slope of A1 increases significantly while A2 is relatively unaffected. In other words, photosynthesis becomes relatively more limited by RuBP regeneration because one of the substrates of carboxylation is increased. The resulting "break point", the nitrogen concentration where A1 equals A2, is decreased considerably. On the other hand, when light is increased (Fig 5.7C), A1 is unaffected but photosynthesis is much less limited by the light reactions (i.e., A2 increases) and the break point moves toward higher N.

Responses to low $p(\text{CO}_2)$ at high elevation. We also examined the ability of our model to predict increases in N for alpine plants growing in environments with reduced partial pressures of CO₂. Several studies have demonstrated this general response in a wide range of life forms (Körner 1989, Körner, Bannister, and Mark 1986, Woodward 1986). Generally, plants growing at high altitudes experience higher irradiances, lower atmospheric $p(\text{CO}_2)$, and decreased soil nitrogen availability (Wielgolaski, Kjølsvik, and Kallio 1975, Rehder and Schäfer 1978, Haselwandter *et al.* 1983). Körner and Diemer (1987), working with two populations of herbaceous plants at 600 m and 2600 m elevation in the Austrian Alps, reported internal CO₂ concentrations of 177 $\mu\text{l/l}$ and 250 $\mu\text{l/l}$, respectively. There was no significant difference in the light environment for the two populations but N averaged 34% greater at the higher elevation. Assuming a moderate σ_f (0.01 $\text{gN g}^{-1} \text{d}^{-1}$) and high PFD we predict a 33% decrease in N_{opt} when internal CO₂ drops from 250 to 170 $\mu\text{l/l}$ (Fig 5.6A). Körner (1989) speculates that alpine plants may respond more to the anthropogenic increase in

atmospheric CO₂ than lowland plants because of their higher leaf nitrogen concentrations. Our analysis predicts that the decline in N_{opt} going from 170 to 270 $\mu\text{l/l}$ is much greater than the change between 240 and 340 $\mu\text{l/l}$ (Fig 5.6A). Despite this large change in N_{opt} , whole-plant growth might still be more stimulated in alpine plants because the largest RGR response also occurs at lower CO₂ (Fig 5.6C).

It is unfortunate that root activities are rarely measured in comparative ecophysiological studies such as Körner and Diemer (1987) since a whole-plant perspective of the costs and benefits of photosynthetic behavior can not otherwise be made. As Givnish (1988) has argued, a closer collaboration between ecophysiologicals, studying leaf function, and root biologists is necessary. Despite this lack of root data, the similarity between our predictions and observations of plants growing at high altitude is encouraging.

5.2.4 Conclusions

The analysis presented here is primarily aimed at determining optimal leaf nitrogen concentrations with the realization that the balance of carbon assimilation by the shoots and nitrogen assimilation by the roots produces a given tissue nitrogen concentration. This balance depends on the root:shoot ratio as well as shoot and root specific activities. We have shown that the responses to both CO₂ and light are adaptive in that they increase the whole-plant relative growth rate. The different responses to light and CO₂ are the result of the way these two factors affect the photosynthesis - leaf nitrogen curve that we generate using the Farquhar model (Farquhar *et al.* 1980). While there is some empirical support for the affects of light on this function there is none that we are aware of for CO₂. In principle, this type of data should be relatively easy to obtain since it does not require growing plants at elevated CO₂, although leaves with several different nitrogen concentrations must be measured.

While this analysis makes precise quantitative predictions, as does any mathematically described theory, the

Figure 5.10: A1 and A2 functions versus leaf nitrogen concentration that were generated by the instantaneous photosynthesis model. See text for discussion. (From Hilbert *et al.* 1991).

predictions must be interpreted qualitatively because of the simplifying assumptions which are necessary in order to arrive at a general and interpretable result. For example, like Davidson (1969) and others, we assume that all of the shoot biomass is active in photosynthesis and that all of the root biomass is active in nutrient absorption. This neglect of structural tissues like stems and non-absorbing roots affects the root:shoot ratios which are predicted to be optimal, but should not change the qualitative result. Perhaps more importantly, nutrient uptake is often not simply proportional to root weight but rather to root length (Nye and Tinker 1977, Chapin 1980). As a consequence, uptake rates per unit weight may decline with size of the root system despite constant specific activity on a length basis. This will mean that root:shoot ratio must increase more than predicted here in order to increase tissue nitrogen concentrations. One could also consider adaptive changes in specific root length as discussed by Robinson (1986). These complications could be included easily in the analysis if the proportionality between root weight and length and the controls on specific root length are known.

We have not considered adaptive changes in specific leaf area since, generally, there is no reason to suspect that specific leaf area and leaf nitrogen concentration are directly related. These variables may be correlated in specific circumstances; for example, plants grown in high light tend to have lower specific leaf areas (Loach 1970, Björkman 1981, Gulmon and Chu 1981) as well as higher leaf nitrogen concentrations (on an area basis) compared with plants growing in low light (Boardman 1977, Langenheim *et al.* 1984). However, Field and Mooney (1986) found a positive correlation between specific leaf area and nitrogen per unit weight for a large number of species growing in the field. When nitrogen availability is varied, specific leaf area and leaf nitrogen concentration are directly correlated (Hirose 1984, Hirose and Kitajima 1986). Also varying nitrogen availability, Gulmon and Chu (1981) found an inverse correlation between nitrogen per unit weight and specific leaf area but no correlation with nitrogen per unit area. Since both positive and negative correlations have been described, it appears

that specific leaf area is a trait that can vary independently and that it may be optimized simultaneously with leaf nitrogen but following an independent optimization criterion.

The most important extension of this work would be to include water availability and controls on its acquisition and use. This may be possible by including the linear relationship between photosynthesis and stomatal conductance of water as leaf nitrogen concentration varies (Givnish 1986b) and by calculating the water status of the plant in relation to root:shoot ratio.

By considering the interdependence of morphological and physiological responses our analysis provides a framework for understanding plant responses to multiple resource limitations and their adaptive value (in terms of maximizing relative growth rate). A whole-plant perspective is necessary in order to understand the adaptive significance of plant traits like photosynthetic capacity. While understanding the details of the photosynthetic process are very important - in this case they help to explain the contrasting effects of CO₂ and light - they are not sufficient without knowledge of root activity and a consideration of the tradeoffs between growing roots and shoots.

5.3.0 An Approach to Simulating Allocation

5.3.1 Background

It is generally assumed that balanced activity is maintained through changes in allocation to shoot and root biomass rather than changes in shoot or root specific activity; for example, when a plant becomes carbon limited due to shading or aboveground herbivory, it compensates by allocating more resources to shoot growth and less to roots (Jameson 1963, Chapin 1980, Painter and Detling 1981, Archer and Tieszen 1986). Interest in Davidson's balanced activity hypothesis, as expressed in Eqn 5.1, has led to a number of related whole-plant allocation models (Thornley 1972, 1976, 1977; Charles-Edwards 1982, Reynolds and Thornley 1982, Johnson 1985, Johnson and Thornley 1987). With the exception of Johnson (1985) who

modifies root specific activity as a function of substrate carbon and nitrogen concentrations, the models do not include the possibility that a plant may alter its specific shoot or root activities. However, specific shoot activity often changes in response to resource availability and can result in balanced growth, although the Davidson hypothesis can not precisely predict the degree to which specific activity changes simultaneously with altered biomass allocation.

Previous allocation models have not considered variable allocation of nitrogen to proteins in the leaf and consequently do not predict altered leaf specific activity in response to the environment. While Charles-Edwards (1979) developed a leaf expansion model that considers allocation to permanent structural material (e.g., cell walls) and to an enzyme pool, his model does not include partitioning between the shoot and root. The model described here extends previous allocation approaches by including variable allocation to the pool of photosynthetically active enzymes in the leaf, resulting in a more robust description of plant response to the environment.

5.3.2 Model Description

The basic model structure is similar to that presented by Johnson and Thornley (1987), who describe the allocation of substrate nitrogen and carbon for growth of roots and shoots. However, the present model divides the shoot into two components; a protein compartment that determines the photosynthetic activity per unit area of leaf and a structural compartment that determines leaf area. The allocation of resources to these two compartments represents a trade-off between leaf area and specific activity. The model has five state variables: the mass of leaf proteins (W_p), structural components in the leaves (W_s), roots (W_r), substrate carbon (W_c), and substrate nitrogen (W_n). A listing of all variables used in section 5.3 is given in Table 5.3. Total plant biomass (W_g) is given by

$$W_g = W_p + W_s + W_r \quad (5.31)$$

Growth rates are assumed to be proportional to substrate carbon and nitrogen concentrations,

$$dW_p/dt = kCN\lambda_p W_p \quad (5.32)$$

$$dW_s/dt = kCN\lambda_s W_s \quad (5.33)$$

$$dW_r/dt = kCN\lambda_r W_r \quad (5.34)$$

where the substrate concentrations are defined as

$$C = W_c/W_g \text{ and } N = W_n/W_g \quad (5.35)$$

and λ_p , λ_s , and λ_r represent the fraction of new growth allocated to leaf proteins, leaf structure, and roots, respectively ($\lambda_p + \lambda_s + \lambda_r = 1$). The parameter k is a growth rate coefficient. The rates of change of the substrate pools are given by

$$dW_c/dt = \sigma_c A - f_{cp} dW_p/dt - f_{cs} dW_s/dt - f_{cr} dW_r/dt \quad (5.36)$$

$$dW_n/dt = \sigma_r W_r - f_{np} dW_p/dt - f_{ns} dW_s/dt - f_{nr} dW_r/dt \quad (5.37)$$

where σ_c is the photosynthetic rate per unit leaf area (A), f_{cp} , f_{cs} , and f_{cr} are the proportions of carbon in leaf protein, leaf structure, and root biomass, σ_r is the specific root activity ($\text{gN g root}^{-1} \text{d}^{-1}$), and f_{np} , f_{ns} , and f_{nr} are the proportions of nitrogen in each of the three biomass compartments. Leaf area (A) is proportional to the mass of shoot structural material

$$A = W_s / rh \quad (5.38)$$

where r is leaf density (g m^{-3}) and h is leaf thickness (m). Leaf density is assumed to be constant while leaf thickness is described empirically as a hyperbolic function of photon flux density (I),

$$h = h_{\max} I / (h_1/2 + I), \quad (5.39)$$

such that leaf thickness is greater for plants growing in high light.

Allocation. The special case of balanced exponential growth (BEG) is useful in defining the allocation parameters λ_p , λ_s , and λ_r . In BEG all of the state variables have the same specific growth rate so that the fractions of the whole-plant weight in root (f_r) and shoot (f_s) are constant, as are the fractions of shoot that are in proteins (f_p) or structural components (f_{cw}). From Eqns 3 - 5, it is clear that the specific growth rates of protein, shoot structure, and root are equal when $\lambda_p = \lambda_s = \lambda_r$. Since the sum of the allocation parameters must also equal one, $\lambda_p = \lambda_s = \lambda_r = 1/3$ in BEG. Following Johnson and Thornley (1987), it is convenient to define the

Table 5.3: List of symbols used in the allocation model (From Hilbert and Reynolds 1991).

Symbol	Definition	Units
A ₁	RuBP carboxylase limited photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
A ₂	RuBP limited photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
BEG	Balanced exponential growth	none
C _i	intercellular CO ₂ concentration	$\mu\text{l/l}$
f _c	fraction of total plant weight in carbon	dimensionless
f _n	fraction of total plant weight in nitrogen	dimensionless
f _p	fraction of leaf biomass in proteins	dimensionless
f _r	fraction of biomass in the root	dimensionless
f _s	fraction of biomass in the shoot	dimensionless
f _{cp}	fraction of carbon in leaf proteins	dimensionless
f _{cr}	fraction of carbon in the root	dimensionless
f _{cs}	fraction of carbon in leaf structure	dimensionless
f _{cw}	fraction of leaf biomass in cell walls	dimensionless
f _{np}	fraction of nitrogen in leaf proteins	dimensionless
f _{nr}	fraction of nitrogen in the root	dimensionless
f _{ns}	fraction of nitrogen in leaf structure	dimensionless
h	leaf thickness	m
h _{max}	maximum leaf thickness	m
h _{1/2}	photon flux density where h is one half maximum	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$
I	photosynthetically active radiation	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$
J _{max}	maximum rate of electron transport	$\mu\text{Eq m}^{-2} \text{ s}^{-1}$
k	growth efficiency	$\text{g biomass g C}^{-1} \text{ fixed}$
N _a	leaf nitrogen concentration	g N m^{-2}
P	partitioning variable	dimensionless
Q	partitioning variable	dimensionless
R _d	dark respiration in leaves	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
V _{cmax}	maximum carboxylation velocity	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
W _c	weight of labile carbon pool	g
W _g	total dry weight of plant	g
W _n	weight of labile nitrogen pool	g
W _p	weight of leaf proteins	g
W _r	dry weight of roots	g
W _s	weight of shoot cell walls	g
β	whole-plant C:N ratio in BEG	gC gN^{-1}
λ _p	fraction of growth allocated to leaf proteins	dimensionless
λ _r	fraction of growth allocated to roots	dimensionless
λ _s	fraction of growth allocated to leaf structure	dimensionless
ρ	leaf density	g m^{-3}
σ _c	shoot specific activity on a leaf area basis	$\text{g C m}^{-2} \text{ d}^{-1}$
σ _s	shoot specific activity	$\text{g C g leaf}^{-1} \text{ d}^{-1}$
σ _r	root specific activity	$\text{gN g root}^{-1} \text{ d}^{-1}$

allocation parameters in terms of a partitioning variable (P). P is defined such that, when some desired condition exists, $P=1$ and the plant allocates resources equally among all components (e.g., $\lambda_p = \lambda_s = \lambda_r = 1/3$). This ensures BEG with constant leaf properties and a constant root:shoot ratio. Johnson and Thornley (1987) determine P analytically by employing the condition that the derivative of the relative growth rate with respect to shoot fraction must equal zero during BEG so that the whole-plant relative growth rate is maximized. In the present model, P would be difficult to obtain in this way since σ_c is a complex function of leaf protein content (see below). Rather, we use the definition of balanced root and shoot activity to define P.

To ensure that the shoot and root activity are balanced when $P=1$, we use Eqn. (1) to define P as

$$P = f_c \sigma_r W_r / (f_n \sigma_c A). \quad (5.40)$$

However, with three allocation parameters and only one control variable (P) there is insufficient information to ensure a unique root:shoot ratio and shoot protein fraction. This is illustrated using an alternative form of Eqn 1 to define balanced activity,

$$f_n / f_c = \sigma_r W_r / (\sigma_c A), \quad (5.41)$$

where it can be seen that, if the carbon and nitrogen fractions of biomass can vary, there are many ratios of root to shoot specific activity that can balance growth. This is a well known property of the balanced activity hypothesis and, as a consequence, it is generally assumed that the ratio (f_n / f_c) in Eqn (5.1) is constant. Requiring that f_n / f_c be constant in BEG leads to a second control variable, Q, given as

$$Q = f_n / \beta f_c, \quad (5.42)$$

where β is the "target" whole-plant nitrogen to carbon ratio. In general terms, the control variables are given by P^q and Q^q , where q determines the degree of control over allocation as in Reynolds and Thornley (1982). Here, q is assumed to equal one.

The λ 's can now be defined as functions of P so that allocation to shoot structure, proteins, and roots is equal when root and shoot activity are balanced, resulting in a constant root:shoot ratio and shoot specific activity. Using an approach

analogous to Johnson and Thornley (1987), we define λ_p , λ_s , and λ_r as functions of P and Q subject to the constraints that $\lambda_p + \lambda_s + \lambda_r = 1$ and BEG occurs only when $P = Q = 1$;

$$\lambda_p = \frac{P}{1+P+Q} \quad (5.43)$$

$$\lambda_s = \frac{Q}{1+P+Q} \quad (5.44)$$

$$\lambda_r = \frac{1}{1+P+Q} \quad (5.45)$$

Eqs 14-16 result in the following behaviours. When $P>1$, root activity is too high for balanced activity so the plant allocates relatively more to leaf proteins (Eqn 14) in order to increase shoot specific activity. When the nitrogen to carbon ratio of the whole-plant biomass is too high ($>\beta$), allocation to shoot structure (the component with the lowest nitrogen content) increases (Eqn 15) in order to decrease the nitrogen concentration of the plant as a whole. Similarly, root allocation is inversely proportional to both P and Q so that, when either root activity or plant nitrogen concentration is too high, there is lower root allocation.

Photosynthesis as a function of leaf proteins. The functional relationship between leaf proteins and leaf specific activity must also be specified. The approach used here is to make photosynthetic rate (σ_c) a function of leaf N concentration (N_a) defined as $f_n p W_p / A$. Specific shoot activity or photosynthetic capacity is usually correlated with leaf nitrogen concentration (Björkman 1968, Evans 1983, Field and Mooney 1986, Gulmon and Chu 1981, Medina 1971, Mooney, Ferrar and Slatyer 1978) which, in turn, is known to vary with soil nitrogen availability (Hilbert 1990), photon flux density (Givnish 1988, Hilbert *et al.* 1991), and carbon dioxide concentrations experienced during growth (Hilbert *et al.* 1991). It is convenient to use the mechanistic model of photosynthesis developed by Farquhar, Von Caemmerer, and Berry (1980) (see Eqns 5.14-5.19).

5.3.3 Results

The simulation model, as given by Eqns 5.31-5.45, was solved using the fourth-

Table 5.4: Parameter values used in the simulations.

Parameter	Value	Source
f_{cp}	0.60	Chapin (1989)
f_{cr}	0.45	Reynolds and Thornley (1981)
f_{cs}	0.45	"
f_{np}	0.16	Field and Mooney (1986)
f_{nr}	0.03	Reynolds and Thornley (1981)
f_{ns}	0.005	estimate
h_{max}	0.0003	estimate
$h_{1/2}$	200	estimate
k	300	estimate
k_1	31	Farquhar <i>et al.</i> (1980)
k_2	827	"
k_3	35.76	Field (1983)
k_4	12.42	"
k_5	92.55	"
k_6	13.85	"
k_7	0.775	"
k_8	-0.238	"
β	0.05	estimate
r	5.0×10^5	estimate

Figure 5.11: A) The predicted response of leaf nitrogen concentration (N_a) and root:shoot ratio (R/S) to increased rates of root specific activity for nitrogen; $PhAR=1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $C_i=240 \mu\text{l l}^{-1}$. B) The predicted increase in whole-plant relative growth rate (RGR) and shoot specific activity (σ_s) in response to increasing root specific activity. (From Hilbert and Reynolds 1991)

order Runge-Kutta method until BEG was achieved. The results presented below were obtained using the parameter values in Table (5.4) and, unless otherwise noted: $\sigma_r = 0.01 \text{ gN g root}^{-1} \text{ d}^{-1}$, $I = 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for a 14-h day, and $C_i = 240 \mu\text{l l}^{-1}$.

Balanced exponential growth solutions. First, we demonstrate model behavior in BEG when resource availabilities are varied. Values for the root:shoot ratio and leaf nitrogen concentration attained in BEG as a function of root specific activity are shown in Fig 5.11A. As in previous biomass allocation models (e.g., Johnson 1985), increasing σ_r decreases the root:shoot ratio (R/S). Unlike these models, however, the present model also predicts an increase in allocation to leaf proteins, increasing the leaf nitrogen concentration (N_a , Fig 5.11A) and shoot specific activity (σ_s , Fig 5.11B). The whole-plant relative growth rate responds hyperbolically to increased σ_r (RGR, Fig 5.11B), increasing more than σ_s because of the decreased R/S at higher σ_r . The combination of higher shoot fraction and higher shoot specific activity stimulates growth to a greater degree than either would alone.

The predicted response to increasing photon flux density is shown in Fig 5.12. Both leaf nitrogen concentration and R/S increase in response to increasing light, the latter reaching a plateau (Fig 5.12A). The increase in N_a is due to the increasing leaf thickness given by Eqn 10. The protein fraction (and thus the nitrogen concentration on a weight basis) actually declines slightly from 10.6 % at $100 \mu\text{E m}^{-2} \text{ s}^{-1}$ to 9.0 % at $1500 \mu\text{E m}^{-2} \text{ s}^{-1}$ (f_p , Fig 5.12B); the specific leaf weight increases because of increased leaf thickness (SLW, Fig 5.12B). In contrast, the increased leaf nitrogen concentration in response to increasing σ_r (shown in Fig 5.11A) is due to an increase in protein fraction from 3 to 12 % with no change in leaf thickness. Root:shoot ratio increases in response to increasing light because the combination of greater PFD and higher N_a increases σ_s significantly; since σ_r is unaffected, a larger root fraction is necessary to balance growth at high light intensities.

Increasing C_i increases R/S and decreases N_a (Fig 5.13A), a response that is exactly opposite to increasing σ_r (Fig 5.11). Increasing C_i elevates σ_s so, in order to achieve balanced growth, a plant has various options: decrease shoot fraction, increase root fraction, and/or decrease N_a to reduce the photosynthetic stimulation. In fact, the model responds to elevated C_i in all of these ways. Since, leaf thickness is not directly influenced by C_i in this model, the decreased allocation to leaf proteins from 10 to 5 % (f_p , Fig 5.13B) significantly decreases N_a .

11. Fig (5.14), the product ($f_r \sigma_r$) is plotted against ($f_s \sigma_s$) for a variety of root and shoot specific activities obtained from the simulations where σ_r , PFD, and C_i were varied to produce Figs 5.11 - 5.7. The balanced activity hypothesis suggests that these two quantities should be proportional during BEG, where, for this model, the proportionality constant is b . As required by the partitioning functions, P and Q , the BEG solutions produce balanced activity with f_n/f_c equalling b . The ratio of nitrogen to carbon substrate also is constant and equal to b . While this ratio is constant, both C and N increase in response to elevated shoot specific activity (higher PFD or C_i) and root specific activity (σ_r).

Response to shoot removal. As one test of the power of the model, as well as to demonstrate its transient behavior, a grazing event was simulated where 75% of the shoots (W_p and W_s) were removed after BEG was obtained. In addition, the substrate carbon and nitrogen pools were reduced such that the resulting C and N substrate concentrations were unchanged. Since the grazing event immediately results in root activity ($\sigma_r W_r$) being much greater than shoot activity ($\sigma_s W_s$), P becomes much greater than one (Fig 5.15A) and allocation is changed to favor construction of leaf proteins (Fig 5.15B). This increased allocation to leaf proteins initially increases Q (Fig 5.15A) since proteins contain much more nitrogen than root and leaf structural components. Consequently, following a lag, allocation to shoot structure increases (Fig 5.15B), and the whole-plant

Figure 5.12: A) The predicted response of leaf nitrogen concentration (N_a) and root:shoot ratio (R/S) to increased photon flux density (PhAR); $\sigma_r = .01 \text{ gN g}^{-1} \text{ d}^{-1}$, $C_i = 240 \mu\text{l l}^{-1}$. B) The change in specific leaf weight (SLW) and the fraction of leaf weight that is made up by protein (f_p) in response to increasing photon flux density. (From Hilbert and Reynolds 1991)

Figure 5.13: A) The predicted response of leaf nitrogen concentration (N_a) and root:shoot ratio (R/S) to increased intercellular concentration of carbon dioxide (C_i); $\sigma_r = .005 \text{ gN g}^{-1} \text{ d}^{-1}$, PhAR = $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. B) The change in leaf protein fraction (f_p) in response to growth at increasing C_i . (From Hilbert and Reynolds 1991)

Figure 5.14: A plot of the product ($\sigma_r f_r$) versus ($\sigma_s f_s$) for the data used to make Figs 5.11-5.13, where the environment was varied by changing root specific activity, PhAR, or C_i . The balanced activity hypothesis predicts that these products are proportional when measured in a variety of environments. (From Hilbert and Reynolds 1991)

nitrogen:carbon ratio (f_N/f_C) returns to the specified value. Since the regrowing shoots have a high protein content, the leaf nitrogen concentration is higher than during BEG and the shoot specific activity is stimulated (Fig 5.15C). Initially, the labile carbon concentration drops while labile nitrogen concentration increases after grazing (Fig 5.15D) - again reflecting the imbalance toward root uptake following grazing. Grazing results in an instantaneous decrease in the whole-plant relative growth rate but the relative growth rate eventually surpasses the rate during BEG prior to the grazing event (Fig 5.16A). The relative growth rates of each component (Fig 5.16B) roughly parallel the allocation parameters (Fig 5.15B).

Sensitivity Analysis. Results from a simple parameter sensitivity analysis are presented in Fig 5.17. Starting with the parameter values listed in Table (5.4), each of the parameters - with the exception of those related to photosynthesis - was independently changed by -50, -25, +25 and +50 % and the model run until BEG was achieved. Two important plant variables, leaf nitrogen concentration and root:shoot ratio were then used to calculate a measure of sensitivity: $(X-X_0)/X_0$ where X_0 is the value of the variable before changing a parameter and X is the value during BEG after changing the parameter. Since the responses of both N_a and root:shoot ratio were mostly linear functions of the percent parameter change, only the response to a 50% increase in the parameters are presented in Fig (5.17). Generally, leaf nitrogen concentration is more sensitive to parameter change than is root:shoot ratio. Leaf nitrogen concentration is most sensitive to h_{max} and r which have an identical affect on N_a through their influence on leaf area (Eqn 10). Both leaf nitrogen concentration and root:shoot ratio are relatively sensitive to the fractions of carbon in root biomass (f_{Cr}) and the fraction of carbon in shoot structural material (f_{Cs}). The fractions of nitrogen in protein (f_{Np}) and shoot structure (f_{Ns}) have a relatively small effect while the fraction of nitrogen in the roots (f_{Nr}) strongly affects both N_a and R/S.

N_a and R/S are relatively insensitive to the remaining parameters (f_{cp} , $h_{1/2}$, and k).

5.3.4 Discussion

While previous allocation approaches have been relatively successful in predicting R/S, the present model has a distinct advantage in that N_a and the correlated photosynthetic rates are also predicted. The predicted inverse relationship between R/S and N_a is the generally observed pattern when soil nitrogen availability is increased (Hilbert 1990, Levin, Mooney, and Field 1989, Ågren and Ingstedt 1987). The model's response to light is consistent with the generally observed pattern of light acclimation (Björkman 1981, Givnish 1988). Plants growing at high photon flux densities generally do have high leaf nitrogen concentrations on an area basis but somewhat lower nitrogen concentrations on a weight basis (Björkman 1981). This result is partly dependent on the empirical relationship between light and leaf thickness that is included in the model. However, the proper simulation of allocation is also necessary for the model results to match empirical observations. Empirically observed R/S in response to photon flux density are variable but increasing R/S are the general expectation. Model responses to C_i are consistent with many studies. The predicted decrease in N_a is often observed when plants are grown under higher than ambient CO_2 conditions (Wong 1979, Larigauderie, Hilbert, and Oechel 1988), especially when soil nitrogen availability is low. Again, observed R/S ratios in response to C_i are variable but increased R/S are frequently observed.

The predicted responses to grazing are qualitatively similar to empirical trends when shoot clipping experiments are performed. Leaf and shoot level photosynthetic rates, for example, often increase following clipping (Dyer *et al.* 1982) and this response can be attributed to increased photosynthetic capacity in leaves produced after defoliation (Detling, Dyer, and Winn 1979). Translocation of labile carbon to roots is severely curtailed following clipping, resulting in a cessation or severe

Figure 5.15: The dynamic response of the model to 75% removal of shoot biomass on day 10 of the simulation; $\sigma_r = 0.01 \text{ gN g}^{-1} \text{d}^{-1}$, $\text{PhAR} = 1000 \text{ } \mu\text{mol m}^{-2} \text{s}^{-1}$, and $C_i = 240 \text{ } \mu\text{l l}^{-1}$. A) The partitioning parameters (P and Q) plotted through time. Balanced activity and BEG are restored when $P=Q=1$. B) The three allocation parameters through time. BEG occurs when $l_p = l_s = l_r = 1/3$. C) Shoot specific activity following the grazing event. D) Concentrations of labile carbon (C) and labile nitrogen (N) following grazing. Figures from Hilbert and Reynolds (1991).

Figure 5.16: A) Simulated whole-plant relative growth rate following 75% shoot removal on day 10. B) The relative growth rates of each of the biomass compartments following grazing. Figures from Hilbert and Reynolds (1991).

Table 5.5: Comparison of allocation models. From Hilbert and Reynolds (1991).

	Thornley 1972	Reynolds and Thornley 1982	Johnson 1985	Johnson and Thornley 1987	Hilbert and Reynolds this manuscript
number of state variables	6	4	4	4	5
shoot specific activity	constant	constant	constant	constant	variable
root specific activity	constant	constant	variable	constant	constant
C and N substrate concentrations	distinct by organ	agregated for whole-plant	agregated for whole-plant	agregated for whole-plant	agregated for whole-plant
C/N fixed in BEG	no	yes	no	no	yes
Allocation method	mechanistic, concentration gradient and resistance	phenomen- ological, function of N, C, W_{sh}, W_r	phenomen- ological, function of N, C, f_{sh}, f_r	teleonomic, maximize rgr, function of $N, C, f_{sh}, f_r, f_c, f_n$	teleonomic, balanced activity, function of $s_s, s_r, f_{sh}, f_r, f_c, f_n$
balanced activity	no	no	no	no	yes
f_c and f_n fixed	yes	yes	yes	yes	no
stability	moderate	low	high	high	high

Figure 7: Results from a parameter sensitivity analysis where each of the parameters were increased 50 % and the percent change in leaf nitrogen concentration (N_a) or root:shoot ratio (R/S) were determined. From Hilbert and Reynolds (1991).

decrease in root growth (Dyer *et al.* 1982, Marshall and Sagar 1968). Labile carbon is then diverted to shoot meristems where the relative growth rate is increased. Under some circumstances, whole-plant relative growth rates are also stimulated by defoliation (Hilbert *et al.* 1981, McNaughton 1979). Thus, our model seems to simulate the general responses to clipping.

The model presented here has features in common with a series of allocation models published in *Annals of Botany* (Thornley 1972, Reynolds and Thornley 1982, Johnson 1985, Johnson and Thornley 1987). Several important characteristics of these models are compared in Table (5.5). The major contribution of the present model is the inclusion of a distinct leaf protein pool that results in variable carbon and nitrogen concentrations of shoot biomass. While the ratio of carbon and nitrogen concentration for the whole-plant (f_C/f_N) is forced to a constant during BEG (Eqn 13), tissue nitrogen concentration of the leaves does vary in response to the above- and belowground environment. This is in contrast to other models where f_C and f_N are constant in time and for all organs (Table 5.5). Given that variation in protein concentration is an important aspect of plant acclimation to resource availability (Mooney and Gulmon 1979, Hilbert 1990), allocation models need to be developed so that the implications of this variability can be explored.

In all of these models, a fundamental question is; how does the whole-plant carbon:nitrogen ratio $[(f_C+C)/(f_N+N)]$ vary in response to changes in root or shoot specific activity? The balanced activity hypothesis requires that when shoot and/or root specific activity are varied, the root and shoot activities in BEG be proportional. In other words, when balanced activity occurs, the carbon:nitrogen ratio of the plant in BEG should be unaffected by the environment (represented by σ_S and σ_R). While the carbon and nitrogen content of structural biomass (f_C and f_N) never change in these models (Table 5.5), the total carbon:nitrogen concentration is variable because of changes in C and N. Since the values of C and N observed in BEG in these models are functions of root and shoot specific activity, they do not produce true balanced activity. The present model uses balanced activity as the teleonomic goal of the plant to define the partitioning functions so that balanced activity is produced (Fig 5.14). While it has been argued that plants do not precisely follow the balanced activity hypothesis, the deviations are not generally large and Davidson's hypothesis remains one of the most important paradigms for the understanding of partitioning and whole-plant growth. Since all of the previous allocation models are aimed, in part, at understanding balanced activity, it seems valuable to formulate a model that explicitly follows this hypothesis.

6.0.0 MODELS OF COMPETITION IN SPECIES MIXTURES BASED ON THE SCALING OF SINGLE PLANT RESPONSES

In order to predict the effects of increasing CO₂ and climate change on plant communities we must understand the ways in which species interactions will change. One of the principal ways this may occur is via *resource pre-emption*. Direct effects on photosynthesis will lead to changes in assimilate translocation, leaf area, root production, etc., which, in turn, will affect the way in which plants obtain resources and thus interact with their neighbors. Here, we present a mechanistic approach that incorporates these factors. The purpose of this work is to develop a general scheme to represent the effects of crowding (e.g. decreased growth rates, altered morphology, and mortality) in our models. Eventually, we will substitute our more complex plant growth model (GePSI) for the simpler model of an isolated plant which is used in this chapter and we will include the competition model in SERECO. However, at the present, this work focuses on the development of an approach that can latter be applied to more complex models. The model will be used to investigate some of the perplexing aspects of multi-species response to elevated CO₂ and stress (e.g., nitrogen, water, temperature, etc.). Material in this chapter is taken from Hilbert, Reynolds, and Bazzaz (1991).

6.0.1 Objectives

The overall goal is to predict plant interactions, resource utilization, and growth of plant populations within a multi-species community. The model should be able to predict changes in population and community biomass, community composition, and resource distribution as a function of increased CO₂ and climate change. There are two specific objectives of the community modeling research:

- 1) To develop a mechanistic plant community model; and
- 2) To use this model as a tool to investigate plant population and community response to global change.

Our goal is to develop a hierarchy of models that are phenomenological or

mechanistic and utilize a common framework for examining the effect of elevated CO₂ on plant community structure. The phenomenological models should be capable of approximating competitive effects without inclusion of complex physiological or morphological details. The addition of physiological and morphological reality in the more mechanistic models should add to the understanding of the potential effects of elevated CO₂ on plant interactions under a range of environmental and community conditions. Light interception models were deemed the most promising approach initially, because they are relatively simple (at least conceptually), can be interfaced with detailed models of photosynthesis and partitioning (Charles-Edwards 1982) and can accommodate light competition models (Rimington *et al.* 1984). We then added the partitioning of biomass between root and shoot and included competition for nitrogen.

A mechanistic plant-centered model of the community must be considered as a first step toward the prediction of community response to elevated CO₂ and climate change. There will be many aspects of the plant population and community not directly incorporated into this scheme, such as phenological changes, senescence, seed dormancy, and seed dispersal, as well as potential genetic changes in the populations, all of which have potential bearing on long-term community structure and function, and may be affected by CO₂ and climate change (Paez *et al.* 1980, Kimball 1983, Bazzaz and Garbutt 1984, Bazzaz *et al.* 1985, Zangerl and Bazzaz 1984, Curtis *et al.* 1989). Many of these aspects of population and community biology will require considerable experimental investigation before we can attempt to model them. However, some of these factors could be incorporated into the plant-centered modeling scheme described below, particularly as further theoretical and experimental studies suggest how CO₂ and climate change may directly or indirectly affect dispersal, phenology, senescence, etc.

6.1.0 Introduction

The effects of CO₂ on plant growth vary considerably among species (Carlson and Bazzaz 1980, Cure 1985, Oechel and Strain 1985). Thus, it has been predicted that elevated CO₂ will bring about change in plant communities by preferentially promoting growth of some species over others (Zangerl and Bazzaz 1984). Experiments of effects of elevated CO₂ on artificial and natural communities of two or more species have shown that there can be rather large, or relatively small, changes in total community production, species' relative contributions to the production, or change in reproductive output of the plants (Carter and Peterson 1983, Bazzaz and Carlson 1984, Zangerl and Bazzaz 1984, Bazzaz and Garbutt 1988, Bazzaz *et al.* 1989, Curtis *et al.* 1989). These studies reveal that 1) outcomes of competition can change under elevated CO₂, and 2) the community-level responses to elevated CO₂ are not simple linear combinations of individual plant responses to CO₂ (Bazzaz *et al.* 1989). Thus, while the output of the whole plant model and a mechanistic understanding of how plants acquire and use resources can provide useful information to the ecosystem-level model, *the summation of individual organism behavior cannot be used to predict community responses without incorporating the system properties that arise from the interaction of neighboring individuals.*

To experimentally examine the outcome of interactions in mixed species communities as a result of elevated CO₂ is an immense task since there are many potential combinations of species and CO₂ levels. At this time, only a few species mixtures have been studied (Carter and Peterson 1983, Patterson *et al.* 1984, Zangerl and Bazzaz 1984, Bazzaz and Carlson 1984, Bazzaz and Garbutt 1988). A more comprehensive approach is to develop mathematical models of plant growth that can be used to examine the dynamics of a plant community from the behavior of the component species grown in monoculture. The development of such models should be guided by a determination of the important interactions at both the population and physiological levels.

Plant community structure is determined by intra- and inter-specific interactions. Thus, a quantitative description of competition should include the morphological and physiological aspects of plants that determine within and between species competition and the outcome in terms of mortality and growth of individual species (McGraw and Wulff 1983). Most models emphasize either the physiology or the population biology of communities, but rarely both. The model described here is an attempt to bridge the gap between physiological and population models, with the specific goal of modeling the physiological and morphological effects of CO₂ on intra- and inter-specific competition in plants and examining the resulting changes in community composition.

While there are a number of plant community models that incorporate various aspects of intraspecific or interspecific plant interactions (Yoda *et al.* 1963, Scott *et al.* 1978, Weiner and Conte 1981, Weiner 1982, Westoby 1982, Law 1983, Pacala 1986, Slatkin and Anderson 1984), most models base their competitive interactions on the state of the organisms, populations, or communities (e.g., size, numbers, distribution) without referring explicitly to the processes of resource capture and use that lead to changes in state. The simplest models of competition in monocultures are empirical models of mean plant weight, yield and plant density. Empirical models include asymptotic models of yield and mean plant weight as a function of planting density (Willey and Heath 1969, Jolliffe *et al.* 1984), the widely used -3/2 law for self-thinning stands (Yoda *et al.* 1963, Hutchings 1979, Westoby and Howell 1981) and models based on derivations of the -3/2 law (Aikman and Watkinson 1980, Westoby 1982). These models do not have a mechanism for incorporating affects of increasing CO₂, and only incorporate climate change empirically.

These descriptive models are unsatisfactory for further development since physiological and morphological realism cannot easily be incorporated in the model structure. A plant community model that is to be responsive to CO₂ must include the important ways in which effects of CO₂ (such

as changes in growth rates, leaf area, root production, etc.) bring about changes in plant-plant interaction. This could be accomplished through a mechanistic, resource-based community model in which plant-plant interactions are indirect, meaning that an individual plant or plant species causes changes in resource distribution, which in turn induces changes in the growth, reproduction, or survival of another plant or plant species (Tilman 1988). Charles-Edwards (1984a, b) developed a model of competition based on equations of light interception and the energy requirements of individual growth points. This approach is particularly satisfying since it models population responses as the result of physiological processes and can easily incorporate more complex physiological models. There are many carbon balance models, e.g., Johnson *et al.* (1983), but these models rarely include population responses. In addition, they are difficult to apply, and are not easily simplified.

Models of inter-specific competition frequently assume light to be the limiting resource. Monteith (1981) presented evidence that light interception by crops does limit crop growth; thus, an assumption of light limited growth may be valid. The simplest of the light competition models are based on Beer's law for light extinction in closed canopies. Rimmington *et al.* (1984) developed a model for mixed species, closed canopies and McMurtrie and Wolf (1983) developed a model of light interception in two layered canopies based on exponential light extinction. More sophisticated models have been developed using finite foliage elements (Acock *et al.* 1978, Holm and Kellomaki 1984) or Lotka-Volterra models (Annikki and Hari 1984). Some models do not explicitly assume light to be the limiting resource, these include an empirical asymptotic model of yield, mean plant weight and plant density by Spitters (1983) and Lotka-Volterra type model by Scott *et al.* (1978).

Tilman (1988) presents a simple model that includes root:shoot partitioning and competition for light and soil nutrients. The model is size structured, following the growth of cohorts with the same date of germination, and allocation switches to seeds after a species specific maximum height is

attained. Tilman's analysis of the model suggests that the basic morphology of a species, described by root:shoot ratio and maximum height, are very important in determining competitive success in a given environment. A limitation of this approach, however, is that morphological and physiological plasticity are not represented. For simplicity, parameters are constant in the model. For example, mortality rates and the root:shoot partitioning are unaffected by resource availability or population density.

6.2.0 Description of the Model

A model of intra-specific competition based on a light interception (assuming intercepted light is the limiting resource) was proposed by Charles-Edwards (1984a, 1984b). In this model, growth of a crop is based on the amount of light intercepted by the canopy and the number of growth points that can be sustained from photosynthesis by the crop. Mortality is proportional to the difference between the number of growth points that can be sustained and the number of growth points present. The models proposed below are conceptually similar to Charles-Edwards' model, but are based on whole plant growth rather than the development of individual growth points. We begin by developing a model for an isolated plant that includes light interception, nitrogen uptake by the roots, and allocation between root and shoot biomass (ISOMOD). This model is then used as the basis of a model for a monospecific stand (MONOMOD) which is then extended to a mixed species stand (MIXMOD). A listing of all symbols used in the model is given in Table 6.1 and a diagram of the ISOMOD is presented in Fig (6.1).

6.2.1 Light interception, nitrogen uptake, and allocation model for an isolated plant (ISOMOD)

The light intercepted by an isolated plant depends on the area it covers and the leaf area density within its canopy. Canopy cover is modeled as a function of biomass using dimensional similarity arguments. Assuming that the shape of the plant remains similar as it grows, canopy cover (C_i , in m^2) is

Figure 6.1: Schematic diagram of the model for an isolated plant (ISOMOD).

Table 6.1: Symbols used in the competition model.

<u>Symbol</u>	<u>Definition</u>	<u>Units</u>
a	root length proportionality constant	m g^{-1}
β	parameter controlling the rate of self thinning	dimensionless
C_i	canopy cover (ISOMOD)	m^2
$C_{j\text{max}}$	maximum canopy cover (MIXMOD)	m^2
C_m	canopy cover (MONOMOD)	m^2
δ_i	rooting density (ISOMOD)	m m^{-2}
δ_m	rooting density (MONOMOD)	m m^{-2}
ϵ	efficiency of converting absorbed light into biomass	g MJ^{-1}
$\epsilon_{1/2}$	N_{conc} where ϵ is 1/2 of maximum	g N g^{-1}
ϵ_{max}	maximum light use efficiency	g MJ^{-1}
f_c	carbon concentration of dry matter	g C g^{-1}
f_j	fraction of incident light absorbed	dimensionless
f_n	nitrogen concentration of dry matter	g N g^{-1}
η_i	efficiency of nitrogen uptake (ISOMOD)	$\text{g N m}^{-1} \text{d}^{-1}$
η_m	efficiency of nitrogen uptake (MONOMOD)	$\text{g N m}^{-1} \text{d}^{-1}$
I_0	photon flux density	$\text{MJ m}^{-2} \text{d}^{-1}$
I_a	total absorbed light	MJ d^{-1}
κ	light extinction constant	dimensionless
LAD_i	leaf area density (ISOMOD)	$\text{m}^2 \text{m}^{-2}$
L_i	leaf area (ISOMOD)	m^2
l_i	total root length (ISOMOD)	m
l_m	total root length (MONOMOD)	m
λ_r	root partitioning coefficient	dimensionless
λ_s	shoot partitioning coefficient	dimensionless
n	population density	individuals m^{-2}
N_{conc}	nitrogen concentration of plant	g N g^{-1}
r	loss rate parameter including respiration	d^{-1}
ρ	canopy cover proportionality constant	$\text{m}^2 \text{g}^{-1}$
RGR_i	relative growth rate of an isolated plant (ISOMOD)	d^{-1}
RGR_m	relative growth rate (MONOMOD)	d^{-1}
R_i	dry weight of roots	g d. wt.
S_i	dry weight of shoots (ISOMOD)	g d. wt.
$SLAR$	leaf area ratio of shoot biomass	$\text{m}^2 \text{leaf g}^{-1} \text{shoot}$
σ_r	root specific activity	$\text{g N g}^{-1} \text{root d}^{-1}$
σ_s	shoot specific activity	$\text{g C g}^{-1} \text{shoot d}^{-1}$
W_i	total dry weight of plant (ISOMOD)	g d. wt.
W_m	total dry weight of plant (MONOMOD)	g d. wt.
μ	mortality rate	individuals d^{-1}

proportional to shoot weight (S_i) raised to the 2/3 power

$$C_i = \rho S_i^{2/3} \quad (6.1)$$

where ρ is a proportionality constant.

Leaf area (L_i) is assumed to be directly proportional to shoot weight

$$L_i = \text{SLAR } S_i \quad (6.2)$$

where SLAR is the leaf area ratio of shoot biomass ($\text{m}^2 \text{ leaf g}^{-1} \text{ shoot}$). The subscript (i) is used throughout to indicate variables for a plant growing in isolation. From Eqns 1 and 2, the leaf area density (LAD_i , analogous to the LAI of a stand, $\text{m}^2 \text{ m}^{-2}$) is

$$\text{LAD}_i = (\text{SLAR}/\rho) S_i^{1/3} \quad (6.3)$$

The fraction of incident light absorbed (f_i) depends on LAD_i and light extinction through the canopy which is given by

$$f_i = 1 - \exp(-\kappa \text{LAD}_i) \quad (6.4)$$

where κ is the light extinction constant. Thus, the total absorbed light (I_a) is

$$I_a = f_i C_i I_0 \quad (6.5)$$

where I_0 is the incident radiation density ($\text{MJ m}^{-2} \text{ d}^{-1}$), and ($C_i I_0$) is the incident light on the area the plant occupies. Net growth of biomass is given by the light absorbed (I_a) times an efficiency of converting absorbed light into biomass (ϵ in g MJ^{-1}):

$$\frac{dW_i}{dt} = \epsilon I_a \quad (6.6)$$

Light utilization efficiency (ϵ) is a complex parameter representing the photosynthetic activity of the plant that can be calculated from the daily photosynthetic integral and the daily light interception. Since dW_i/dt can be written as the product of the daily net photosynthetic integral (∇_F) and a proportionality constant (q) that converts $\text{g}(\text{CO}_2)$ to $\text{g}(\text{biomass})$, ϵ equals $q \nabla_F / I_a$. So, given sufficient data, a photosynthesis submodel of any complexity could be substituted for ϵ .

Dry weight allocation can be incorporated in the model by defining parameters that determine the fractions of new biomass that go to growth of shoots (S_i) and roots (R_i). Now,

$$\frac{dS_i}{dt} = \lambda_s \frac{dW_i}{dt} - \gamma_s S_i \quad (6.7)$$

$$\frac{dR_i}{dt} = \lambda_r \frac{dW_i}{dt} - \gamma_r R_i \quad (6.8)$$

where λ_s and $\lambda_r = (1 - \lambda_s)$ are the shoot and root partitioning coefficients, while γ_s and γ_r are rate parameters for the loss of biomass due to a number of factors. The partitioning coefficients can be defined to produce balanced activity as defined by

$$\text{root mass} \times \text{root specific activity} = (\text{shoot mass} \times \text{shoot specific activity}) \quad (6.9)$$

(Davidson 1969, Reynolds and Thornley 1981) where f_n is the nitrogen concentration of dry matter and f_c is the carbon concentration. Charles-Edwards (1976) derived the partitioning coefficients

$$\lambda_r = \frac{f_n \sigma_s}{f_c \sigma_r + f_n \sigma_s} \quad (6.10)$$

$$\lambda_s = \frac{f_c \sigma_r}{f_c \sigma_r + f_n \sigma_s} \quad (6.11)$$

where σ_r is the root specific activity ($\text{gN g}^{-1} \text{ root d}^{-1}$) and σ_s is the shoot specific activity ($\text{gC g}^{-1} \text{ shoot d}^{-1}$). Eqns 6.7-6.11 provide a simple method for the dynamic allocation of biomass to the root and shoot so that changes in partitioning due to changes in nutrient availability or carbon availability can be explicitly accounted for.

Since growth is a function of light interception and depends primarily on photosynthesis, shoot specific activity is easily defined from the rate of biomass growth (Eqn 6.6) times the fraction of biomass that is carbon (f_c) divided by the shoot weight

$$\sigma_s = (f_c / S_i) (dW_i/dt) \quad (6.12)$$

In order to calculate σ_r , a model of nitrogen uptake is also needed. This can be quite simple but the method must also allow some means of representing root competition at the population level. Consequently, for an isolated plant, we begin with the assumption that the efficiency of nitrogen uptake per unit root length (η_i in $\text{gN m}^{-1} \text{ root d}^{-1}$) is a function of the rooting density (δ , in $\text{m root m}^{-2} \text{ soil}$). While this density can vary in a population of plants, for an isolated plant, we further assume that root density is constant for a given soil environment. Nitrogen uptake is then given by the product

Figure 6.2: Examples of output from ISOMOD showing the growth dynamics of an isolated plant.

of η_i and total root length (l_i). Assuming geometric similarity, root length is proportional to weight raised to the one third power. That is,

$$l_i = a R_i^{1/3}, \quad (6.13)$$

where a is a proportionality constant. Root specific activity is then

$$\sigma_r = \eta_i l_i / R_i = \eta_i a R_i^{-2/3}. \quad (6.14)$$

Using this function for root specific activity in the partitioning functions (Eqns 6.10 and 6.11) allows us to include the response of plants to nitrogen nutrition.

Substituting the definition of σ_s (Eqn 6.12) into the allocation function (Eqn 6.11) and the result into the shoot growth equation (Eqn 7) gives

$$dS_i/dt = \sigma_r S_i dW/dt / (\sigma_r S_i + f_n dW/dt) - \gamma_s S_i \quad (6.15)$$

where the dependence of shoot growth on root specific activity, shoot weight, and whole plant growth rate can be readily seen. Similarly, it can be shown that

$$dR_i/dt = f_n (dW/dt)^2 / (\sigma_r S_i + f_n dW/dt) - \gamma_r R_i \quad (6.16)$$

Including the feedbacks which exist between nitrogen uptake, root:shoot ratio, and shoot specific activity is possible without substantially increasing the complexity of the model. Since root specific activity and root weight are known, the total plant nitrogen pool (N) can be easily calculated from

$$dN/dt = \sigma_r R_i \quad (6.17)$$

The light utilization efficiency (ϵ) can then be made a function of the nitrogen concentration for the plant as a whole ($N_{conc} = N/W$). Here we use a simple hyperbolic function

$$\epsilon = \epsilon_{max} N_{conc} / (\epsilon_1/2 + N_{conc}) \quad (6.18)$$

which is a simple but fairly realistic way to represent the basic feedback between plant nitrogen status and photosynthetic capacity.

Eqns (1) - (18) completely specify the model for a plant growing in isolation (ISOMOD). The model was coded in STELLATM using the 4th order Runge-Kutta method with a time step of two days. Typical results from running the model are given in Fig (6.2). Dry weight of both roots and shoots initially increase exponentially

(Fig 6.2A) but then begin to decline because the relative growth rate declines with plant age (Fig 6.2C). Whole plant nitrogen concentration declines with plant age (Fig 6.2B), in part because the ratio of root to shoot specific activity declines (Fig 6.2D). Shoot specific activity is high initially because of the high plant nitrogen concentration and a lack of self shading. Root specific activity declines with age because of the nonlinear relationship between root length and root weight.

Fig (6.3) presents the response (shoot and root weight at day 200) of ISOMOD to changing light at both low and high soil nitrogen availability. Increasing light increases total plant size and increases root:shoot ratio. Increasing nutrition greatly stimulates growth, especially at high light, and decreases root:shoot ratio. All of these responses are consistent with the generally expected trends in plant growth in response to light and nitrogen availability.

6.2.2 Monospecific Stand Model (MONOMOD)

The growth of a single species population can be modeled analogously to ISOMOD but with the addition of competition for light and nutrients and density dependent mortality. Assuming that competition for space limits the canopy cover of an individual to $1/n \text{ m}^2$, where n is the population density (numbers m^{-2}), canopy cover for an individual in the population (C_m) is now

$$C_m = \text{MIN}[C_i, 1/n]. \quad (6.19)$$

Thus, canopy cover of an individual growing in a monospecific stand will be the same as that of an isolated plant (C_i) until all the available area is occupied; after that time, cover is directly constrained by the population density. The remaining variables (leaf area, leaf area density, fraction of light absorbed, the total absorbed light, root length, the allocation parameters, and shoot activity) are defined exactly as in ISOMOD. There is no explicit consideration of mutual shading in the model, however, Eqn 17 indirectly affects the degree of self shading since, at high densities, plants will be more slender (smaller canopy cover) and have a

Figure 6.3: Shoot and root biomass at day 200 of the simulation using ISOMOD where light and nitrogen availability are varied.

higher lead area density - a trend that is observed across species.

Competition for nitrogen is assumed to be due to increased root density in the soil which lowers the uptake rate of nitrogen per unit root length. Root density for individuals within the stand (δ_m) will be the same as for isolated plants (δ_i) until the total density per m^2 exceeds δ_i . If the root length of a plant in the stand is l_m and the plant density is n , then the average root density ($m\ m^{-2}$) is $n \cdot l_m$ so the stand root density is

$$\delta_m = \text{MAX} [n l_m, \delta_i] \quad (6.20)$$

The efficiency of nitrogen uptake for plants in the stand (η_m) can then be represented by

$$\eta_m = \eta_i (\delta_i / \delta_m) \quad (6.21)$$

which, along with Eqn 18, implies that the efficiency of nitrogen uptake is inversely proportional to root density once the average density is greater than that of an isolated plant.

The rate of growth for an individual plant within the population is exactly analogous to that for an isolated plant (Eqn 6)

$$dW_m/dt = \epsilon l_a - r W_m \quad (6.22)$$

with l_a now defined for an individual within the stand and assuming that ϵ and r have the same values as in ISOMOD.

The rate of mortality (μ) is a function of the ratio of the relative growth rate of a plant in the population (RGR_m) and the relative growth rate of an isolated plant (RGR_i). Thus, the mortality rate (μ) is

$$\mu = \beta (1 - RGR_m / RGR_i) \quad (6.23)$$

where $RGR_m = \frac{1}{W_m} \frac{dW_m}{dt}$, $RGR_i = \frac{1}{W_i} \frac{dW_i}{dt}$, and β is a parameter controlling self thinning. The change in density is then

$$dn/dt = -\mu n \quad (6.24)$$

Running MONOMOD without root competition results in the classic self thinning pattern which approaches a slope of -2/3 in a log - log plot of density and average plant weight (Yoda *et al.* 1963). An example of output from the model is given in Fig (6.4). With root competition, the self thinning curves are somewhat different and diverge considerably from Yoda's law when competition for nutrients is intense (Fig 6.5).

6.2.3 Model for a Mixed Species Community (MIXMOD)

The major problem for a mixed species model is to calculate the average canopy cover for each species and the appropriate root densities. For two species, the maximum canopy cover is still $1\ m^2$ so

$$C_1 n_1 + C_2 n_2 = 1 \quad (6.25)$$

where C_1 and C_2 are the canopy covers of individuals of species 1 and 2 and n_1 and n_2 are the population densities of the two species. The canopy cover of individuals of each species can be determined by the size of each species when grown individually. Canopy covers for plants of the same weight (but different species) differ because of different proportionality constants (ρ). We can assume that

$$C_1 / C_2 = \rho_1 / \rho_2 \quad (6.26)$$

which implies that species will tend to keep their characteristic shape when grown in a mixed species stand. While density will affect C_1 and C_2 , the species that has a larger canopy cover when grown in isolation will still have a greater cover in a mixed stand. Equations (25 and 26) define a system of two linear equations that can be solved for C_1 and C_2 to give

$$C_1 = \rho_1 / (\rho_1 n_1 + \rho_2 n_2) \quad (6.27)$$

and

$$C_2 = \rho_2 / (\rho_1 n_1 + \rho_2 n_2) \quad (6.28)$$

In general, for s species, the maximum canopy cover for an individual of species j (C_{jmax}) is

$$C_{jmax} = \rho_j / \sum_{k=1}^s \rho_k n_k \quad (6.29)$$

Thus, in MIXMOD, canopy cover of an individual of species j is

$$C_j = \text{MIN} [C_{ij}, C_{jmax}] \quad (6.30)$$

where C_{ij} denotes canopy cover of an isolated plant of species j in ISOMOD.

Root competition in MIXMOD uses the same approach as MONOMOD except that the rooting density must be scaled according to the different uptake efficiencies of different species. Scaling the total root lengths of each species ($n_j l_j$) by the ratio of the appropriate efficiencies (η_j) gives the equation

$$\delta_j = \text{MAX} [(1/\eta_j) \sum_{k=1}^s \eta_k n_k l_k, \delta_{ij}] \quad (6.31)$$

Figure 6.4: The self thinning relationship produced by MONOMOD when root competition is ignored. The classical self thinning curve (Yoda *et al.* 1963) is produced.

Figure 6.5: The self thinning relationship produced by MONOMOD when root competition is included. At very low soil nitrogen availabilities the model diverges from the Yoda self thinning curve.

Figure 6.6: Simulated percent cover for a mixed community of Johnson grass (JG) and Soybean (SB) at two levels of CO₂ and light.

where δ_j is the scaled rooting density seen by each species. This equation is analogous to Eqn 18 and δ_{ij} is the rooting density of an isolated plant of species j . The first term in the brackets is the sum of the scaled root lengths for each species

$$\delta_j = (\eta_1/\eta_1) n_1 l_1 + (\eta_2/\eta_1) n_2 l_2 + \dots + (\eta_k/\eta_1) n_k l_k \quad (6.32)$$

which adjusts the "effective" root lengths by the efficiency of nitrogen uptake. Aside from the change in the definition of C_i and δ_j , the mixed species model is the same as MONOMOD. Of course, each species will have its own characteristic parameter set ($\rho_j, \beta_j, \epsilon_j, \eta_j, LAR_j, \kappa_j$).

As a preliminary test of the behavior of MIXMOD we have run the model with two species, Johnson Grass and Soybean. Where possible, parameters were estimated from data on these two species grown in the Duke Phytotron (Patterson *et al.* 1984). Fig (6.6) presents the simulated percent cover of these two species when grown at high and low light and high and low CO_2 . As one would expect, the C4 plant (Johnson grass) is competitively superior at high light while the C3 plant (Soybean) does better at low light. CO_2 has a relatively small effect compared to light but does improve the competitive ability of the C3 plant.

6.3.0 Discussion

The approach to competition developed here appears promising for the mechanistic understanding and prediction of competition at high CO_2 . While the model is relatively simple it nonetheless includes many of the most important morphological and physiological parameters that characterize plant species and their competitive abilities in various environments. While the model has not yet been rigorously tested, the qualitative behavior is reasonable. For example, the patterns of growth through time are reasonable (Fig 6.2) and root:shoot ratios respond realistically to light and soil nitrogen availability (Fig 6.3). Self thinning in MONOMOD generally behaves as expected (Fig 6.4) although the behavior at low soil N availability (Fig 6.5) should be further explored. Finally, the behavior of the model for two species is reasonable; coexistence of species with dominance of one species over another that is realistic given species characteristics and resource availabilities.

Most importantly, the approach developed here is a general scheme that can be easily modified to fit a particular situation with more or less detail included as is dictated by the available data and specific goals. In fact, this scheme can be used with much more complex simulation models of plant growth such as our whole-plant model (GePSI).

7.0.0 ECOSYSTEM MODELING

7.1.0 Introduction

Modeling at the ecosystem scale is intended to integrate results from the leaf, canopy, whole plant, and competition models with additional modules that simulate ecosystem level processes such as nutrient cycling, soil water, and decomposition. The goal is to develop an ecosystem-level simulation model, using a modular and generic structure so that it is transferable and adaptable to a variety of ecosystems. There are four objectives of the ecosystem level modeling research:

- 1) to incorporate plant response to elevated CO₂ into an ecosystem framework in order to predict the primary ecosystem effects of global change (see Fig 2.1);

- 2) to permit realistic simulations of ecosystem response to global change at conditions beyond those used to calibrate the model;

- 3) to validate the total system-level response against various ecosystem field studies or data sets of response to climate change and elevated CO₂;

- 4) to use the validated ecosystem model to test specific hypotheses and make predictions about ecosystem response to global change that may be undiscoverable within the time frame of experimental data collection.

Much of the information presented in this chapter is based on material that has been submitted for publication elsewhere (Kemp, et al. 1990; Kemp, et al. 1991; Cornelius et al. 1991; Reynolds et al. 1991; Leadley and Reynolds 1991).

7.2.0 Development of SERECO

SERECO consists of a linkage between plant growth and competition models and modules representing the soil and atmospheric environment (Fig 7.1). Three soil modules were developed specifically to be able to respond to changes in climate or secondary effects of elevated CO₂. Our ability to predict the response of ecosystems to climate change and elevated atmospheric CO₂ depends upon our ability to accurately

determine the amount and distribution of water in the soil as a function of the direct and indirect effects of climate change and CO₂. The importance of soil water to ecosystem processes is particularly important in arid and semi-arid regions. Most existing soil water models are applicable to agricultural situations and/or mesic environments, so there was a need for a more general soil water model that will be effective across a variety of ecosystem types, particularly those of semi-arid regions. Thus, we developed a process-based model (SOWAT in Fig 7.1; Cornelius et al. 1991) capable of predicting the dynamics of soil water as a function of the principal controlling factors of: 1) water input (rainfall and infiltration), 2) water loss (runoff, evaporation, and transpiration), and 3) physical properties of the soil. The model was validated with data collected as part of the monitoring associated with the Jornada Long-term Ecological Research program located in the desert/grassland region of southern New Mexico, U.S.A. The model can be used for predicting soil water contents under future climates or environmental conditions, and is particularly suited for semi-arid regions, such as desert, shrubland, and grassland.

Development of an ecosystem model that is capable of responding to climate changes also depends on predicting the dynamics of soil temperatures in response to climate change. Soil temperatures affect numerous ecosystem processes, including evaporation, the dynamics of soil organisms, plant root growth, seed germination, nutrient uptake, and decomposition. As a consequence, response of ecosystems to climate change may be mediated through effects of climate changes on soil temperatures. We therefore developed a simple process-based model (SOTEMP in Fig 7.1; Kemp et al., 1991) capable of predicting soil temperatures from the principal controlling factors of: 1) energy exchange at the surface, and 2) conduction and storage of heat in the soil profile. The model was validated with data collected as part of the monitoring associated with the Jornada Long-term Ecological Research program

SERECO Ecosystem Model

Figure 7.1: Scheme showing the modules of SERECO and their principal interrelationships.

located in the desert/grassland region of southern New Mexico, U.S.A. The model can be used for predicting soil temperatures in sites for which there are no soil temperature data, or for predicting soil temperatures under future climates or environmental conditions. By predicting soil temperature from surface conditions and soil thermal diffusivity (which is a function of soil moisture), soil temperature behavior in this model will be responsive to changes in surface environment associated with climate change.

The third soil module developed for response to global change was DECOMP (Fig 7.1; Moorhead and Reynolds 1991). Because of the importance of substrate carbon-nitrogen (C:N) ratio in controlling decomposition (Melillo et al. 1982; Paul and Juma 1981), and because of the potential for elevated CO₂ to cause changes in plant C:N tissue (Lemon 1983), one of the more important indirect effects of CO₂ at the ecosystem level may very well be changes in decomposition and nutrient cycling due to changes in C:N ratio of plant residues. To account for this phenomenon in SERECO it is crucial that the decomposition module be based on processes that are a function of substrate C:N. DECOMP was developed to track soil litter decomposition as a function of litter C:N ratio, soil temperature, and soil moisture. The model effectively responds to changes in plant litter C:N (as a function of CO₂ during plant growth and climate-induced changes in soil temperature and moisture).

CANDO and COMPETE modules for grassland ecosystems. The implementation of the SERECO for the grasslands includes several features not shown in Fig (7.1) or discussed in the CANDO module for canopy environment or the COMPETE module for annual plant communities. The principal requirement for the simulation of grassland communities is to account for the aerial distribution of shoot biomass and its change in distribution during the growing season. In the tallgrass prairie shoot biomass changes significantly throughout the growing season and may be quite different from year to year, depending upon seasonal distribution of moisture. The extent to which each species' develops leaf area and the position in the

canopy which this area occupies has important consequences with regard to the distribution and availability of light to its leaves and its neighbors. Thus, a specific CANOPY module is included in SERECO to account for the aerial distribution of shoot biomass. This module includes functions that predict the distribution of leaf, stem, and dead phytomass into particular layers of the canopy.

Upon germination from seed or sprouting from the root crown, shoots grow in height as a species' specific function of the amount of stem biomass. The average height of a species determines its aerial distribution of phytomass into canopy layers. We have represented the entire prairie canopy by a small number of layers of approximately equal total phytomass. Although, it is desirable to divide the canopy into a large number of thin layers so that each layer would have a relatively uniform light environment within, the computational requirements and lack of data for validation greatly limits the number of layers. Based on measurements of the distribution of phytomass in the canopy at the end of the growing season in two relatively moist years, we chose to divide the simulated canopy into five layers: 0-10 cm, 10-20 cm, 20-30 cm, 30-45 cm, and 45-150 cm. Shoot biomass of each species was apportioned equally among layers that were fully occupied by the species (based on its total height), and fractionally into the uppermost layer if it was not fully occupied. Stem biomass and standing dead biomass were apportioned similarly.

A second requirement for simulation of grassland ecosystems with SERECO was to account for the spatial distribution of roots in the soil. In this case we assume that although there is considerable annual turnover in roots, the average rooting depth of each of these perennial species changes little during the year and that each species has a constant, effective rooting depth over which water and nitrogen are available. It is further assumed that soil water and nitrogen which is available to the plant species is the maximum that occurs in any of the soil layers that the species has roots. For the purposes of calculating soil water and nitrogen, the soil is arbitrarily divided into 6 to 8 layers, depending on the thickness of the actual soil

profile in the prairie region being simulated. Soil layers used for the prairie region of Central Kansas were: 0-15 cm, 15-30 cm, 30-60 cm, 60-90 cm, 90-120 cm, and 120-150 cm.

7.3.0 Application of SERECO

7.3.1 Response of grassland (prairie) ecosystems to climate change.

Introduction. In order to predict how ecosystems will respond to global climate change it is necessary to understand how climate directly and indirectly influences ecosystem structure and function. Furthermore, if we are to have confidence in model predictions of ecosystem response to future climates, a simple, but important, requisite is that the models reliably predict ecosystem responses to current and historical climate. Thus, a principal element of our research is to investigate responses of ecosystems to climate, through 1) analyses of historical vegetation responses to climate and 2) ecosystem-level simulations of response to historical climate. This research focuses on the prairie of Central North America, specifically central Kansas. This region was chosen because historical weather records (Borchert 1971; Wigley et al. 1980; Kellogg and Schwere 1981) and simulation modeling (Manabe and Wetherald 1986; Kellogg and Zhao 1986) of regional climate suggest that the prairie regions of North America (Great Plains and adjacent lowlands of the Mississippi and Missouri River Valleys) may be particularly sensitive to, or strongly affected by, global climate change. Secondly, there are two sites in central Kansas having relatively long-term records of vegetation and climate. One site, near Manhattan, documents vegetation changes of a tallgrass prairie community over a 50-year period (Towne and Owensby 1984), and the other site, near Hays, documents vegetation changes of a mixed prairie community over a 35-year period (Tomanek and Hulett 1970). Also, our work represents part of a collaboration with the staff at Kansas State University who are studying the effects of elevated CO₂ on the tallgrass prairie near Manhattan. This collaboration forms an integral part of the development of models

for predicting ecosystem responses to the combined effects of climate change and elevated CO₂.

Historical patterns of prairie response to climate. Historical records of undisturbed vegetation provide one way to ascertain the effect of relatively recent climate fluctuations on grassland ecosystems. Year to year changes in vegetation should reflect primarily the year to year changes in weather. Longer-term changes in the vegetation could be expected to be related to climatic changes (Greenland and Swift 1991).

Fig (7.2) shows long-term variation in annual production (estimated as peak above-ground biomass), of unburned, ungrazed plots of tallgrass prairie near Manhattan (Towne and Owensby 1984). Total annual production varied from a low of about 60 g/m² in 1934, the driest year of nearly a decade of drought in the 1930's, to a high of about 750 g/m² in 1981, a year of moderately high rainfall. However, total above-ground production was not significantly correlated with monthly, seasonal, or annual rainfall (maximum r^2 obtained was between total annual production and summer rainfall; $r^2 = 0.15$; n.s.). The only significant correlation uncovered was a slight trend toward increasing production over the course of the observations ($r^2 = .25$, $p < 0.10$). The extent to which climate may have induced changes in this grassland plant community is not completely evident from these data since there is no record for the individual species, although the authors indicate there was no change in the relative species abundances.

Another historical vegetation record is from the mixed prairie about 200 km west of Manhattan near Hays (Tomanek and Hulett 1970). Fig (7.3) shows the average cover (basal area) of 4 principal species in 12, 1-m² plots located in a little bluestem community type. In this community, as in the tallgrass prairie, total above-ground cover was not correlated with monthly, seasonal, or annual rainfall (maximum r^2 obtained was with the relationship between total cover and annual rainfall; $r^2 = 0.10$; n.s.). Nor was the cover of any species significantly correlated with rainfall.

Figure 7.2: Average total aboveground biomass at the end of each summer growing season in unburned, ungrazed tallgrass prairie near Manhattan, KS. There is no record for 1935-37, 1945-53, 1967, and 1971 (adapted from Towne and Owensby 1984).

Figure 7.3: Average peak cover (basal area) of grasses in unburned, ungrazed mixed prairie near Hays, KS (adapted for Tomanek and Hulett 1970).

Prior to 1932 the mixed prairie community was dominated by little bluestem and big bluestem, but during the drought of the 1930's, both species declined greatly. They were replaced by two drought tolerant grasses--sideoats grama, initially, and then blue grama two or three years later. The moist summers of the 1940's resulted in a slow recovery of big bluestem and a decline in both grama grasses. However, this moist period did not result in a return of the community to its pre-drought condition, in which little bluestem was the most abundant species (Weaver 1943; Tomanek and Hulett 1970). Thus, in contrast to the tallgrass prairie, the mixed prairie appears to have undergone a rather long-lasting change in species composition following the drought of the 1930's.

Determining why this occurred requires a greater understanding of how the many other factors that control plant distribution changed as a result of drought or climate shifts. For example, weather changes may have led to changes in plant competitors or herbivores, or may have caused changes in soils through erosion or loss of organic matter. However, most of these factors weren't monitored, and we have only the record of the vegetation and weather changes. Simulation models offer one way of investigating some of these indirect factors.

Model Simulations. For simulation of a tallgrass prairie ecosystem, SERECO was parameterized for six species (or lifeforms)--two C₄ tallgrass dominants (big bluestem and little bluestem), a drought-tolerant C₄ shortgrass (blue grama), a C₃ grass, a C₃ forb, and a C₄ forb. Parameter values were determined based on data in Risser et al. (1981), Weaver (1968), and Knapp (1985a,b). The model was parameterized using a 10-year sequence of random Manhattan weather so as to produce a steady-state composition of vegetation similar to what could be expected under non-drought conditions (50% big bluestem, 30% little bluestem, 15% C₃ grass, and 5% forb; Weaver and Albertson 1956; Towne and Owensby 1984).

The model simulation was run over the period from 1900-1982 using actual daily maximum and minimum air temperatures and precipitation from Manhattan, Kansas. Solar radiation and wind values were generated using the climate simulator of Richardson, et al. (1987). The model was initialized with small, equal root biomass for each plant form (50 g/m²). In order to compare simulations with observed plant biomass, as determined from harvests at the end of the growing season (Towne and Owensby 1984), we show simulated biomass for the second week of August. Some species had greater peak biomass before or after this time, but this period was usually within one or two weeks of peak total above-ground biomass in the simulation. Results of the simulation are shown in Fig (7.4). Because of the low starting plant biomass, there is a transition or succession in the modeled community. Initially, C₄ forbs and blue grama had the highest biomass, but they were both eliminated from the community by the tenth year of simulation. There was also a significant trend for big bluestem biomass to increase during the course of simulation ($r^2 = 0.44$, $p < 0.01$), a situation that is consistent with the increase in biomass in the observed record.

The simulated total above-ground biomass is compared to observations (Towne and Owensby 1984) beginning in 1928 in Fig (7.5). Simulated above-ground biomass tends to overestimate observed. This may be due to differences between the conditions of the model and the experimental plot (e.g., no insect herbivory in the model), or it may be the result of a systematic model error. However, by and large, the model results correspond quite well with the actual year to year changes in community biomass. The average simulated plant composition for the period from 1928 to 1982 was: 55% big bluestem, 28% little bluestem, 10 % C₃ grass, and 7% forb. This compares favorably to the average field composition of 50% big bluestem (+indiangrass), 28% little bluestem, 17% C₃ grass, and 4% forb (Towne and Owensby 1984). The simulation results reproduce closely the observed responses of

Figure 7.4: Simulated production of biomass of the principal species of a tallgrass prairie community based on response to actual weather of Manhattan, KS.

Figure 7.5: Comparison of simulated total aboveground biomass of a tallgrass prairie community with observed values (observations from Towne and Owensby 1984).

tallgrass prairie to the droughts of the 1930's and of the 1950's. The drought of the 1930's was characterized both in the model predictions and the data as of short duration (essentially 1934) from which all species recovered relatively quickly. The drought of the 1950's was more protracted but with less severe reduction in biomass. There is no indication in the model simulation of long-term vegetation change associated with drought in the tallgrass prairie community. This contrasts with the mixed prairie communities to the west, which were impacted for a decade or more by the drought of the 1930's (Weaver 1943, 1968).

Next, we used SERECO to predict the response of mixed prairie to weather changes. SERECO was parameterized for two tallgrasses (big bluestem and little bluestem), two drought-tolerant shortgrasses (blue grama and sideoats grama), and forbs and subshrubs. Parameter values were determined from data in Risser et al. (1981) and Weaver (1968). The model was parameterized using a 10-year sequence of random weather from Hays, Kansas so as to produce a steady-state composition of vegetation similar to what found under non-drought conditions (60% little bluestem, 20% big bluestem, 5% sideoats grama, <1% blue grama, and 15% forb and subshrubs; Weaver and Albertson 1956; Tomanek and Hulett 1970).

There were several discrepancies between the model predictions and the observed changes in mixed prairie reported by Tomanek and Hulett (1970; Fig 7.6). The most notable difference between model simulation and observation was that the model did not predict the great reduction in little bluestem that occurred during the early 1930's. Neither did the model predict as great a decline in big bluestem as was observed during the 1930's. Although the model correctly predicted a temporary increase in drought tolerant grasses, the predicted increases preceded by several years the observed increases. Because the drought-induced changes in mixed prairie observed by Tomanek and Hulett (1970) were representative of changes that were widespread throughout the prairie (Weaver 1968), we conclude that the present model of mixed prairie is not adequate to predict

response of mixed prairie to climate change. Major modifications of the model will be implemented in an effort to overcome these limitations. One of the most important changes will be implementing improved decomposition and nutrient cycling modules (as described in Moorhead and Reynolds 1991). These modules will provide for a greater control of grassland productivity by nutrients, consistent with recent research that indicates grassland productivity is limited at least as much by decomposition and nutrient availability as by water (Breman and deWit 1983; Knapp and Seastedt 1986). We believe that the importance of nutrients is underscored by the lack of correlation between rainfall and productivity in both the tallgrass and mixed prairie historical vegetation data. It also seems likely that the interaction between water and nutrient availability could be a factor causing both 1) the greater impact of drought on the dominant tallgrasses of the mixed prairie than seems to be accounted for by drought alone, and 2) the lag in response to drought of drought-tolerant grasses in the mixed prairie.

Conclusions. We know that long-term climatic changes, such as those associated with the Ice Ages, can have large impacts on ecosystems (e.g., Dort and Jones 1970). However, there is little evidence or understanding of the effects on ecosystems of climatic changes at the scale of decades to a century. These are precisely the kinds of changes that will be associated with global climate forcing from elevated CO₂ in the near term. We believe that understanding how relatively short-term climate influences ecosystems is an essential step toward making reliable predictions about the effects of future climate change on ecosystem structure and function. The historical prairie vegetation records that we examined indicate that climate fluctuations have induced significant changes in plant cover and species composition in mixed prairie but have had much less effect on tallgrass prairie. This may be because the tallgrass prairie is more resistant to climatic fluctuations, or the climatic changes in the tallgrass prairie were relatively less than in the mixed prairie. If

Figure 7.6: Comparison of simulated aboveground biomass of a mixed prairie community with observed values (observed values derived from basal area in Tomanek and Hulett 1970).

the historical climate fluctuations at these two sites were, in fact, relatively similar, then we would predict that the mixed prairie would be more susceptible to, or affected by, future climate change than the tallgrass prairie.

Model predictions of prairie vegetation dynamics did not reveal this difference between prairie types in response to climate. However, the simulation of mixed prairie vegetation did not correlate well with the observed historical record. Thus, further model development will be required before we can draw conclusions about the influence of climate on mixed-prairie ecosystem structure and function. We believe that the most significant changes currently needed are improved decomposition and nutrient cycling modules, which will allow more effective simulation of interactions between nutrient and water limitations of grassland productivity. An improved model will help provide information about the apparent differences between the tallgrass and mixed prairie responses to climate. However, the relatively close agreement between tallgrass prairie model simulations and observed vegetation responses suggests that the current ecosystem-level model (SERECO) is well on its way to becoming a useful tool for providing predictions about ecosystem response to global climate change.

7.3.2 Response of arid ecosystems to climate change: Spatial and temporal variability in rainfall

Introduction. A second group of ecosystems for which we are modeling responses to climate change are arid/semi-arid ecosystems. While it is usually assumed that productivity in arid and semi-arid regions is controlled by water (e.g., Macmahon and Schimpf 1981), the relationship between the amount or availability of water and actual plant production is not direct. Le Houerou et al. (1988) found that arid ecosystems were highly variable in response to water inputs. In their study, the variabilities in rainfall and mean annual above-ground primary production were examined for a variety of vegetation types in arid and semi-arid sites around the world. The variability in annual

production was 50% greater than the corresponding variability in annual rainfall on sites receiving less than 600 mm (Fig 7.7).

The great diversity of sites evaluated by Le Houerou, et al. (1988) makes it difficult to understand what caused the high variability in plant production in relation to rainfall, but their conclusions clearly contradict existing, conceptual models of desert ecosystem dynamics. For example, Schlesinger et al. (1990) suggest that desert shrub communities should show less variation in production than grasslands because the former are deeper rooting. Furthermore, the 'pulse and reserve' paradigm of Noy-Meir (1973) states that desert plant reserves buffer vagaries in water input, thereby reducing variability in production relative to rainfall. How do we reconcile these divergent conclusions? We propose three alternative explanations to this phenomenon: 1) Interactions between various aspects of water input, such as timing, frequency and intensity of precipitation events, and the particular requirements of individual plant species enhance the variability of productivity in arid and semi-arid regions. 2) Topographic and edaphic characteristics of the landscape modify the pattern of spatial distribution and retention of water, potentially affecting production. 3) Factors other than water availability, such as herbivory or nutrient limitations, may also exert a significant effect on productivity under certain conditions. If we are to be able to make predictions of the way arid and semi-arid ecosystems will respond to future global climate changes, we must understand the way in which these systems are controlled by the climate and the interaction of the climate with other environmental factors. That is the goal of this research.

Rainfall patterns and plant responses. Timing, seasonality, intensity and volume of rainfall events may be important contributors to variability in plant production (Cunningham et al. 1979). Years with high rainfall in winter may provide greater available moisture than years with high rainfall in summer, because of higher evaporative demand in summer. Deserts with a strong seasonal aspect to their moisture may have decreased productivity in

years when the moisture falls out of season, because of a smaller suite of plants able to use it (Shreve 1942; Kemp 1983), or inability of the dominant plants to use it (Cunningham et al. 1979; Fisher et al. 1988). Many small rainfall events may not be as effective as a single large rainfall event because of a lack of deep soil recharge and/or a lack of triggering germination or growth responses in desert plants (Beatley 1974). On the other hand, frequent, small rainfall events may lead to greater production than few, widely separated ones (Ludwig and Flavill 1979, Sharifi et al. 1988) perhaps because of increased nitrogen mineralization (Fisher et al. 1988) and less runoff.

Variability in diversity of plant species and guilds may be an important cause of variation in production response to rainfall. Shallow rooted evergreen perennials would be able to utilize small, erratically spaced rainfall events, deep-rooted perennials would require larger or sequential rainfall events to recharge deep soil moisture, and ephemerals would require large rainfall events that would trigger germination (Noy-Meir 1973; Beatley 1974). Ephemerals would be susceptible to seasonal drought since they must pass through a seedling stage (most vulnerable to drought) every year. Most of the studies listed by Le Houerou et al. (1988) reported only above ground production. For perennials, above ground plant production may be more variable from year to year than total production since biomass allocation may shift in response to stress (Cunningham et al. 1979). Changes in above ground production or standing crop may reflect allocation to below ground reserves in drought years.

Topography and Soil Texture.

Topographic and edaphic factors may decrease or enhance the effectiveness of rainfall by amplifying or dampening its expression in plant production. Steep sites or fine textured surface soils limit infiltration, particularly of larger rainfall events.

Le Houerou et al. (1988) reported that, in arid climates, variability in production is much greater in fine- than in coarse-textured topsoils, and larger in shallow than in deep soils. They contend that fine textured soils may have no

production in dry years and very large production in wet years, while sandy soils exhibit a much more regular production. In general, net primary production is higher on coarse- than fine-textured soils in arid and semi-arid regions (c.f., Shreve 1942, Noy-Meir 1973, Le Houerou, et al. 1988). Sala et al. (1988) analyzed production data from 9500 arid and semiarid sites throughout the central United States and found that sandy soils (with low water-holding capacity) are more productive than loamy soils when precipitation is less than 370 mm; the opposite pattern occurs when precipitation exceeds 370 mm.

This relationship between texture and production in arid climates is opposite that found in mesic environments. Hence, Noy-Meir (1973) referred to this phenomenon as the "inverse texture effect". He also identified three factors underlying this relationship: 1) there is less runoff and greater infiltration in coarse- than fine-textured soils; 2) the depth of wetting by a given rain event is inversely proportional to soil water storage capacity (since water storage capacity decreases with sand and stone content of the soil, the depth of wetting is greater for coarse than for fine soils given equal infiltration amounts); 3) total evaporative loss is lower in sandy, gravelly, and rocky soils than in fine-textured soils (Alizai and Hurlbert 1969) because it is directly proportional to the water storage capacity of the top 20-30 cm of soil.

Much of the rationale for the inverse texture hypothesis is based on the differing ramifications of physical location of water in soils of mesic vs arid environments. In mesic climates, loss of soil water occurs primarily through drainage, or deep percolations beyond the root zone. However, rainfall is rarely great enough to penetrate beyond the rooting depth of plants in dry climates, so soil moisture loss is predominately through evapotranspiration (Noy-Meir 1973). The balance between the advantages of coarser textured soils (less evaporation loss) and their disadvantages (more drainage loss) appears to shift within the range of 300-500 mm annual rainfall.

Herbivory. Although our discussions have centered on the direct effects of

changing moisture regimes on plants, herbivores also influence patterns of primary production. Although they typically consume only a small percentage of net primary production in temperate ecosystems (Golley 1960, O'Neill 1976, Owen and Weigert 1976), herbivores may control rates of production (Golley 1973, Mattson and Addy 1975), regulate energy flow and nutrient flux to decomposers (Chew 1974, Lee and Inman 1975, McNaughton 1976, Parker 1983), and increase ecosystem stability (Lee and Inman 1975, Petruszewicz and Grodzinski 1975). Thus, a comprehensive understanding of effects of climate change on arid ecosystems requires an analysis of the interaction between climate and herbivory on the ecosystem.

The most obvious effect of herbivory on primary production results from the consumption of plant materials. However, herbivory can influence subsequent plant growth and physiology, including leaf and shoot level photosynthetic rates (Dyer, Detling, Coleman, and Hilbert, 1982), internal allocation of labile carbon (Dyer et al., 1982; Marshall and Sagar, 1968). Under some circumstances, whole-plant growth rates are stimulated by defoliation (Hilbert et al. 1981; McNaughton 1979). The effects of herbivory may indirectly alter resource levels (e.g., soil water) and impact other ecosystem processes, such as decomposition. Several authors have suggested that the most important indirect effect of herbivores on ecosystem function is the rapid cycling of living plant matter into the decomposer compartment (Chew 1974, Lee and Inman 1975, McNaughton 1976, Parker 1983). Grasshopper grazing in grasslands produce litter and frass equal to 25% of annual above ground productivity (Mitchell and Pfadt 1974). Since this material decomposes rapidly, grazing can actually increase nutrient availability. Phytophagous insects of *Larrea* have been shown to increase the flux of nitrogen from canopy to soil and, consequently, influence nutrient cycling (Lightfoot and Whitford, 1990).

Decomposition. Finally, there are other ways in which interactions among organisms or ecosystem processes may lead to lags or indirect responses to change in rainfall

amount. Productivity has been reported to decline in the second year of two consecutive wet years (Charley 1972; Ludwig and Flavill 1979), most likely as a result of soil nutrient depletion. Thus, decomposition and other aspects of nutrient dynamics may play a fundamental role in the production response of desert ecosystems to rainfall patterns.

Methods. Three major tasks are being addressed by our modeling efforts in arid ecosystems: (1) describing processes that occur at specific locations on the landscape; (2) characterizing transport of energy and materials between locations; and (3) interfacing local and transport processes in a landscape framework. These process models will contribute to our basic understanding of the rates, directions, and magnitudes of important fundamental processes controlling ecosystem response to changing resource availabilities in the face of local disturbances and/or global changes. We are building a suite of models that will allow us to address questions at distinct time and space scales since activities at lower levels (e.g., physiological processes) operate at faster time and smaller spatial scales than activities at higher levels (e.g., ecosystem and landscape processes) (Reynolds and Acock 1985a,b). In this section we present only the results of modeling at a specific location using SERECO.

SERECO was parameterized for an arid shrubland ecosystem in the northern Chihuahuan Desert. Modeled species included creosotebush (*Larrea tridentata*) and 3 guilds and annual species (spring, summer, and winter growing).

Shrub module. The shrub model (SHRUB) is based upon a carbon balance, primary production model originally developed for creosotebush (*Larrea tridentata*) (Cunningham and Reynolds 1978, Reynolds et. al. 1980, Reynolds and Cunningham 1981). This model balances carbon losses (respiration, leaching, etc.) and gains (photosynthesis), with excess carbon being partitioned between vegetative and reproductive growth depending upon the current physiological condition of the plant. The model has been modularized, as described by Reynolds et. al. (1988), which

makes the model more general, easier to understand, and therefore easy to modify for use with other shrub species, [e.g., mesquite (*Prosopis glandulosa*)]. The current version uses a simple net CO₂ exchange model (Reynolds et. al. 1979), which is being updated to a canopy photosynthesis model (Reynolds et. al. 1988). SHRUB assumes that structural nitrogen follows structural carbon flows in fixed ratios, and that the nitrogen concentration of tissue remains fixed through time. The N balance submodel of the current version of SHRUB has N uptake a function of soil temperature, soil N concentration, and whole plant substrate N concentration (Johnson and Thornley 1987), and there is a feedback between whole plant N concentration and photosynthesis that has been based upon data from Lajtha and Whitford (1989). Recent data show internal cycling of N (i.e., retranslocation of structural N) to be very important in the eco-physiology of *Larrea* (Lajtha and Whitford 1989), thus, we plan to add internal cycling to the N balance model. A variable root:shoot allocation scheme (similar to that of Johnson [1985] and Johnson and Thornley [1985, 1987]) has also been incorporated into the model, with allocation being a function of the relative C:N ratio of the internal substrate pool. Root growth in SHRUB has been modified to partition new biomass between soil layers to optimize water uptake (similar to Protopapas and Bras 1987). Other planned modifications to SHRUB include the development of more detailed models for plant architecture, 'population' dynamics of roots and shoots, and whole plant water balance. These modifications will allow more dynamic feedbacks between the soil water model (SOWAT) and the decomposition model (DECOMP), which will be necessary for simulation of the process of resource island development. We will also be adapting and parameterizing SHRUB for mesquite (*Prosopis glandulosa*). Current and planned modifications to SHRUB will result in a model easily adaptable for use with other shrub species, and which will be sensitive to a wide range of environmental conditions, (e.g. climate change, nutrient limitations, elevated CO₂, disturbance, etc.).

Annual forb module. The three guilds of annual forbs were model using simplified versions of GEPSI. Because of the importance of environmental factors such as moisture, temperature, and nitrogen in controlling desert vegetation, the emphasis of the herbaceous plant model (HERB) in SERECO is to simulate physiological responses of plants to the abiotic environment (as opposed to plant-plant interactions). This does not mean that plant-plant interactions are ignored, and, in fact, plants can have a specific impact on each other in the model via their extraction of nitrogen and water, thereby reducing the amounts of the resources in the environment (see COMPETE). In addition, the growth activities of perennials and life cycles of annuals in this arid lands version of SERECO are controlled by a mechanistic phenology submodel (PHENANN, Bachelet, et al. 1988) that predicts growth, germination, and flowering responses to environmental cues of temperature, moisture, and photoperiod.

Model validation. Data for model parameters and validation were collected as part of the Jornada Long Term Ecological Research Program. Model simulations were first done under 10-year sequences of historic weather to determine the capacity of the model to predict natural variation in primary production. Simulations were then carried out for sequences of years with simulated greater variation in rainfall or with changes in frequency of certain kinds of rainfall years (types) , e.g., El Nino, La Nina, Median.

Results. Model simulations showed that total annual primary production was quite variable from year to year under ambient climate variation--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 the year to year variation of vegetation production over the variation in rainfall (Table 7.1). This was, again,

Figure 1: Coefficient of variation in annual productivity (CVP) vs coefficient of variation in annual rainfall (CVR) (from data presented in Le Houerou et al. 1988).

Table 7.1: Simulated variation in production of shrubs and annuals in response to variations in rainfall. Results are from ten, 10-Year simulations of artificially induced variations in annual rainfall amounts.

Life Form Group	Coef. of Variation of Rainfall	Coef. of Variation of Production	CVP / CVR
Annuals			
Winter Season	0.55	1.36	2.47
Spring Season	1.00	1.88	1.89
Summer season	0.70	1.45	2.09
Total	0.56	1.03	1.83
Creosotebush			
Shoot	0.56	0.40	0.79
Root	0.56	0.51	0.73
Reproductive	0.56	1.24	3.66
Total	0.56	0.41	0.80
Le Houerou (1988) (77 arid rangelands)	0.34	0.49	1.47

observed to be the result of variation in production of herbaceous species. Changing the frequency of rainfall types was found to have an immediate 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 associated with El Nino years. Short term shifts in shrub production were not observed; however, the long term production of shrubs could be affected by either a long term climatic shift, or by changing levels of CO₂. These aspects of global change will be investigated in a followup study, using a version of SERECO and GEPSI parameterized for the long-term affects of elevated CO₂.

7.3.3. Response of an Arctic sedge to climate change - from Leadley & Reynolds (1991)

Introduction. The third ecosystem we investigated with regard to its response to global change is Arctic tussock tundra. The potential response of arctic vegetation to global climate change has been the subject of much recent debate (Chapin et al. 1991), largely because it is widely accepted that the polar regions of the earth will bear the brunt of global temperature increases (Chen and Drake 1986). One species that has received considerable attention from experimentalists is the sedge *Eriophorum vaginatum*. *Eriophorum* is widely distributed throughout arctic regions of the world (Bliss 1981) and is an important component in ecosystems where it occurs because its tussock-forming habit affects soil nutrient cycling and microclimate (Chapin et al. 1979). In addition, it is one of the principal invaders of disturbed areas (Chapin and Chapin 1980, Gartner et al. 1986).

All studies of *Eriophorum*-dominated tussock tundra have been short-term relative to the time scale over which climate change is likely to occur. While short-term experiments provide valuable information about response mechanisms, they may not be indicative of long-term changes in plant growth because of homeostatic adjustments that occur over longer time scales (Osmond et al. 1980, Oechel and Strain 1985). In

addition, plant response to manipulation of single factors may not provide enough insight into the response to disturbance because of the complex interactions between environmental factors that limit growth of tussock tundra species (Chapin and Shaver 1985 a,b). Unfortunately, long-term, multi-factor experiments are both difficult and expensive.

Thus, simulation models, while not a replacement for experiments, provide a link between short-term, single factor experiments and understanding of long-term, multi-factor disturbances (Reynolds and Acock 1985, Pereira and Landsberg 1989). Numerous simulation models have been developed for arctic tundra, some specifically designed to address effects of disturbance on tussock tundra (e.g. Miller et al. 1984). In a review of arctic vegetation models, Reynolds and Leadley (in press) found that most of these growth models were either highly complex and mechanistic and, hence, not appropriate for long-term simulations, or were highly empirical and, therefore, are not suitable for long-term extrapolation. The exception to this was the Northern Ecosystem Carbon Simulator (NECS) developed by Miller et al. (1983) to specifically address the long-term effects of climate change on northern ecosystems. NECS was developed with a long time step (a mix of months and years) but contained enough mechanism to capture the essence of processes that control plant growth in the arctic. However, NECS was not validated and some predictions conflict with recent experimental findings (Reynolds and Leadley in press).

We developed a simulation model, which, like NECS, utilizes a mechanistic framework to address potential long-term effects of climate change on arctic vegetation. Because of its ecological importance in arctic ecosystems and the large amount of data available on *Eriophorum* growth and physiology, we chose this species as a test case to model the potential response of arctic plants to global climate change and elevated CO₂. Included are the effects of light, temperature, season length, nitrogen availability, and CO₂ concentration on *Eriophorum* growth. The model was parameterized using published studies of the growth responses of *Eriophorum* to nutrients;

validation was based on field studies on growth responses of *Eriophorum* to temperature and shading and the effects of elevated CO₂ and temperature on photosynthesis. Because the model that was developed for this exercise is substantially different than SERECO, we present a detailed description of the model.

Model description.

Overview of Eriophorum growth. Detailed descriptions of the growth habit of *Eriophorum* are given in Chapin et al. (1979), Fetcher and Shaver (1982, 1983), and Robertson and Woolhouse (1984). Briefly, a single *Eriophorum* ramet (= tiller) consists of live leaf blades, leaf sheaths, a perennial rhizome, and roots. The shoot meristem differentiates into a flower bud after several years, and the ramet flowers and dies the subsequent year. Leaves and sheaths grow sequentially throughout the arctic summer; some of the leaf and sheath survive the winter. Dead leaves and sheaths may remain attached to the rhizome for several years. The root system is annual. Successful reproduction in *Eriophorum*, like most other arctic plants, is almost exclusively vegetative. Mother tillers produce one to two daughter tillers every year after maturing.

Eriophorum tussocks develop through the accumulation of partially decomposed ramets. Tussocks are dominated by *Eriophorum* in early stages of development but gradually become invaded by other plants as the tussock ages. The mound or mushroom-shaped tussock is crowned with leaves and sheaths; rhizomes lie just beneath the surface of partially decomposed litter and roots explore the tussock following the thaw front. Because of the extreme spatial heterogeneity within a tussock, Shaver et al. (1986) and Chapin et al. (1986) sampled *Eriophorum* productivity by removing cores from the center of tussocks. Their data and all simulation output we present are expressed using a "core" as the unit of area (0.00332 m²).

Model structure. The temporal resolution of the model is one year. Plant physiological activity is restricted to the arctic summer, defined here as the time between spring snowmelt (late May) and before freezing of the soil (mid-September).

A diagram of the model is shown in Fig 7.7. State variables (boxes) represent the overwinter status of the plant, i.e., the status the plant would have on January 1 of each year. Carbon (C) and nitrogen (N) are divided into overwinter labile components (labile C and labile N) and overwinter structural components (structural C and structural N). (Carbon is used here as carbon plus the sum of the mass of all non-nitrogen elements, i.e., hydrogen and oxygen plus mineral elements.) Overwinter structure is the sum of overwinter leaf, root, and other (i.e., stem, leaf sheath, and reproductive organs) plant structure.

Parameterization and Fitting.

Below, we provide a description of the various fluxes of carbon and nitrogen, including uptake (C uptake and N uptake), conversion of labile plant components into structure (growth), losses of labile components (labile C loss and labile N loss), and the losses of structural material (structural loss). Estimates of parameters for these functions were obtained in two steps: 1) Initially, from published papers, reports, and best guesses; sources and ranges of these estimates are discussed below. These estimates were difficult to make since the model has an annual time step, whereas most of the observed responses on *Eriophorum* are from short-term experiments. 2) These initial estimates were then modified based on fitting the model to data collected by Chapin, Shaver and co-workers in a 3-yr study of the response of *Eriophorum* to nutrients, temperature, and shading (Chapin et al. 1986, Shaver et al. 1986). The model was fitted to their unfertilized treatments assuming plants were in steady-state growth; response to fertilizer application was simulated as deviations from steady-state. In Table 7.2, a listing of all parameter and their values used in the simulations is given.

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Table 7.2. Description and values of variables, parameters, and graphical functions. Dashes indicate that the value varies during simulation.

<u>NAME</u>	<u>DESCRIPTION</u>	<u>UNITS</u>	<u>VALUE</u>
C growth	carbon growth rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
C uptake	net annual carbon uptake	$\text{g m}^{-2} \text{yr}^{-1}$	----
c_{eff}	light utilization efficiency	g/MJ	----
c_{max}	maximum light utilization efficiency	g/MJ	2.5
CO ₂	CO ₂ concentration	$\mu\text{L/L}$	Table 7.3
f_{C}	fraction of labile carbon not retranslocated	dimensionless	0.25
f_{I}	fraction of incoming light intercepted	dimensionless	Fig 7.8a
f_{N}	fraction of labile nitrogen not retranslocated	dimensionless	0.15
f_{new}	fraction of new structure that is leaves	dimensionless	----
f_{old}	fraction of overwinter structure that is leaves	dimensionless	0.1
f_{other}	fraction of new structure other than leaves and roots (i.e., stems, leaf sheaths, and reproductive organs),	dimensionless	----
growth	structural growth rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
I_{ave}	average daily incident radiation	$\text{MJ m}^{-2} \text{day}^{-1}$	----
I_0	incident light during the growing season	$\text{MJ m}^{-2} \text{yr}^{-1}$	Table 7.3
labile C	labile carbon	g/m^2	----
labile C loss	labile carbon loss rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
labile N	labile nitrogen	g/m^2	----
labile N loss	labile nitrogen loss rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
leaf structure	leaf structural biomass	g/m^2	----
new structure	structure grown in one year	g/m^2	----
N availability	soil nitrogen availability	$\text{g m}^{-2} \text{yr}^{-1}$	Table 7.3
N growth	nitrogen growth rate	$\text{g m}^{-2} \text{yr}^{-1}$	----

Table 1 (continued)

<u>NAME</u>	<u>DESCRIPTION</u>	<u>UNITS</u>	<u>VALUE</u>
N uptake	net annual nitrogen uptake rate	$\text{g m}^{-2} \text{ yr}^{-1}$	----
overwinter biomass	overwinter structure plus overwinter labile carbon and nitrogen	g m^{-2}	----
overwinter structure	overwinter structural dry weight	g/m^2	----
peak biomass	overwinter biomass plus production	g/m^2	----
production	annual carbon and nitrogen uptake	g/m^2	----
rgt	relative growth rate	yr^{-1}	----
r_{max}	maximum relative growth rate	yr^{-1}	2.0
root structure	root structural biomass	g/m^2	----
$S_{\text{c},[\text{C}]}$	Scalar, effect of labile carbon on C uptake	dimensionless	Fig 7.8d
S_{CO_2}	Scalar, effect of CO_2 concentration on C uptake	dimensionless	Fig 7.8e
$S_{\text{f},[\text{C}]}$	Scalar effect of labile carbon on fraction of new structure allocated to leaves	dimensionless	Fig 7.8j
$S_{\text{f},[\text{N}]}$	Scalar effect of labile nitrogen on fraction of new structure allocated to leaves	dimensionless	Fig 7.8k
$S_{\text{g},[\text{C}]}$	Scalar effect of labile carbon on growth	dimensionless	Fig 7.8f
$S_{\text{g},[\text{N}]}$	Scalar effect of labile nitrogen on growth	dimensionless	Fig 7.8g
S_{I}	Scalar effect of light saturation on C uptake	dimensionless	Fig 7.8b
SL_{act}	Actual length of growing season	days	Table 7.3
SL_{ave}	Average length of growing season	days	100
SL_{rel}	Scalar effect of relative season length on growth	dimensionless	0-1
$S_{\text{s},[\text{C}]}$	Scalar effect of labile carbon on structural loss	dimensionless	Fig 7.8h
$S_{\text{s},[\text{N}]}$	Scalar effect of labile nitrogen on structural loss	dimensionless	Fig 7.8i
S_{T}	Scalar effect of temperature on C uptake and growth	dimensionless	Fig 7.8c

Modeling the Response to Global Change

Table 1 (continued)

<u>NAME</u>	<u>DESCRIPTION</u>	<u>UNITS</u>	<u>VALUE</u>
structural C	structural carbon	g/m^2	----
structural C loss	structural carbon loss rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
structural loss	structural loss rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
structural N	structural nitrogen	g/m^2	----
structural N loss	structural nitrogen loss rate	$\text{g m}^{-2} \text{yr}^{-1}$	----
total N	total overwinter nitrogen concentration	g/m^2	----
t	time	yr	----
T	average temperature over the growth season	$^{\circ}\text{C}$	Table 7.3

Carbon uptake. Net annual carbon uptake is given by:

$$C_{\text{uptake}} = c_{\text{eff}} \cdot f_l \cdot I_0 \quad (7.1)$$

where

$$c_{\text{eff}} = c_{\text{max}} \cdot S_l \cdot S_t \cdot S_{c,[C]} \cdot S_{\text{CO}_2} \quad (7.2)$$

Variable c_{eff} is the efficiency of converting intercepted light energy into carbon and f_l is the fraction of incident light (I_0) intercepted. The value of c_{eff} is determined from the product of a maximum efficiency (c_{max}) and scalars for light saturation (S_l), air temperature (S_t), labile carbon feedback ($S_{c,[C]}$) and atmospheric CO_2 concentration (S_{CO_2}). Reported values for c_{eff} average 1.5 g/MJ for many species of plants under ideal growth conditions (Cannell 1989, Leadley et al. 1990). We set c_{max} at 2.5 g/MJ; in all simulations, c_{eff} typically ranged from 1.7 - 2.0 g/MJ.

Eqn (7.1) is equivalent to the light interception formulation of Monteith (1977, 1981), which has been used to describe the growth of many agricultural species and trees and has been rigorously validated (see Pereira and Landsberg 1989). Since it is extremely difficult to directly relate short-term processes to longer term dynamics (O'Neill 1988), the major advantage of this approach is the use of long-term, stand-level parameters, rather than short-term, organ-level parameters (e.g., single leaf photosynthetic rates), the latter of which was used by Miller et al. (1983) in the NECS model.

Fractional light interception (f_l) was assumed to be a hyperbolic function of leaf structural biomass, similar to those used for crop canopies (e.g., Leadley et al. 1990); the specific relationship for *Eriophorum* (f_l , Fig 7.8a) was arrived at in the model fitting. Incident radiation (I_0) was computed as the amount of radiation received during the arctic summer. Incident radiation provides an indirect effect of season length on carbon uptake since it is assumed to change in direct proportion to relative season length.

The light limitation scalar (S_l , Fig 7.8b) accounts for light saturation of carbon uptake by the canopy. This is computed as a function of the average daily radiation (I_{ave} ,

Fig 7.8b), which is equal to total incident radiation received over a growing season divided by actual season length (SL_{act}). Canopy photosynthesis usually saturates at higher light intensities than single leaves, so the canopy saturation response was assumed to be intermediate between the single leaf light responses for *Eriophorum* measured by Johnson and Tieszen (1976), Limbach et al. (1982), and Woolhouse and Robertson (1984) and a linear response as assumed in the Monteith (1981) model (Eqn 7.1).

The scalar response to temperature (S_t , Fig 7.8c) was derived from single leaf photosynthetic response curves for *Eriophorum* (Johnson and Tieszen 1976) and from the temperature response of *Eriophorum* growth in controlled environments (Kummerow and Ellis 1984). In both cases, these data suggest that net CO_2 uptake and growth peak at 10 - 15 °C and remain positive even at 0 °C.

The effect of CO_2 on carbon uptake is represented by S_{CO_2} (Fig 7.8d). This relationship was based on measurements of the non-acclimated photosynthetic response of *Eriophorum* leaves to CO_2 concentration (Tissue and Oechel 1987).

The effect of carbon uptake due to labile carbon concentrations is given by $S_{c,[C]}$ (Fig 7.8e). This functional form resulted in both stable and realistic levels of labile carbon concentrations under a variety of steady-state conditions, which is consistent with observations that *Eriophorum* usually maintains very high labile carbon concentrations under a wide range of conditions (ca. 40-50% labile carbon in overwintering rhizomes, Chapin et al. 1986). Similar functional forms for labile carbon feedback inhibition have been used in tree and aridland shrub models (Reynolds et al. 1980).

Nitrogen uptake. Chapin and Shaver (1985b) and Shaver et al. (1986) have shown that additional nitrogen increases productivity of *Eriophorum* (and other tussock tundra species) more than phosphorus or potassium; hence, we treat only nitrogen. Nitrogen uptake is set equivalent to nitrogen availability:

Figure 7.7: Conceptual view of *Eriophorum vaginatum* model. Boxes represent state variables, arrows are fluxes, valves signify control over fluxes, and clouds represent infinite sinks or sources.

VALUE OF SCALAR

Figure 7.8: Scaling functions used in the model. See Table 7.2 for parameter descriptions.

$$N \text{ uptake} = N \text{ availability} \quad (7.3)$$

We initially assumed N uptake to be a function of soil temperature, root biomass, and N availability; however, we found the model was only sensitive to N availability, a conclusion that is supported by experimental evidence (see Discussion).

Growth. Growth is defined as the conversion of labile carbon and nitrogen fractions (i.e., fractions of C and N that are mobile or are readily re-mobilized including sugars, starch, proteins, etc.) to structural components (i.e., fractions that are not readily re-mobilized, such as cellulose, lignins, etc.). Growth rate is given by:

$$\text{growth} = \text{rgr} \cdot \text{overwinter structure} \quad (7.4)$$

where

$$\text{rgr} = r_{\max} \cdot \text{SL}_{\text{rel}} \cdot \text{MIN}(S_{g,[C]}, S_{g,[N]}) \cdot S_t \quad (7.5)$$

The relative growth rate of the plant (rgr) is the product of $r_{\max}$ (a maximum growth rate), relative season length (SL_{rel}), and scalars representing the effects of labile carbon ($S_{g,[C]}$) and nitrogen ($S_{g,[N]}$) status and temperature (S_t) on growth. The function MIN indicates that the minimum value of the two scalars is used.

The maximum relative growth rate ($r_{\max}$) more closely corresponds to productivity:biomass (P/B) ratios than to short term estimates of relative growth rate, since the model has an annual resolution. Shaver and Chapin (in press) estimated P/B ratios of ca. $0.37 \text{ g g}^{-1} \text{ yr}^{-1}$ for tussock graminoids (which included *Eriophorum* and *Carex bigelowii*) in undisturbed tundra. From these data (and using early season biomass for B), we estimated a P/B for *Eriophorum* of ca. $1.7 \text{ g g}^{-1} \text{ yr}^{-1}$. We initially set $r_{\max}$ to this value, but it was adjusted upwards to 2.0 in the model fitting.

The functional forms of the labile carbon and nitrogen scalars ($S_{g,[C]}$ and $S_{g,[N]}$, Fig 7.8e and g) were determined by model fitting. We assume that labile carbon and nitrogen do not limit growth at concentrations typically observed in the field under nonfertilized conditions (ca. 45% and 2%, respectively, Fig 7.8). Temperature was assumed to affect growth rate and carbon uptake similarly (Fig 7.8c).

Following the findings of Miller et al. (1976) and Stoner et al. (1978), who found a near-linear response of net productivity to season length in their simulations, the effect of season length on rgr was assumed to be a linear function of the relative length of the growing season (SL_{rel}), i.e.,

$$\text{SL}_{\text{rel}} = \text{SL}_{\text{act}} / \text{SL}_{\text{ave}} \quad (7.6)$$

where SL_{act} is the actual season length and SL_{ave} is the average season length.

Structural carbon and nitrogen growth were assumed to be constant fractions of growth, i.e.,

$$C \text{ growth} = 0.995 \cdot \text{growth} \quad (7.7)$$

$$N \text{ growth} = 0.005 \cdot \text{growth} \quad (7.8)$$

These fractions, 0.995 and 0.005 respectively, were roughly based on data from Chapin (1989).

Losses. Structural losses are computed as:

$$\text{structural loss} = \text{growth} \cdot S_{s,[C]} \cdot S_{s,[N]} \quad (7.9)$$

where $S_{s,[C]}$ and $S_{s,[N]}$ are scalars representing the effect of labile carbon and nitrogen, respectively, on structural losses. The functional forms of these scalars (determined during model fitting) are shown in Fig (7.8f and g), respectively. We assume that annual structural growth and losses are in balance (i.e., structural loss/growth = 1) when labile carbon and nitrogen concentrations equal 45% and 2%, respectively (i.e., $S_{s,[C]} = S_{s,[N]} = 1$, Fig 7.8). This ratio varies depending upon the concentrations of these labile pools, i.e., growth exceeds structural losses under favorable concentrations and structural losses exceed growth under unfavorable concentrations.

Structural carbon and nitrogen losses are assumed to be the same proportions of structural losses as the proportions of carbon and nitrogen in structural growth, i.e.,

$$\text{structural C loss} = 0.995 \cdot \text{structural loss} \quad (7.10)$$

$$\text{structural N loss} = 0.005 \cdot \text{structural loss} \quad (7.11)$$

Losses of labile carbon and nitrogen are assumed to be proportional to structural losses and to the ratio of labile to structural biomass for carbon and nitrogen, i.e.,

$$\text{labile C loss} = \text{structural loss} \cdot \text{labile C} / \text{structural C} \cdot f_C \quad (7.12)$$

$$\text{labile N loss} = \text{structural loss} \cdot \text{labile N} / \text{structural N} \cdot f_N \quad (7.13)$$

where f_C and f_N are the fractions of labile carbon and nitrogen not re-translocated. Although initial estimates of f_C and f_N were based on data from Chapin (1989), the final values were considerably lower because the leaves, leaf sheaths, roots, and reproductive structures have lower labile carbon and nitrogen concentrations than rhizomes, yet constitute a larger fraction of senescent tissue than rhizomes.

Partitioning. Biomass produced during a year at the growth rate given in Eqn (7.4) is termed new structure. The amount of leaf and root structure at any point in time can be calculated from the old structure, new structure, and partitioning coefficients. Leaf structural biomass is given by:

$$\text{leaf structure} = f_{\text{old}} \cdot \text{overwinter structure} + (1 - f_{\text{other}}) \cdot f_{\text{new}} \cdot \text{new structure} \quad (7.14)$$

where f_{old} is the fraction of overwinter structural biomass that is leaves, f_{other} is the fraction of new structure other than leaves and roots (i.e., stems, leaf sheaths, and reproductive organs), and f_{new} is the fraction of new structure that is leaves. We assume f_{old} and f_{other} are fixed (Table 7.2), but f_{new} can vary depending on labile carbon and nitrogen concentrations, because this allows changes in partitioning to lag changes in labile pools as appears to occur in *Eriophorum* (Shaver et al. 1986), i.e.,

$$df_{\text{new}} / dt = S_{f,C} + S_{f,N} \quad (7.15)$$

where $S_{f,C}$ and $S_{f,N}$ are the labile nitrogen and carbon scalars (Figs 7.8f, i, respectively). The functional forms of $S_{f,C}$ and $S_{f,N}$ were determined during model fitting.

No roots overwinter, so root structure is given by

$$\text{root structure} = (1 - f_{\text{other}}) \cdot (1 - f_{\text{new}}) \cdot \text{new structure} \quad (7.16)$$

The root:leaf ratio is then equal to root structure divided by leaf structure.

Peak biomass. Modelled peak biomass is equal to the overwinter labile and structural biomass plus integrated net carbon

and nitrogen uptake. The derivation of peak biomass follows. The change in overwinter labile carbon is given by:

$$d(\text{labile C}) / dt = \text{C uptake} - \text{C growth} - \text{labile C loss} \quad (7.17)$$

Integration of Eq. (7.17) gives:

$$\text{labile C}(1) = \text{labile C}(0) + \int \text{C uptake} \cdot dt - \int \text{C growth} \cdot dt - \int \text{labile C loss} \cdot dt \quad (7.18)$$

where $\text{labile C}(0)$ and $\text{labile C}(1)$ are overwinter labile carbon biomass at the beginning and the end of a 1 yr integration (denoted by $\int$), respectively. Similar integrations can be performed for overwinter labile nitrogen and overwinter structure. Summing the integrations for labile carbon, labile nitrogen, and overwinter structure gives:

$$\begin{aligned} \text{peak biomass} &= \text{labile C}(0) + \text{labile N}(0) + \text{overwinter structure}(0) + \int \text{C uptake} \cdot dt + \int \text{N uptake} \cdot dt \\ &= \text{labile C}(1) + \text{labile N}(1) + \text{overwinter structure}(1) - \int \text{labile C loss} \cdot dt - \int \text{labile N loss} \cdot dt - \int \text{structural loss} \cdot dt \end{aligned} \quad (7.19)$$

Peak biomass can be broken down into two components: overwinter biomass and production. Overwinter biomass is given by:

$$\text{overwinter biomass} = \text{labile C}(0) + \text{labile N}(0) + \text{overwinter structure}(0) \quad (7.21)$$

Production is given by:

$$\text{production} = \int \text{C uptake} \cdot dt + \int \text{N uptake} \cdot dt \quad (7.22)$$

Carbon and nitrogen concentrations. Overwinter labile carbon and labile nitrogen concentrations ($[\text{labile C}]$ and $[\text{labile N}]$) are given by:

$$[\text{labile C}] = \text{labile C} / (\text{overwinter structure} + \text{labile C} + \text{labile N}) \quad (7.23)$$

$$[\text{labile N}] = \text{labile N} / (\text{overwinter structure} + \text{labile C} + \text{labile N}) \quad (7.24)$$

Total overwinter nitrogen concentration ($[\text{total N}]$) is given by:

$$[\text{total N}] = (\text{structural N} + \text{labile N}) / (\text{overwinter structure} + \text{labile C} + \text{labile N}) \quad (7.25)$$

Discussion.

Key assumptions. We make several key assumptions about mechanisms that

regulate resource uptake and growth in *Eriophorum*. While this modelling exercise does not specifically address the validity of these assumptions, it does show that a model based on these assumptions can generate responses that are consistent with the observed behavior of *Eriophorum* growth over a wide range of conditions.

Nitrogen uptake. We assume that nitrogen uptake is usually limited only by nitrogen availability. Chapin et al. (1980) concluded that in wet meadow tundra, "Seasonal changes in depth of thaw, soil temperature, and the quantity and activity of root biomass influence the seasonal pattern of nutrient absorption. However, simulations suggest that these parameters are less important than seasonal changes in soluble soil phosphorus in determining the seasonal pattern of phosphorus uptake." Indeed, Chapin and Bloom (1976) suggest that there are poor correlations between phosphorus uptake and root biomass and soil temperature, but almost perfect agreement in the pattern of phosphorus availability and phosphorus uptake. Although data for nitrogen are limited, there is evidence to suggest that nitrogen uptake in *Eriophorum* is relatively independent of the quantity and activity of root biomass.

Shaver et al. (1986) found that the total amount of nitrogen contained in *Eriophorum* did not change despite nearly three-fold changes in root biomass across various treatments. Chapin et al. (1979) found that *Eriophorum* roots occur at very high densities within the thawed portions of tussocks. Based on calculations of the zones from which roots could extract nitrogen from the soil, they suggested that nitrogen uptake would be relatively insensitive to increased root biomass. Our experience in fitting the model is consistent with these data since the best fit was achieved when we assumed that nitrogen uptake was independent of root structure. It also appears that nitrogen uptake in *Eriophorum* is relatively insensitive to temperature. Marion and Kummerow (1990) found that there was no significant difference in nitrogen uptake kinetics of *Eriophorum* roots between 5 and 20 °C. In nitrogen impoverished soils, root uptake kinetics play a minor role in

regulating nitrogen uptake since uptake is controlled by the rate of supply of nitrogen from the soil and species that grow in such soils have considerable capacity for luxury uptake (Chapin 1980, 1991).

Carbon uptake. We assume that carbon uptake in *Eriophorum* is largely limited by light interception and not by nutrients or water. Chapin and Shaver (1985a) concluded that on a community basis, for arctic vascular plants "the major limiting factors to photosynthesis are the available leaf area and its state of development" and that in arctic plants, "nutrients stimulate growth processes rather than directly affecting photosynthesis."

Bigger and Oechel (1982) found photosynthetic rates in *Eriophorum* to be non-responsive or may even decrease with the addition of fertilizer containing nitrogen. Tieszen (1978) found that photosynthetic rates in several arctic species were not correlated with leaf or soil nitrogen concentration over a wide range of productivities. In a study of the downslope movement of fertilizer, the photosynthetic rates of three tussock tundra species were largely unaffected by increased leaf nitrogen concentration (Oberbauer et al. 1989). There is no evidence that *Eriophorum* experiences water stress under most circumstances (Oberbauer and Miller 1979). Plant growth in tussock tundra does respond to addition of water, but this has generally been ascribed to effects on soil aeration and nutrient availability (Oberbauer and Miller 1982, Chapin et al. 1988, Oberbauer et al. 1989).

Carbon limits to growth. The assumption that carbon status does not generally limit growth in *Eriophorum* is supported by several properties: First, *Eriophorum* maintains very high levels of labile carbon under a wide range of environmental conditions (e.g., Chapin et al. 1986, Tissue and Oechel 1987). Second, labile carbon concentrations typically increase during the periods of rapid growth of *Eriophorum* (Chapin et al. 1986). Third, photosynthetic rates of *Eriophorum* are insensitive to many perturbations that would tend to increase rates if carbon was limiting growth (Warren-Wilson 1966, Billings et al.

1984, Bigger and Oechel 1982, Tissue and Oechel 1987).

Nitrogen limits to growth. Another key assumption we make is that nitrogen does not limit relative growth rate (rgr) at typical nitrogen concentrations in field-grown *Eriophorum*. It is often assumed that rgr is limited by plant nutrient status in nutrient poor environments, but there is a growing body of evidence suggesting that plants from these environments adapt to have maximal relative growth rates commensurate with low nutrient availability (Chapin 1991). Indeed, work with the arctic wet meadow graminoid *Dupontia fisheri*, suggests that leaf growth occurs at maximal rates at leaf phosphorus concentrations observed in the field (phosphorus has been identified as the most common limiting element in arctic wet meadows) (Chapin et al. 1980).

We found that increases in production due to fertilization are best explained by increased overwinter biomass via reduced losses and by assuming no effect on rgr. (This assumption is the opposite of a conclusion drawn by Shaver et al. (1986), i.e., fertilization increases production by increasing rgr and does not change overwinter biomass. However, they did not measure overwinter biomass and considerable growth occurred before their first harvest of the season.).

There is evidence to suggest that fertilization reduces losses, but does not alter rgr. First, the data of Fetcher and Shaver (1983) show that survivorship of older *Eriophorum* tillers increases after fertilization and that there is a shift in the age structure towards young tillers that have very high survivorship. Second, nitrogen fertilization typically affects *Eriophorum* growth only on time scales of greater than one year. For example, Kummerow and Krause (1982) found that most nitrogen fertilization treatments had little effect on *Eriophorum* biomass in a 18 week experiment. Also, Shaver et al. (1986) observed the greatest response to fertilization in *Eriophorum* occurred in the third year after fertilization. One straightforward explanation for these observations is that increased productivity in *Eriophorum* usually requires long-term increases in overwinter biomass and is not

dependent on short-term changes in RGR. In addition, we found that simulated labile carbon concentrations were too low if RGRs were allowed to increase after fertilization (see below). Fortunately, the outcome of most of the simulations was not too sensitive to this assumption (see below), given that there is little solid evidence to choose between the alternatives.

Losses. The biomass dynamics of perennial plants, such as *Eriophorum*, are as dependent on the rate of loss as it is on the rates of resource uptake and growth. Unfortunately, processes that control senescence of plant tissue and death of ramets are poorly understood in general and very poorly understood in the arctic. There are two predominant methods of determining losses in previous models for arctic plants (Reynolds and Leadley in press): 1) losses are fixed (e.g., in NECS [Miller et al. 1983] losses were set equal to growth, so that overwinter biomass could never increase), or 2) losses are determined by poor carbon or nitrogen balance (e.g., Bunnell and Scoullar 1982, Miller et al. 1984). It is clear that the first approach will cause serious errors in systems where overwinter biomass changes in response to disturbance. The problem with the second approach is in its implementation, i.e., usually the carbon or nitrogen balance of the organ or plant is calculated and the organ or plant dies when carbon or nitrogen have been depleted. This implies a strong cause and effect relationship between the short-term resource depletion and tissue loss. There is, however, no evidence that organ senescence or tiller death in *Eriophorum* is caused by resource depletion. Shaver et al. (1986) observed high labile carbon and nitrogen levels during periods when substantial tiller death occurred in *Eriophorum*. Shaver and Billings (1976) found that labile carbon concentrations did decline in arctic species as they aged, but the concentrations were high enough in older ramets (ca. 10 to 30%) to suggest that carbon depletion does not lead to ramet death. Current evidence suggests that carbon or nitrogen depletion of a plant may not be the principal cause of organ loss or ramet death (Nooden 1988). Indeed, poor nutrient status may decrease or increase longevity of ramets depending on the type of

plant (Nooden 1988). We suggest that this evidence argues against a short-term mechanistic relationship between carbon and nitrogen depletion and losses, as has been used previously, and in favor of a long-term correlative relationship between carbon and nitrogen status and losses, as was used in this model.

Model sensitivity to parameterization. There are several important aspects of model behavior related to parameterization. The amount of carbon and nitrogen uptake required to support growth is sensitive to the amount of structural and labile carbon and nitrogen lost. In particular, the fractions of labile carbon and nitrogen not remobilized (f_C and f_N) exert considerable control over the amount of growth that can be supported. We have only moderate confidence in our estimates of these parameters. In addition, there are no published data on stand light interception (f_l) or light utilization efficiencies (c_{eff}) for *Eriophorum* and there are very little data on nitrogen availabilities or nitrogen uptake by plants in tussock tundra that can be related to annual measures of nitrogen availability in the center of *Eriophorum* tussocks.

The sensitivity of the model to changes in the response of growth to labile nitrogen concentration ($S_{g,[N]}$) was explored to determine the consequences of assuming that nitrogen does not typically limit relative growth rate (see above). We provide an example of the effects of increasing the sensitivity of growth to high labile nitrogen concentrations; the results are representative of parameterizations that match observed peak biomass. At normal labile nitrogen concentrations, i.e., 2%, the $S_{g,[N]}$ scalar was reduced from 0.6 to 1.0 (by dividing the x-axis of the $S_{g,[N]}$ scalar by 2; see Fig 7.8g). The value of r_{max} was increased to 3 to compensate for the lower value of $S_{g,[N]}$ at normal labile nitrogen concentrations. A fertilization simulation was then run with these changes. The results were virtually the same as the steady-state conditions obtained prior to fertilization, i.e.: 1) slightly higher production in the year of fertilization (i.e., 1978); 2) slightly lower peak biomass in 1979 and 1980 (11.8 vs. 12.6

g/m^2 in 1980) as a result of lower overwinter biomass (4.3 vs. 6.0 g/m^2 in 1980), but higher production (7.5 vs. 6.6 g/m^2 in 1980); and 3) lower labile carbon concentrations in both years (30 vs. 36% in 1980). The most acute problem with allowing relative growth rate to increase at high labile nitrogen concentrations was that labile carbon was depleted; this was particularly true in the shade simulations.

Independent Confirmation of Model. The microcosm work of Billings et al. (1984) provides independent confirmation of the response of arctic vegetation to elevated CO_2 observed by Tissue and Oechel (1987) and of the interaction between elevated CO_2 and nitrogen. Billings et al. (1984) observed a large increase in the biomass of coastal tundra after fertilization, but found no significant effect of elevated CO_2 and no interaction between elevated CO_2 and fertilization. Likewise, Oberbauer et al. (1986) found no effect of elevated CO_2 on the biomass of three tussock tundra species grown in controlled-environment chambers.

The simulated light utilization efficiency, c_{eff} (Eqn 7.2), was typically ca. 1.7 - 2.0 g/MJ . This value seems high considering that measured values for most agricultural plants range from 1.0 - 2.0 g/MJ , and native plants in nutrient poor environments are usually considered to have lower photosynthetic rates than agricultural plants. Indeed, the maximum rate of leaf photosynthesis in *Eriophorum* is typically 13-18 $mmol CO_2 m^{-2} s^{-1}$ (see review by Oberbauer and Oechel 1989, but note exception in Limbach et al. 1982), which is considerably lower than maximum rates measured for crops (e.g., 30-44 $mmol CO_2 m^{-2} s^{-1}$, Gordon et al. 1982). There are, however, several factors that suggest c_{eff} , which is a measure of whole canopy photosynthesis, is relatively high in *Eriophorum* compared to crops. First, c_{eff} for crops usually includes only aboveground production, whereas c_{eff} in the model includes above- and belowground production. Second, leaf photosynthesis measurements in *Eriophorum* are typically made on all age classes of leaves (see exception in Defoliart et al. 1988), while

photosynthesis measurements in crops are usually made on young, fully expanded leaves. Maximum leaf photosynthetic rates are much lower when averaged over an entire canopy than are rates of young, fully expanded leaves (e.g., Gordon et al. 1982 measured single leaf photosynthetic rates of $8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in old and very young soybean leaves). Third, single leaf photosynthetic rates do not account for nighttime respiration; crops have a negative CO_2 balance at night, while *Eriophorum* can maintain positive CO_2 uptake 24 hours per day over much of the growing season because of the long arctic days. Because single leaf photosynthetic rates can be misleading and give little information about integrated carbon uptake by whole canopies, there is a need for direct measurement of light utilization efficiency in *Eriophorum*.

The rates of nitrogen availability used in the simulations are much higher than estimated annual nitrogen uptake in tundra obtained on a square meter basis. However, nitrogen uptake estimates at this scale are probably far too low for *Eriophorum*, because *Eriophorum* tussocks have a greater capacity to extract and absorb nitrogen than intertussock areas (Chapin et al. 1979). Shaver et al. (1986) reported that nitrogen in *Eriophorum* increased ca. 50 mg core^{-1} from a low in mid-June to its seasonal high in September. We estimated nitrogen availability to be $15 \text{ g m}^{-2} \text{ yr}^{-1}$ from these data compared to $9 \text{ g m}^{-2} \text{ yr}^{-1}$ used in the model. This difference is reasonable because the estimate from Shaver et al. (1986) probably included nitrogen remobilization from dying ramets.

Model Limitations. Our goal in this modeling effort is to make long-term predictions of the potential response of *Eriophorum* to climate change based on an understanding of mechanism, coupled with fitting to short-term data sets. Unforeseen competitive effects and other changes in the ecosystem that occur outside the range of expectations could, of course, make these predictions moot. The effects of inter-specific competition have not been accounted for although it is not clear that there are strong short-term, inter-specific competitive effects

in *Eriophorum* (Fetcher 1985). Thermal erosion, loss of permafrost, and invasion of tussock tundra by shrubs or trees are examples of changes that may occur in a warmer climate, but have not been accounted for.

An inherent limitation of the model is that it has an annual resolution. This limits the extent to which within-season variability can be accounted for (i.e., non-linear responses that occur within season cannot be fully accounted for in an annual model). We have begun to test the response of this model with another model of *Eriophorum* growth which has a daily resolution to determine the amount of error this introduces (see below). Another limitation is the lack of validation data for long-term disturbances, especially those involving changes in nutrient availability. In particular, there is not enough evidence from short-term experiments to exclude the possibility that other nutrients might become more limiting than nitrogen in the long-term. Given the lack of long-term data, we do not have enough information to understand how *Eriophorum* responds to environmental variability, even though there is evidence suggesting that *Eriophorum* productivity may vary substantially from year to year in response to normal environmental fluctuations (Chapin and Shaver 1985b). An associated problem is the inadequacy of the environmental data available for the short-term validation data sets used. As a consequence, we have had to assume constant environmental conditions.

Predicted response to climate change. The effect of a 50-yr period of climate change on peak biomass (overwintering biomass plus seasonal production) in *Eriophorum* was explored using the model. We use climate change here to refer to linear increases over a 50-yr period in temperature (from 8 to 13 °C), season length (from 100 to 120 days), and atmospheric CO_2 (from 340 to 680 mL/L). Similarly, a wide range of nitrogen availabilities (from 9 to $18 \text{ g m}^{-2} \text{ yr}^{-1}$) was also examined because of its importance in productivity. Three scenarios (see Table 7.3) were simulated: Scenario 1) climate change with no change in nitrogen availability; Scenario 2) an increase in nitrogen

availability with no change in climate; and Scenario 3) climate change with an increase in nitrogen availability.

In Scenario 1, the model predicts that a simultaneous increase in the direct effects of temperature, season length, and CO₂, with no change in nitrogen availability, would result in a slight decrease in peak biomass (Fig 7.9a). This is a result of decreasing overwinter biomass that is not offset by a slight increase in seasonal production. In Scenario 2, a simulated long-term doubling of nitrogen availability resulted in a ca. 70% increase in peak biomass (Fig 7.9a), whereas with concurrent changes in climate and nitrogen availability (Scenario 3) the model predicted a slight decline in peak biomass compared to increases in nitrogen alone (Fig 7.9a). In essence, the model predicts that climate change will have substantial effects on *Eriophorum* only indirectly through changes in nitrogen availability.

The relationship between long-term growth dynamics and nitrogen availability (from 9 to 27 g m⁻² y⁻¹) was explored further. Prevailing wisdom suggests that rates of nitrogen cycling and, hence, availability to plants, will increase with climate change, although the degree of increase is uncertain (Chapin 1984, 1987). Figure (7.9b) shows that simulated peak biomass responds linearly up to a doubling of current nitrogen availabilities. Therefore, at low to moderate increases in nitrogen availability, the predicted response of *Eriophorum* to climate change is linearly (and almost exclusively) dependent on our ability to predict the effects of climate change on nitrogen cycling. At nitrogen availabilities >2x current availabilities, the relationship flattens out very rapidly (Fig 7.9b). This occurs because the plant becomes limited by carbon uptake. Thus, if nitrogen availabilities more than double in the future, *Eriophorum* may shift from being a nutrient-limited to a carbon-limited system and, consequently, increased season length and elevated CO₂ concentrations may play an important role in controlling *Eriophorum* productivity.

Conclusions. Long-term studies will be crucial for resolving how nutrients and

other environmental factors effect *Eriophorum* productivity. Short-term experiments and simulations miss many of the responses that are important in determining the ultimate consequence of disturbances and, therefore, great care should be used in extrapolating short-term responses over long periods. For example, elevated CO₂ will increase *Eriophorum* photosynthesis in the short-term, but not the long-term (Tissue and Oechel 1987). High nutrient availability does not affect root:leaf ratios in the short-term (Kummerow and Krause 1982), but does in the long-term (Shaver et al. 1986). Mortality and senescence are poorly correlated with carbon and nitrogen status in the short-term, but are correlated in the long-term. Simulated productivity is highly dependent on season length in the short-term, but independent of season length in the long-term. Models that are based on mechanism and designed for long-term simulations provide a basis for reconciling the apparent discrepancies between many short- and long-term responses to disturbance.

Simulation results and experimental evidence indicate that nitrogen availability is the factor that ultimately limits *Eriophorum* productivity under a wide range of conditions. Shaver and Chapin (1986) suggest there are several mechanisms regulating the response of tussock tundra vegetation to increased nutrient availability that have received little attention. They identify the "missing elements" as 1) an adequate understanding of plant allocation patterns, 2) controls on mortality of plant parts, and 3) controls on shoot density. Our modeling effort suggests that these "missing elements" are the principal mechanisms of response to nutrients. Our simulations suggest that increased productivity in response to nitrogen addition is caused by changes in allocation patterns and increases in overwinter biomass mediated by losses. We believe the reason Shaver and Chapin (1986) found "relative differences between species in photosynthetic rate, nutrient uptake, etc., were not good predictors of relative responsiveness of whole-plant productivity", is that these processes are not casual. We suggest that the response of *Eriophorum* to nitrogen fertilization is not regulated by

direct limitations on photosynthetic or nutrient uptake rates.

Figure 7.9 A) Simulated response of *Eriophorum* peak biomass to climate change. Three scenarios (see Table 7.3) were simulated: Scenario 1) climate change with no change in nitrogen availability; Scenario 2) an increase in nitrogen availability with no change in climate; and Scenario 3) climate change with an increase in nitrogen availability. B) Simulated response of *Eriophorum* to long term changes in nitrogen availability.

8.0.0 SUMMARY AND GENERAL CONCLUSIONS

8.1.0 Introduction

The ultimate goal of our research is to develop a general ecosystem model to investigate 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. 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 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 conclusions concerning the process of scaling up (see Chapter 2).

Our philosophy is that each level has its own characteristic set of processes and special modeling challenges that can be worked on in relative isolation from work at other levels (see Table 8.1). 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 occurring 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 in GePSI rather than the full model described in Chapter 3. As described in Chapter 4, the major challenge in modeling whole-plant growth is the development of a flexible and realistic allocation model. In doing so, 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 GePSI 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 global change as they progress from the physiological level of organization to the ecosystem level. Furthermore, this allows us to answer some global change questions directly at each level of interest. This approach will be apparent to the reader from the organization of this report, where detailed descriptions of model development at each level are given separately in the preceding chapters. 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 CO₂ and climate change primarily result from the complex interactions that begin at the leaf level and culminate in altered ecosystem structure and function. This chapter attempts to summarize the lessons learned at each level and put them into the context of ecosystem response to global change.

8.2.0 Major conclusions

8.2.1 Leaf Level

At the level of the leaf, the short-term and long term responses to elevated CO₂ must be distinguished. In the short-term, stomata respond to changes in ambient CO₂ but the biochemical properties of the leaf are fixed. When plants are maintained in an elevated CO₂ 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 CO₂ may be substantial or relatively small. In some cases, net photosynthesis of plants grown and measured at 680 μ bar is actually less than that of 340-grown plants.

The photosynthesis model has been validated under current CO₂ levels (Harley *et al.* 1986; Harley and Tenhunen 1989) and responds realistically to short-term increases in CO₂, 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 CO₂.

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 CO₂ 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, within the individual leaf or within the plant as a whole. This affect cannot be

evaluated at the leaf level of organization alone. If nitrogen 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 discussed in Chapter 5 provide criteria with which to predict *a priori* the total shoot nitrogen content while the analysis of optimal distribution of nitrogen within the canopy (Chapter 4) can predict the spatial distribution of this nitrogen. 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.

The remaining challenge at the leaf level is to build up a data base characterizing changes in photosynthetic characteristics (i.e., model parameters) for a wide range of species, and ultimately to begin elucidating the controls which determine how different leaves respond to environmental change. Changes in leaf behavior result primarily from changes in the allocation of critical nutrients, particularly N. Thus, in order to understand leaf response to environmental change, leaf level processes must be integrated into a whole plant context, in which canopy structure and resource allocation play a critical role.

8.2.2 Canopy Level

The canopy module has been used to investigate components of within-canopy interactions important for predicting whole-plant photosynthetic response to elevated CO₂. This work concluded that a more complex formulation of the light-interception calculations included in the Caldwell *et al.* (1986) version of the model was necessary for predicting photosynthetic and transpirational response to elevated CO₂. This more complex formulation entailed 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 CO₂. Further complexity in the light interception module (such as that provided by considering several classes of leaf inclinations) was deemed less valuable for refining estimates of gas exchange, particularly at elevated CO₂. More value was attributed to the inclusion of leaf and canopy energy balances, since gas exchange response to elevated CO₂ is highly dependent on temperature.

Additional work with the canopy model has focused on the interactive effects of canopy acclimation to growth at high CO₂ (e.g. increased leaf area), leaf acclimation (reduced photosynthetic capacity due to changes in leaf N), and whole-plant photosynthesis. The conclusions of this work are that 1) canopy gas exchange is sensitive to the acclimation to elevated CO₂, 2) leaf acclimation reduces canopy photosynthesis and transpiration beyond that expected from elevated CO₂ 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 CO₂ and elevated CO₂ without acclimation.

This model is quite effective in describing the aggregate behavior of a population of leaves with known properties. Further work, however, needs to be done that investigates the effects of altered photosynthetic capacity and morphological characteristics due to growth at high CO₂ concentrations. Analysis and modeling at the whole-plant level will be used to guide this work since a major focus at the plant level is the allocation of N to leaves in response to light and CO₂. Several analyses of the optimal distribution of N within a canopy (Field 1983; Cowan 1986; Charles-Edwards *et al.* 1987; Hirose and Werger 1987, and our analysis in Chapter 4) will also prove useful. A second area of important work is the development of a simplified canopy module that can be incorporated in the whole-plant

model (GePSI). Our goal is a model structure that accounts for the CO₂ and temperature responses, while reducing the number of layers, leaf angles, etc. necessary in the canopy model.

8.2.3 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 CO₂ concentrations; and 2) phenomenological allocation models are effective in predicting changes in root:shoot ratio, leaf photosynthetic capacity, and plant growth at high CO₂ 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, this result seems consistent with empirical results.

The prototype version of GePSI was effective at predicting root:shoot ratios but was not designed to predict altered photosynthetic rates due to changes in leaf N concentration. This was due to a limitation of the allocation module previously used in GePSI where the efficiencies of resource assimilation were not mechanistically predicted. This has been a general limitation of all root:shoot partitioning models. They require that specific root and shoot activities be specified as parameters. We have developed a new allocation module 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 CO₂, 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.

Future developments will mainly involve coupling the simplified canopy module and the new allocation model, along with the soil and plant water relations modules; and simplification of GePSI for use in the plant community model.

8.2.4 Plant Population and Community Level

Previously, our plant community model had been adapted from the SPUR ecosystem model (Richardson *et al.* 1987). This model incorporates generalized growth responses of plant functional groups to a suite of environmental variables (light, temperature, soil water, and nitrogen). However, the model 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 CO₂ is neither directly nor indirectly involved in any of the phenomenological growth functions.

In developing a new, mechanistic community model, we decompose the system (community) into its component parts (plants, populations, and species) and describe the behavior of the system through the interaction of these parts. Implicit in this approach is the assumption that effects of elevated CO₂ 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 (MacMahon *et al.* 1978; Huston *et al.* 1988).

In developing this model we have devised a theoretical framework of the problem of plant community structure and function with respect to variable CO₂ 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 (e.g., Weiner 1982; Slatkin and Anderson 1984; Pacala 1987) and physiologically-based (Johnson and Thornley 1985; Reynolds and Acock 1985) explanations of plant competition and interaction and, as such, contributes to the goal of linking population biology and physiological ecology of plants (McGraw and Wulff 1983). 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.

Future work will entail parameterizing and validating the community model with experimental data sets that have been collected (or planned) by DOE CO₂ Consortium, especially population and community research at Harvard University in the laboratory of F. A. Bazzaz.

8.2.5 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 (based in large part upon the models and results discussed in previous sections), 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 in the ecosystem. We have developed two kinds of ecosystem models in this phase of the research. The first (SERECO) is intended to be a more or less direct integration of the results of our modeling plant leaf, canopy, and allocation processes. The model consists of simplified versions of the leaf, canopy, and allocation modules coupled to modules representing the abiotic environment. As such, the model has a relatively high degree of mechanism and addresses processes that occur over the course of the day, particularly plant photosynthesis, respiration, and allocation. The second model has a more coarse temporal resolution, designed for the purpose of investigating slower processes, such as those associated with the growth of Arctic tussock tundra.

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 global 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 reported herein preliminary results of modeling the response of three different ecosystems--prairie, desert, and arctic tundra--to changes in the abiotic environment. We compare these results with actual responses of these ecosystems documented in vegetation records.

Responses of grassland ecosystems to climate change. 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 SERECO 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.

Response of arid ecosystems to climate change. This modeling work examined the response of arid/semi-arid ecosystems to variability in rainfall. Model simulations with SERECO 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. In this case, the model simulations are not only corroborated by the finding of high variability of production in desert ecosystems (LeHouérou *et al.* 1988), but offer an explanation for this variability.

Response of an Arctic sedge to climate change. The effect of climate change on peak biomass (overwintering biomass plus seasonal production) in *Eriophorum* (a tussock-forming sedge) was explored using a simple ecosystem model 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 CO₂. 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.

Conclusions. The grassland and desert versions of SERECO produced relatively long-term simulations and successfully predicted responses of prairie and desert ecosystems to changes in or variability in climate. Response to climate is an essential feature of a model that is to be used in making long-term predictions of ecosystem response to global climate change. The Arctic tussock tundra model predicted the response of a sedge to environmental manipulations and provided some indications of the effects of a 'greenhouse' climate on this Arctic system.

The ecosystem models will require considerable refinement in order to have the capacity to predict responses of communities and ecosystems to the combined effects of elevated CO₂ and climate change. Much of this refinement can be based on the modules

currently being developed at the different levels of plant organization. Future work will include incorporating into the ecosystem model simplified modules of plant, canopy, and community models that are responsive to atmospheric CO₂. 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 CO₂ 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 CO₂.

8.3.0 Summary of Processes and Our Modeling Capability

Table 8.1 lists the processes that we are modeling at each hierarchical level, briefly describes the approach we are using, and the uncertainties related to these processes. Future modeling work will focus on removing these uncertainties where possible and suggesting promising avenues for experimental work. A continued effort to link information among the various levels will also need to be made.

Table 8.1: Primary processes that are modeled at each hierarchical level, our current modeling capabilities, major limitations or uncertainties.

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
LEAF LEVEL			
Leaf photo-synthesis rate	<p>C₃ model is mechanistic, based on limitation of photosynthesis by either Rubisco activity, rate of electron transport or rate at which inorganic phosphate is recycled via starch and sucrose synthesis.</p> <p>C₄ model is semi-empirical.</p> <p>Model predicts rate as a function of temperature, light, intercellular CO₂ and O₂, and has been validated for plants grown in both ambient and elevated CO₂.</p>	<p>How do model parameters change in elevated CO₂ for different species, and what controls these changes?</p> <p>What is the importance of limitations arising from inorganic P under natural conditions, and are they likely to increase as CO₂ increases?</p>	Sections 3.3.3 3.3.4 3.4.0
Photorespiration	<p>Photorespiration is dealt with explicitly, based on Michaelis-Menton kinetics, competitive with respect to CO₂ and O₂, and stoichiometry of the integrated Calvin and photorespiratory cycles.</p> <p>Possible effects of incomplete carbon recycling in photorespiration are now incorporated.</p>	Behavior under phosphate limited conditions remains to be validated experimentally.	Section 3.4.0
Feedback on photosynthesis via source-sink imbalance	Feedbacks are incorporated as changes in model parameters to the extent that they represent short-term regulation of metabolism, they will not follow the observed relationships with leaf nitrogen.	If source-sink imbalance persists, will nitrogen be re-allocated either towards or away from starch and sucrose production?	Section 3.4.0

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
LEAF LEVEL (continued)			
Effect of nitrogen allocation on photosynthesis	Key model parameters are all assumed to be linear functions of leaf nitrogen concentration. Thus, allocation of nitrogen to the leaf determines leaf photosynthetic response.	Is nitrogen allocation the primary means by which leaves alter their photosynthetic capacity in high CO ₂ ? Are photosynthetic parameters always linearly correlated with nitrogen? Do all C3 species utilize nitrogen with the same efficiency? What determines allocation of N among root and shoot?	Sections 3.3.4 3.5.0 5.2.0
Rubisco activity	Activation state of Rubisco is ignored - e.g. assumed to be fully activated.	Activation state declines with short term exposure to elevated CO ₂ . Does the activation state recover over time? If not, how will this affect the relationship between Rubisco activity and nitrogen?	
Stomatal conductance	Empirical model, assumes that stomatal conductance is proportional to photosynthesis, modified by CO ₂ and humidity. Currently requires an iterative solution.	Is the model applicable to a wide range of species? Is model response to elevated CO ₂ realistic? Do model parameters change with acclimation to elevated CO ₂ ?	Sections 3.3.2, 3.3.3
CANOPY LEVEL			
Radiation transfer	Calculates profiles of direct PAR, NIR and diffuse PAR, NIR in a canopy.	Non-random leaf distribution can be accounted for by using an empirical cluster parameter, but the accuracy of the calculated radiation profiles will be reduced.	Section 4.2.0
Momentum transfer	Calculates profile of wind speed in a canopy.	Characteristics of turbulence within a canopy are not well understood and canopies with broad leaves will be most affected.	Section 4.1.1

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
Heat and vapor transfer	Calculates profiles of air temperature and vapor pressure in a canopy.	Characteristics of heat and vapor transfer within a canopy are not well understood and canopies with broad leaves will be most affected.	Section 4.1.1
Leaf energy balance	Determines leaf temperature based on energy balance.	Same as above.	Section 4.1.3
Sunlit and shaded leaves	Leaves in each layer are divided into a number of sunlit and shaded classes.	Penumbra is not taken into account, but it is assumed not to be very important.	Section 4.1.2
Stem shading	Considers interception of radiation by stems.	Stem morphology is not included and the deviation from the random distribution may result in minor errors.	Section 4.1.2
Photosynthesis	Calculates photosynthesis of each sunlit and shaded leaf class.	Age effects on acclimation are not well understood.	Section 4.1.3
Transpiration	Calculates transpiration of each sunlit and shaded leaf class.	Stomatal response to water stress is described in Ba'll's model but need more experimental validation.	Section 4.1.3
Water-use efficiency	Calculates water-use efficiency of each sunlit and shaded leaf class.	Same as above.	
N allocation within a canopy	Calculates vertical leaf nitrogen distribution by coordination theory.	Need direct experimental validation.	
PLANT LEVEL			
Carbon and nitrogen allocation within and among organs	Phenomenological model, based on balanced activity hypothesis, distinguishes leaf structure and leaf proteins as well as roots.	No generally accepted mechanisms are known. Partitioning within roots is not included and storage of C and N is poorly understood.	Section 5.3.2

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
PLANT LEVEL (continued)			
Leaf expansion and growth	Growth of shoots and photosynthetic activity of leaves depending on C and N availabilities. Detailed leaf expansion models exist and can be incorporated in GePSI.	Changes due to CO ₂ or temperature are not well characterized.	Section 5.3.2
Root growth	Growth dependent on allocation of C and N.	Morphological changes and root exudation are uncertain.	Section 5.3.2
Flowering and fruiting	A simple submodel exist for our <i>Larrea</i> version of GePSI.	Effects of global change on allocation to reproductive parts is almost unknown.	
Seed production	Seed production is modeled in the <i>Larrea</i> version of GePSI.	The effects of global change on seed production is little known for most native species.	
Interactions with other resources and environmental variables	Interactive responses of allocation and growth to CO ₂ , light, and nitrogen are represented.	Less understanding of the role of water limitations.	Sections 5.2.3, 5.3.2, 5.3.3
Responses to Herbivory	Fairly realistic responses to shoot removal are possible.	Effects of phloem and xylem feeders as well as root grazers are not well known.	Section 5.3.3

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
COMMUNITY LEVEL			
Growth as affected by neighbors	Leaves and roots of individuals are packed into a smaller ground area so specific activities are reduced by self shading and competition for nutrients.	The general pattern of gross morphological change in response to competition is not well known.	Sections 6.2.1, 6.2.2, and 6.2.3
Mortality	Mortality depends on the degree to which relative growth rates are decreased in a population, compared with the growth rate of isolated plants.	Size structure is not now included and may influence the patterns of mortality.	Sections 6.2.1 and 6.2.2
Reproduction	Not presently included since the model is for a single growing season but could be represented easily if sufficient data are available.	Limited data for most species - especially in relation to global change.	
ECOSYSTEM LEVEL			
Total above ground biomass; productivity	Responses of dominant plant species of grassland, desert, and Arctic tundra ecosystems to environment changes of moderate duration.	Validation of model responses over the long term.	Sections 7.3.1, 7.3.2, 7.3.3
Ecosystem physiognomy; biome classification	Changes in ecosystem physiognomy is accounted for by changes in dominance among those growth forms included in the model.	Models do not account for immigration of new dominant forms into an ecosystem.	

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
ECOSYSTEM LEVEL (continued)			
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.	Changes in species diversity are only through attrition, there is no provision for species additions.	Section 7.3.1
Succession	Successional aspects of ecosystems are implicitly accounted for in models if the successional species are included in the model formulation.	Models are not specifically succession models and do not account species migration into new habitats.	Section 7.3.1
Plant-animal interactions	Presently, only herbivory is included in ecosystem models; herbivores remove vegetation according to prescribed choices; rate of removal based on quality.	How will herbivory be affected by changes in plant species, forage quality, etc.?	
Rates of decomposition & nutrient cycling	Decomposition (and thus nutrient cycling) is a direct function of microbial activity and nutrient concentration of litter, and is responsive to changes in litter quantity and quality.	Will microflora species composition change with changing global environment? What effect would this have on rates of decomposition?	Section 7.3.3
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 global change.	Validation data are severely lacking, particularly for whole systems.	Section 7.3.1
Hydrology	Distribution of water in soils can be predicted from a combination of soil, plant, and atmospheric factors that are fully coupled in SERECO.	Present models are patch models and do not account for lateral movement of water; runoff is empirically determined.	Section 7.3.1

PROCESS	OUR MODELING APPROACH AND CAPABILITY	MAJOR LIMITATIONS OR UNCERTAINTIES	TEXT
Biogeochemical 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, particularly over the long term.	The models do not include inorganic chemical processes involved in long-term bio-geo-chemical carbon cycling within an ecosystem.	
Keystone guilds	For ecosystems in which the role of a keystone guild has been adequately defined (very few), this information could be incorporated empirically into SERECO.	It would be very difficult to model the response of a keystone guild to global change based on the small data bases that currently exist for any keystone guild.	
Effects of fire, pollutants, disturbance, etc.	It is beyond the scope of our present ecosystem models to address the interactions of global atmospheric change with other external environmental changes. These questions might be pursued using models specific for fire effects, pollutants, etc. and imposing the addition of atmospheric changes upon them.	Validation data are severely lacking, particularly for whole systems and for long periods of time. Major challenge is to understand and predict long term responses based on short term data.	

8.4.0 Concluding Remarks

Modeling the response of plants and ecosystems to climate change is a formidable task requiring a predictive understanding in the disciplines of physiology, organismic biology, population dynamics, community dynamics, and systems ecology. Our approach has been, and will continue to be, the development of state-of-the-art-models in each of these areas. In this way we can ask, and hopefully answer, important questions about climate change at each level. Since most questions concerning climate

change are themselves scale specific, this is an eminently practical approach. On the other hand, answers to questions at each level depend, to one degree or another, on both lower and higher levels. For example, to predict how individual plants will be affected by climate change we must know how their physiology is affected (one level down) and something about their environment (one or more levels up); we also must include other plants, the soil, atmosphere, and radiative environment. Developing the methodology to do this effectively remains one of the greatest challenges in global climate change research.

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