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Final Technical Report

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by

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TITLE: Modeling the response of plants and ecosystems to CO2 and climate change.

OVERVIEW OF OBJECTIVES: Our objectives can be divided into those for plant modeling and those for ecosystem modeling and experimental work in support of both. We worked in a variety of ecosystem types, including pine, arctic, desert, and grasslands.

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

Ecosystem level modeling (ECOS: Ecosystem Simulator): 1) To incorporate models of plant responses to elevated CO_2 into a generic ecosystem model in order to predict the direct and indirect effects of elevated CO_2 and climate change on ecosystems; 2) To validate model predictions of total system-level response (including decomposition) against various ecosystem field studies of elevated CO_2 and climate change; 3) To use the ecosystem model to test specific hypotheses and to make predictions about primary, secondary and tertiary effects of elevated CO_2 and climate change on ecosystems for conditions and time frames beyond those used to calibrate the model; and 4) To use the ecosystem model to study effects of change in CO_2 and climate at regional and global scales.

Supporting experimental work: Occasionally we conducted some experimental work that we deemed important to the development of our models. This work was mainly physiological work that we could perform in the Duke University Phytotron, using existing facilities.

SUMMARY OF RESULTS: Note: only products explicitly citing DOE Grant No. DE- FG05-92ER-61493 are included here.[1]

At the plant-level, we developed a modeling capability for a number of important processes affected by elevated CO_2, including the direct effects of CO_2 on photosynthesis to account for reduced enzyme activity in response to changing leaf nitrogen allocation, carbon partitioning and photosynthetic acclimation, foliar nitrogen adjustments and whole-plant growth, all of which have been integrated into a generic plant simulator (GePSi). At the ecosystem-level we have stressed the translation of CO_2 effects on plants through the ecosystem and interactions with other environmental factors, including the scaling of leaf CO_2 effects to canopies, decomposition and nutrient cycling, soil temperature and water flux, and complex plant-ecosystem dynamics, all of which have been integrated into a generic ecosystem simulator (ECOS). Here we provide brief summaries and overviews of our major

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[1] In a few cases, an incorrect grant No. was actually published (e.g., "-614005" or, in one instance, some unknown grant No. (starting with 83ER...!) was used that must have been invented by one of my coauthors. (In a series of papers by coauthor BassiriRad, a random number generator must have been used for acknowledging this grant as the last series of numbers are all different.) In any case, I cite only those products that were actually supported by this grant.

findings to date with regard to the development of **GePSi** and ECOS and experimental work in support of development of these models.

GePSi and modularity: One of our goals was to develop a modular-based model for use in global change research. Over the years with DOE support, we have presented definitions of modularity and genericness based on sets of criteria and rules for model design and which encompass the goal of developing an efficient and flexible structure for plant and ecosystem models. In have concluded that model structure should be based on modules that 1) relate directly to real world components or processes; 2) have input and output variables that are measurable values; and 3) communicate solely via these input and output variables. Such a model structure has the advantage that it can be incrementally improved by simply replacing one module with another that has the same input and output variables. The underlying mechanism in the replacement module can be different, which facilitates the incorporation of the latest experimental research results and allows modelers to readily test alternative hypotheses about mechanisms. Thus, modularity and genericness open models to contributions from many authors, facilitate the comparison of alternative hypotheses, and extend the life and utility of simulation models.

Towards our goal of developing a modular design for GePSI and ECOS, we published a special issue of *Ecological Modelling* on modularity in plant growth models (Reynolds & Acock, 1997b). The papers collected in this volume take up this theme of modular generic designs for plant models. They are based on ideas originally presented at a symposium the PI organized entitled, “Modularity in Plant Models” sponsored by the International Society of Ecological Modelling, and held in conjunction with the annual meeting of the Ecological Society of America in 1994 (Knoxville, TN). While this volume focuses on plant models, the concepts apply to all types of ecological modelling.

The paper by Reynolds and Acock (1997a) lists criteria and rules for good modular design that have been developed by computer scientists. The authors distinguish between model design and implementation. Because plant modellers have not developed a language for discussing model design, the authors explain some of the criteria and rules of modular design by using parallel examples from model implementation. Genericness is defined in a similar way to modular design, i.e., criteria and rules are introduced for ensuring that model designs are applicable to a range of managed and unmanaged ecosystems. The expected advantages of designing models to be modular and generic are discussed. Chief among these is the ability to improve models incrementally, as experimenters gain new understanding of plant behavior.

The subsequent papers emphasize the implementation process, often referring to object-oriented design (OOD) and programming (OOP) as means of facilitating and enhancing modularity in plant and ecosystem models. OOP has so far been used almost exclusively for modelling systems where the interactions between components are discrete and sequential. In plant models the interactions between components are complex, continuous and parallel and most plant modellers simulate these interactions by strictly controlling the order in which processes are calculated. This introduces a procedural element into the OOD, but this can be accommodated in the OOP language, C++, which is described by Acock and Reynolds (1997). As a example of this approach, Chen and Reynolds (1997) present the generic plant simulator (**GePSi**) for simulating native woody shrubs and trees and Luo, Field, and Mooney (1997) summarized some of the general problems they encountered in modifying **GePSi** to conduct preliminary modelling studies of the effects of elevated carbon dioxide on plant and ecosystem processes at the Jasper Ridge grassland in northern California. This exercise addresses several of the conceptual issues presented in this volume concerning the purported benefits of genericness, modularity, and OOP in plant modelling.

ECOS: photosynthesis and growth: Luo et al. (1997) used **GePSi** as a part of **ECOS** to examine the often observed phenomenon that there is a disproportional increase in photosynthesis and plant biomass. This was done at the Jasper Ridge CO2 site. Elevated CO_2 concentrations often lead to increased photosynthetic carbon uptake in plants but his does not necessarily result in a proportional increase in plant biomass. We examined this paradox for the Jasper Ridge grasslands in northern California that have been exposed to elevated CO_2 since 1992. We evaluated the effects of physiological adjustments on plant growth and carbon balance of the dominant species. *Avena barbata* using GePSi and ECOS. Without physiological adjustments, an observed 70% increase in leaf photosynthesis in elevated CO_2 was predicted to increase plant biomass by 97% whereas experimental measurements suggested 5 and 13% decreases in 1992 and 1993, respectively, and a 40% increase in 1994. Simulations with an increase in carbon allocation to roots by 29%, or leaf death rate by 80%, or non-structural carbohydrate storage by 60%, or leaf mass per unit area by 25% each predicted an approximately 40% increase in plant biomass in 1994 under elevated CO_2. It follows that greater suppression of the biomass responses to elevated CO_2 in 1992 and 1993 resulted from variable combinations of these physiological adjustments. This modelling study concludes that (a) an increase in carbon loss of (b) a decrease in carbon-use efficiency or (c) an increase in carbon allocation to root growth will result in an increase in biomass growth that is less than that in leaf photosynthesis under elevated CO_2. Alternatively, if carbon loss is reduced (e.g. depressed respiration) and/or carbon allocation to leaf growth is increased, biomass growth may be stimulated more than leaf photosynthesis by atmospheric CO_2 concentration. Moreover, this modelling exercise suggests that physiological adjustments may have substantial effects on ecosystem carbon processes by varying ecosystem carbon influx, litterfall and litter quality.

GePSi: Nutrient uptake: We also developed a model of nutrient uptake for use in GePSi. We did the testing of this based on data from arctic ecosystems (Leadley, Reynolds & Chapin, 1997). A model of nutrient uptake was used to determine the factors that control the uptake of ammonium, glycine, and nitrate for an important arctic sedge, *Eriophorum vaginatum*, because the factors that regulate the nitrogen (N) uptake of plants is natural ecosystems are not well understood and a growing number of studies suggest that organic forms of N, including glycine, are an important source of N for *E. vaginatum* and other plants. *E. vaginatum* was selected as an exemplary system to explore nitrogen (N) uptake of a native species in situ, because it appears to be strongly N limited in the field, its N nutrition has been extensively studied, and its root growth habits make it well suited to modeling nutrient uptake. The model account for N supply from microbial mineralization and other sources, flux of N through the soil to the root surface, and uptake by the plant root. We included glycine in our simulation of N uptake because laboratory experiments have shown that *E. vaginatum* can use glycine and other low-molecular-mass amino acids as a source of N. However, the extent to which glycine contributes to the N nutrition of *E. vaginatum* in the field is unknown. Based on these simulations we concluded that: (1) ammonium, glycine, and nitrate could all potentially make significant contributions to the N nutrition of *E. vaginatum*. The relative contribution of glycine is difficult to asses, because its behavior in the soil has not been characterized. However, glycine and ammonium contributed in roughly equal proportions for most model parameterizations. (2) The importance of factors that regulated modeled ammonium and glycine uptake can be ranked as follows: supply rate > [soil factors (buffer capacity and diffusion coefficient) = root density] > root uptake kinetics. Supply rate was the only factor that regulated nitrate uptake. These simulation results with GePSi and other considerations suggest that N uptake kinetics of roots and soil-solution concentrations may not be reliable predictors of whole-plant N uptake in tundra or other natural ecosystems.

GePSi: canopy nitrogen distribution: It has long been observed that leaf nitrogen concentrations decline with depth in closed canopies in a number of plant communities. This phenomenon is generally believed to be related to a changing radiation environment and it has been suggested by some researchers that plants allocate nitrogen in order to optimize total whole canopy photosynthesis. Although optimization theory has been successfully utilized to describe a variety of physiological and ecological phenomena, it has some shortcomings that are subject to criticism (e.g., time constraints, oversimplifications, lack of insights, etc.). Chen et al. (1993) used a new scheme in GePSi as an alternative to the optimization theory of plant canopy nitrogen distribution, which we term coordination theory. We hypothesize that plants allocated nitrogen to maintain a balance between two processes, each of which is dependent on leaf nitrogen content and each of which potentially limits photosynthesis. These two processes are defined as W_c, the Rubisco-limited rate of carboxylation, and W_j, the electron transport-limited rate of carboxylation. We suggest that plants allocate nitrogen differentially to leaves in different canopy layers in such a way that W_c and W_j remain roughly balanced. In this scheme, the driving force for the allocation of nitrogen within a canopy is the difference between the leaf nitrogen content that is required to bring W_c and W_j into balance and the current nitrogen content. We were able to show that the daily carbon assimilation of a canopy with a nitrogen distribution resulting from this internal coordination of W_c and W_j is very similar to that obtained using optimization theory.

ECOS: Decomposition: The decomposition component of the ECOS modeling project entailed three basic efforts: 1) to evaluate and extend traditional modeling approaches (e.g., GENDEC) to other ecosystems, 2) to expand the existing model to address dynamics of recalcitrant materials during decay as well as to address the interface between plants and decomposers, and 3) to explore alternative approaches to evaluating and predicting patterns of litter decay. Herein, we summarize our accomplishments to date. Our general decomposition model is called GENDEC.

1. Modeling overview and applications to other ecosystems We (Moorhead *et al.*, 1996) examined a suite of common decomposition models and noted that two basic approaches exist: (1) empirical models that generally ignore underlying processes when describing system behavior, and (2) mechanistic models that reproduce system behavior by simulating underlying processes. Empirical models are easy to formulate, require few data for development or use, and generally are very accurate within the range of conditions for which they are built. The greatest limitation to empirical models is their unreliability for novel conditions. Mechanistic models tend to be more applicable to novel situations because they incorporate biological processes underlying the phenomenon of interest explicitly. However, they also are more complex, requiring more types of information (e.g., underlying physiological processes) to develop and use. Moreover, interpretation of model behavior can be difficult for complex models. Thus, the value of a model to any particular study depends on the match between study goals and model formulation.

The decomposition model used in ECOS was based on generalized descriptions of decomposition processes for a wide variety of systems with a effort to avoid site-specific idiosyncrasies. It was initially developed to simulate decomposition in a warm desert and subsequently was modified for use in moist tussock tundra ARDEC (Moorhead, Linkins & Everett, 1996; Moorhead & Reynolds, 1993). Recently, this model was used to evaluate litter decay in Long-Term Intersite Decomposition Experiment Team (LIDET) project (LIDET 1995). This study focused on decay of two litter types of contrasting quality over a two-year period at four sites in North America (Moorhead et al., in review): an arctic tussock tundra (Alaska, USA), a warm desert (New Mexico, USA), a temperate deciduous forest (Massachusetts, USA) and a tropical rain forest (Puerto Rico). Predictions tended to underestimate litter mass loss in the tropical forest and overestimate decay in the desert and tundra (Moorhead et al., in review). Moreover, mechanisms describing loss of nitrogen from high quality litter and nitrogen immobilization by low quality litter were not fully captured by model structure. These results emphasize the need for greater resolution of climate and litter quality controls (only possible through large scale, cross-site studies like LIDET) to further refine decomposition models.

2.a. Recalcitrant organic matter dynamics One of the important limitations to GENDEC and ARDEC was that long-term dynamics of recalcitrant compounds (lignins, humic complexes, etc.) were not included in model formulation. This was not particularly relevant to the desert or arctic systems since there is so little soil organic matter, litter or humus present in the desert and much of the organic matter in tussock tundra is arrested in a fairly early stage of decay. Moreover, decomposition is so slow in the tundra that humification processes probably are not important over decade-long simulations (perhaps even centuries). However, it is important to consider these dynamics in other ecosystems.

Our efforts in this area focused on the progressive transformation of plant compounds to microbial products (Fig. 1 Moorhead & Sinsabaugh, 1998). In essence, litter compounds are used to create microbial biomass, which partly consists of recalcitrant cell wall materials. Eventually, the progressive transformation of this material slows to a rate determined by the turnover of the accumulated recalcitrant materials as the more readily degraded compounds are utilized. This process was incorporated in GENDEC by dividing the dead microbial pool into three major fractions (1) cytoplasm, (2) acid-soluble cell wall components (e.g., cellulosic fractions), and (3) acid-insoluble cell wall materials. Comparisons of model behavior to experimental observations was possible for a suite of litter types examined in a field study by Aber et al. (1984). Close agreement between simulations and observations existed for overall litter decay (mass loss), and dynamics of labile and recalcitrant compounds (Table 1). However, the dynamics of cellulose decay (acid-soluble) is a complex process controlled by different factors at different times. For example, the relatively high availability of more labile compounds at early stages of decay inhibits degradation of cellulose (Linkins et al. 1984), nitrogen limitations at any time during decomposition will inhibit cellulose decay (Berg et al. 1975), and the hydrolysis of cellulose is greatly reduced at temperatures below 10o C (Linkins et al. 1984). No apparent pattern emerged for cellulose degradation from either observation or simulations (e.g., Fig. 2).

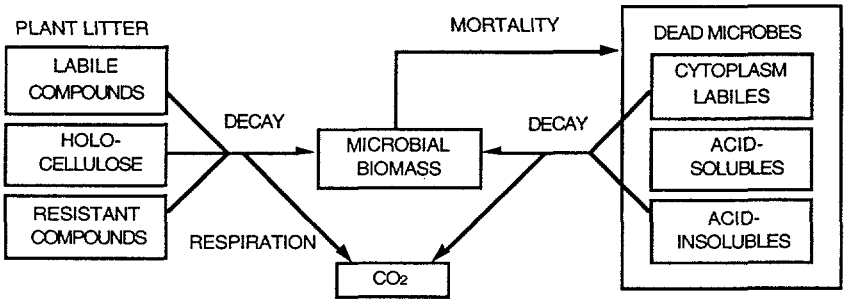

Fig. 1. Carbon flow diagram for modified GENDEC model.

Table 1. Correlations (r^2) between observed (Aber et al. 1984) and simulated (Moorhead and Sinsabaugh, 1998 in review) characteristics of litter residues during decomposition (N = 11).

Litter Type	Mass	Extractives	Acid-Solubles	Acid-Insolubles
maple	0.9661	0.7792	0.0416	0.7933
aspen	0.9529	0.6851	0.7098	0.7758
white oak	0.9930	0.6159	0.0375	0.8806
pine	0.9850	0.8900	0.0843	0.8548
hemlock	0.9615	0.8968	0.2580	0.8817
red oak	0.9914	0.4654	0.3204	0.9293

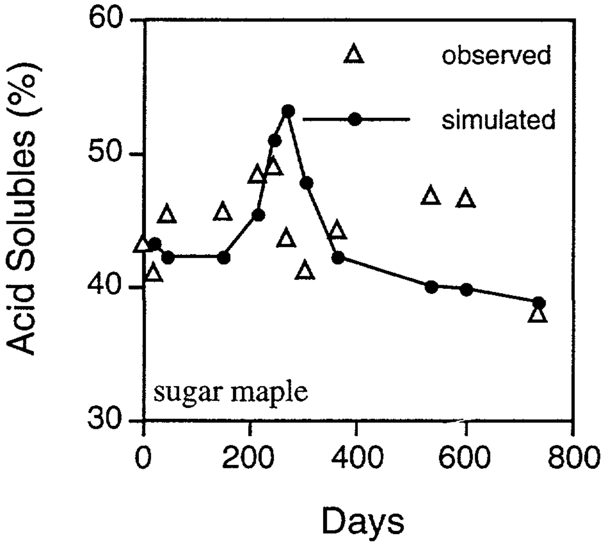

Fig. 2. Cellulose content of sugar maple leaf litter throughout decomposition.

<u>2b. Plant-microbe interactions</u> The decomposition of dead organic matter provides a large fraction of many mineral nutrients required for plant growth. Conversely, plants produce most of the dead organic matter that is processed by decomposers. Thus, plants and decomposers not only benefit by association, but mutually depend on each other for critical resources. However, both groups of organisms may immobilize mineral forms of nutrients, becoming competitors under nutrient-limiting conditions. Indeed, competition among plants and saprophytes for nutrients often has been shown to decrease plant production when nutrients are immobilized within decomposing litter but the effects of plants on litter decay have not been examined. The nature of this interaction has important implications to nutrient cycling, and the allocation of mineral nutrients among growing plants and microbiota utilizing decaying litter presents difficulties to integrated plant-soil models.

A greenhouse study was conducted to examine this interface (Moorhead, Westerfield & Zak, 1998). Litter was incubated in pasteurized and unpasteurized soils, with and without the presence of prairie grasses (*Bouteloua gracilis* or *Schizachyrium scoparium*), to determine if competition between plants and saprophytes altered rates of litter decay. A soil pasteurization treatment was included to ascertain if the presence of VAM inocula would affect the competitive interaction. Analyses of variance detected significant effects ($P < 0.5$) of soil pasteurization, plant species and litter presence on root mass; and significant effects of plant species and litter presence on shoot and total plant mass. The degree of mycorrhizal colonization varied little between plant species but mycorrhizae were entirely absent in pasteurized soils; soil pasteurization usually reduced plant growth. Analyses of covariance detected (1) a highly significant negative relationship ($P < 0.01$) between litter mass loss and plant growth (as covariates; Table 2), when controlling for the effects of time, and (2) a significant positive relationship ($P < 0.05$) between litter nitrogen content and mass loss (as covariates; Fig. 3), when controlling for the effects of time and soil pasteurization. These relationships would be expected if exploitative competition for nutrients existed between plants and decomposers such that nutrient uptake by plants reduced concomitant litter decay. Moreover, this relationship between plant growth and litter decay may be useful in devising a preliminary allocation scheme for mineral nitrogen among plants and microflora when this element is limiting.

Table 2. Results of ANCOVA examining the relationship between percent litter mass loss (arcsine-square-root transformed), date and soil pasteurization as main effects, and total plant mass as a covariate (Moorhead et al. 1997).

Source	Sum of Squares	Degrees Freedom	Mean Squares	F-value	Probability of F
Date	15138	3	5046	149.000	<.001
Soil	9	1	9	.276	.601
Total Plant Mass	423	1	423	12.480	<.001
Error	3861	111	34		
Total	19230	119			

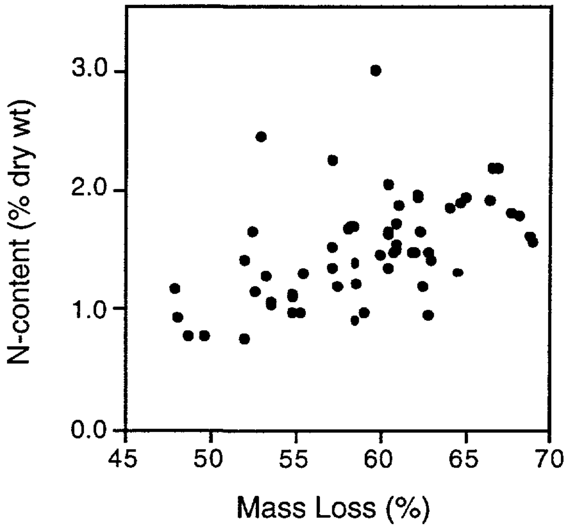

Fig. 3. Relationship between nitrogen content

and mass loss of litter.

3.a. Alternative approaches — Dust loading alters belowground enzyme activities In the acid tussock tundra of northern Alaska, dust from gravel roads affects soil physical-chemical characteristics, microclimate and plant communities. As the Dalton Highway road stretches 577 km from Fairbanks to Prudhoe Bay, dust deposited along both sides of the route directly affects approximately 1154 km^2 of total area. We hypothesized that decomposition and nutrient cycling also could be affected, and found that activities of extracellular enzymes associated with cellulose decay and phosphorus mineralization in soils were inversely proportional to dust loading along this highway (Moorhead et al. 1996). Overall, endocellulase, exocellulase and phosphatase activities within 5 m of this gravel road were reduced by 88%, 74% and 45%, respectively, of activity levels at 500 m (Table 3). Detailed examinations of soil components showed that phosphatase enzyme activities were displaced from organic matter complexes by dust inputs and became adsorbed onto mineral materials. This decreased the rate of enzyme-mediated reactions. Mathematical models incorporating these reduced levels of enzyme activities projected substantial reductions in carbon (from cellulose) and phosphorus mineralization (Table 4). Moreover, reduced carbon utilization by decomposer microbiota, resulting from slower cellulose decay, also decreased microbial immobilization of nitrogen, thus increasing simulated net nitrogen mineralization (Table 4). Such changes in soil nutrient dynamics would be expected to affect the structure of plant communities, as has been reported for vegetation adjacent to the Dalton Highway. However, concurrent changes in other environmental characteristics of the soil environment near this road (e.g., drainage) limit our ability to establish causal relationships.

Table 3. Soil characteristics (0-30 cm) along a dust depositional gradient in a tussock tundra, Alaska (Moorhead et al. 1996).

Distance From Road (m)	Organic Carbon Content (% dry wt)	Dust Loading (g m^{-2} d^{-1})	Endocellulase Activity (units g^{-1} h^{-1})	Exocellulase Activity (µg glucose g^{-1} h^{-1})	Phosphatase Activity (µm pNPP g^{-1} h^{-1})
5.0	14.01	0.750	30	90	2900
7.5	15.12	0.660	40	120	3100
10.0	15.78	0.580	120	205	4100
50.0	34.55	0.075	175	275	4250
500.0	39.11	0.010	250	350	5250

3.a. Alternative approaches — Elevated CO_2 alters belowground enzyme activities. Plant and ecosystem responses to elevated atmospheric CO_2 concentrations sometimes are inconsistent or transitory, because factors other than carbon availability also limit plant production. Indeed, plant growth at elevated CO_2 may be constrained by nutrient availability's. However, impacts of CO_2 on nutrient cycling and soil organic matter dynamics are less direct and more uncertain.

Table 4. Simulated impacts of modifying cellulose decay rate (k_2), due to road dust inputs, on carbon and nitrogen dynamics in a tussock tundra soil, Alaska (Moorhead et al. 1996).

Fraction of k_2	Cellulose Carbon (g m^{-2})	Mineral Nitrogen (mg m^{-2})	Nitrogen Turnover (g m^{-2})	Respired Carbon (g m^{-2})	Microbial Nitrogen (g m^{-2})	Overall C:N
0.1	3834	1.51	4.56	45.83	3.04	36.22
0.2	3828	1.28	4.56	49.32	3.27	36.20
0.3	3823	1.05	4.56	52.80	3.51	36.19
0.4	3816	0.82	4.56	56.28	3.74	36.17
0.5	3811	0.59	4.56	59.75	3.97	36.16
0.6	3805	0.37	4.57	63.22	4.20	36.14
0.7	3799	0.14	4.57	66.68	4.43	36.13
0.8	3798	0.02	4.57	70.12	4.66	36.10
0.9	3788	0.02	4.57	73.54	4.88	36.05
1.0	3782	0.02	4.57	76.95	5.11	36.00

Moorhead and Linkins (1997) found that a three-year exposure to a CO_2 concentration of 680 µmol mol^{-1} altered the enzymic characteristics of root surfaces, associated ectomycorrhizae, and in soils surrounding roots in a tussock tundra ecosystem of north Alaska, USA (Fig. 4). At elevated CO_2, phosphatase activity was higher on *Eriophorum vaginatum* root surfaces, ectomycorrhizal rhizomorphs and mantles associated with *Betula nana* roots, and in Oe and Oi soil horizons associated with plant roots. Also, endocellulase and exocellulase activities at elevated CO_2 were higher in ectomycorrhizal rhizomorphs and lower in Oe and Oi soil horizons associated with roots. These results suggest that arctic plants respond to raised CO_2 by increasing activities associated with nutrient acquisition, e.g., higher phosphatase activities on surfaces of roots and ectomycorrhizae, and greater cellulase activity in ectomycorrhizae. Changes in enzyme activities of surrounding soils are consistent with an increase in carbon exudation from plant roots, which would be expected to inhibit cellulase activities and stimulate phosphatase activities of soil microflora. These data were used to modify existing simulation models describing tussock phosphatase activities (Moorhead et al. 1993) and litter decay (ARDEC; Moorhead and Reynolds 1993, 1996). Model projections suggest that observed increases in phosphatase activities at 680 µmol mol^{-1} CO_2 could augment total annual phosphorus release within tussocks by more than 40%, at present levels of root and ectomycorrhizae biomass (Table 5). This includes a nearly three-fold increase in potential phosphatase activity of *E. vaginatum* roots, per unit of surface area. Observed reductions in cellulase activities could diminish cellulose turnover by 45% in soils within rooting zones, which could substantially increase mineral nitrogen availability in soils due to lowered microbial immobilization (Table 6).

Table 5. Simulated impacts of enhanced rates of maximum phosphatase activities (V_{max}; µmol g^{-1} h^{-1}) on annual phosphorus release (mg P tussock^{-1} y^{-1}) in a tussock tundra soil (Moorhead and Linkins 1997).

Tussock	CO_2; 340 µmol mol^{-1}		CO_2; 680 µmol mol^{-1}		Change (%)
Component	V_{max}	P-Released	V_{max}	P-Released	in P-Released
New Roots	53.90	5.9	136.91	15.1	+155.9
Yellow Roots	53.90	9.8	136.91	24.8	+153.1
Organic Soil	25.96	106.6	36.34	149.2	+40.0
Mineral Soil	5.62	33.1	5.62	33.1	+0.0
Total		155.4		222.2	+43.0

Table 6. Simulated impacts of reduced endocellulase activities on cellulose decay and nitrogen dynamics in a tussock tundra soil (Moorhead and Linkins 1997).

Response	340 µmol mol^{-1} CO_2	680 µmol mol^{-1} CO_2	Change (%)
Cellulose decay (g C m^{-2} y^{-1})	57.6	31.9	-44.7
Respired carbon (g C m^{-2} y^{-1})	77.0	61.5	-20.1
N-release (g N m^{-2} y^{-1})	4.6	4.6	-0.2
N-pool (µg N m^{-2})	19.2	479.6	+2404.4
Organic C:N	36.0	36.2	+0.4

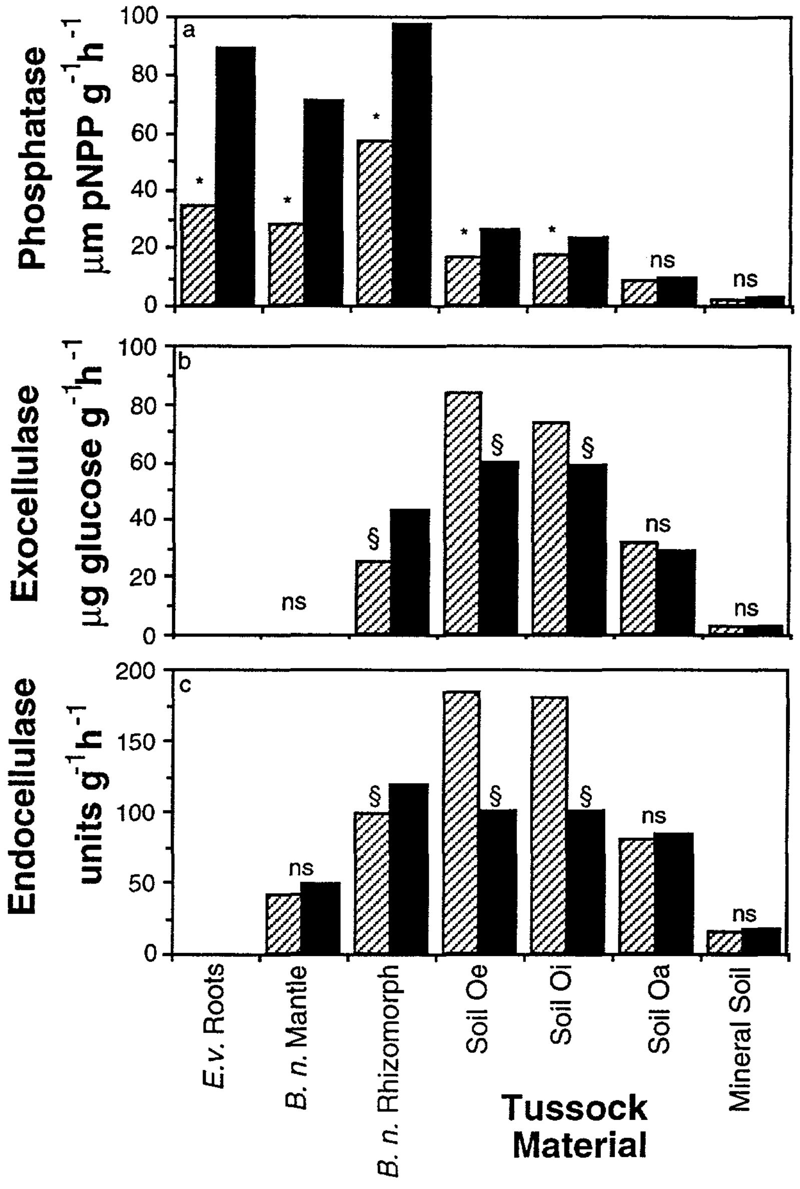

Fig. 4. Extracellular enzyme activities in tussock tundra soils: a. phosphatase, b. exocellulase and c. endocellulase (units based on changes in solution viscosity), at 340 and 680 μmol mol^{-1} CO$_2$ (cross-hatched and solid bars, respectively). * denotes significant differences between treatments for particular rhizosphere component ($P < 0.05$), § denotes differences between treatments for rhizosphere components ($0.10 > P > 0.05$).

3.c. Alternative approaches — Predicting patterns of enzyme activities. Considerable research has focused on gaining a mechanistic understanding of litter decay, and capturing this understanding in simulation models. Models of decay vary with respect to detail, but most utilize decay rate coefficients for particular chemical constituents of litter, derived from empirical observations of turnover. Recent studies have shown that the activities of extracellular enzymes are correlated with decay, and represent instantaneous measures of biochemical processes responsible for the hydrolysis of particular chemical compounds. Thus, rates of turnover may be viewed as surrogates for enzyme activities.

Moorhead and Sinsabaugh (in review) modified GENDEC to predict activities of extracellular enzymes. Initial simulations were performed to insure that dynamics of the carbon fractions of litter (extractive, acid-soluble and acid-insoluble compounds) were consistent with observations (Table 1). Turnover rates of these carbon fractions were viewed as surrogates for the activities of suites of enzymes normally associated with the degradation of key chemical components of these fractions (e.g., cellobiose, sucrose, starch, cellulose, hemicellulose, lignins). Patterns of simulated turnover were similar to observed patterns of extracellular enzyme activity from field and laboratory experiments (Fig. 5). These results suggest that traditional modeling approaches can be used to predict patterns of enzyme activities, although existing data are not yet sufficient to conduct a rigorous quantitative test of this approach. Conversely, assays of extracellular enzymes could be used to test models of litter decay with much less difficulty than long-term measurements of changes in litter chemistry.

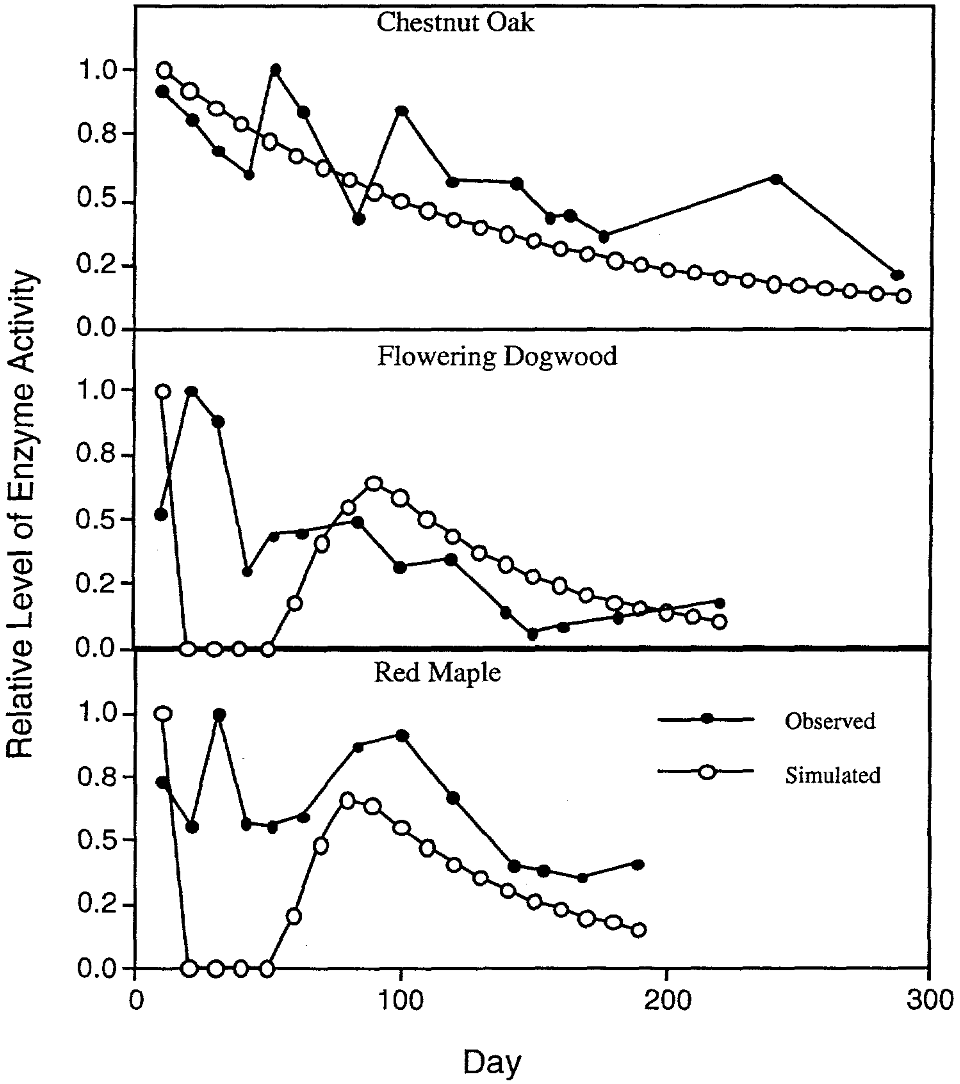

Fig. 5.

Simulated rates of turnover for acid-soluble fractions of litter and observations of overall cellulase activities during a laboratory study (Moorhead and Sinsabaugh, in review).

4-CO2 effects on grassland decomposition: At the DOE site at the Konza Prairie, we did some field work on decomposition to help us with **ECOS**. Standing dead and green foliage litter was collected in early November 1990 from *Andropogon gerardii* (C_4). *Sorghastrum, nutans* (C_4), and *Poa pratensis* (C_3) plants that were grown in large open-top chambers under ambient or twice ambient CO_2 and with or without nitrogen fertilization (45 kg N ha^{-1}) (Kemp *et al.*, 1994). The litter was placed in mesh bags on the soil surface of pristine prairie adjacent to the growth treatment plots and allowed to decay under natural conditions. Litter bags were retrieved at fixed intervals and litter was analyzed for mass loss, carbon chemistry, and total Kjeldahl nitrogen and phosphorus. The results indicate that growth treatments had a relatively minor effect on the initial chemical composition of the litter and its subsequent rate of decay or chemical composition. This suggests that a large indirect effect of CO_2 on surface litter decomposition in the tallgrass prairie would not occur by way of changes in chemistry of leaf litter. However, there was a large difference in characteristics of leaf litter decomposition among the species. *Poa* leaf litter had a different initial chemistry and decayed more rapidly than C_4 grasses. We conclude that an indirect effect of CO_2 on decomposition and nutrient cycling could occur if CO_2 induces changes in the relative aboveground biomass of the prairie species.

Review of Models: We wrote a number of reviews dealing the the role of models in predicting the effects of elevated CO2 and climate change on plants and ecosystems (Reynolds, Acock & Whitney, 1993; Reynolds, Hilbert & Kemp, 1993; Reynolds *et al.*, 1996; Reynolds & Strain, 1994).

EXPERIMENTAL FINDINGS:

In terms of modeling uptake of nutrients in **GePSi**, we encountered a number of interesting issues. The nitrogen requirement of plants is predominantly supplied by NH_4^- and/or NO_3^- from the soil solution, but the energetic cost of uptake and assimilation is generally higher for NO_3^- than for NH_4^+. We did and experiment in the phytotron and found that CO_2 enrichment of the atmosphere enhanced the root uptake capacity for NO_3^-, but not for NH_4^-, in field-grown loblolly pine saplings (BassiriRad *et al.*, 1996b). Increased preference for NO_3^- at the elevated CO_2 concentration was accompanied by increased carbohydrate levels in roots. The results have important implications for the potential consequences of global climate change on plant- and ecosystem-level processes in many temperate forest ecosystems.

We did a similar experiment for loblolly pine. Root growth and physiological uptake capacity for NH_4^+ and NO_3^- were examined for seedlings of loblolly and ponderosa pine grown for 160 days under two CO_2 levels, ambient (35 Pa) and ambient plus 35 Pa (70 Pa) . Fraction of biomass allocated to active fine roots as well as total N (NH_4^++ NO_3^-) absorption per unit root dry mass were unaffected by CO_2. On a whole-plant basis, elevated CO_2 led to a significant increase in N acquisition in loblolly but not in ponderosa pine. However, even in loblolly pine where CO_2 significantly increased plant N acquisition, the relative increase, in biomass far exceeded the gain in N, i.e. a 60% increase in total dry weight was accompanied by only a 30% increase in N gain in response to high CO_2 is largely caused by inability of the root systems to sufficiently compensate for increased N demand. Elevated CO_2 significantly altered root uptake capacity of the different N forms, i.e., high

CO_2 significantly increased NO_3^- absorption rates, but decreased NH_4^+ absorption rates in both species though the decrease in loblolly was insignificant. However, elevated CO_2 increased root respiration rate in loblolly pine whole significantly decreasing it in ponderosa pine. This indicates that CO_2-induced changes in plant preference for inorganic N forms is not simply regulated by root energy status. If changes in plant preference for inorganic N forms represent typical responses to elevated CO_2, the results could have important implications for N dynamics in managed and natural plant communities.

In another series of phytotron experiments, we examined responses of a tussock sedge, *Eriophorum vaginatum* L., to changes in atmospheric CO_2 concentration and soil temperature (BassiriRad *et al.*, 1996c). This was done to help us better characterize interactions in GePSI. We were particularly interested in phosphorus (P) acquisition and below ground plant characteristics that regulated its uptake in response to CO_2 enrichment. Plants were grown at two CO_2 partial pressures, 35 and 70 Pa, three soil temperature regimes, 5, 15, and 25°C and a constant ambient air temperature of 15°C. Elevated CO_2 increased total plant biomass production, but decreased tissue P concentration. Although high CO_2 enhanced root carbohydrate concentration, it inhibited root respiration with no significant effect on root PO_4^{3-}-absorption capacity or root;shoot ratio. Surprisingly, there were no compensatory adjustments, e.g. increased root;shoot ratio or PO_4^{3-} absorption capacity, was largely responsible for the observed decline in tissue P concentration under elevated CO_2 conditions. This could ultimately limit long-term growth responses of *Eriophorum* to CO_2 enrichment in the field where P availability is limiting. We found that uptake of PO_4^{3-} in response to elevated CO_2 was independent of changes in root respiration, but changes in root respiration could have important implications for ecosystems carbon budget under elevated CO_2 levels. Our data indicated that although root respiration on a per unit biomass basis declined in response to CO_2 enrichment, this effect was counterbalanced by increased root biomass, so that high CO_2 stimulated root respiration on a whole-plant basis by 30%. This might help to explain why long-term exposure to high CO_2 increases CO_2 efflux from *Eriophorum*-dominated ecosystems.

Next, we examined changes in root growth and $^{15}NH_4^+$ uptake capacity of loblolly pine (*Pinus taeda L*) and ponderosa pine (*Pinus ponderosa* Douglas Ex Laws) seedlings that were grown in pots in a phytotron at CO_2 partial pressures of 35 or 70 Pa with NH_4^+ as the sole N source (BassiriRad *et al.*, 1996a). Kinetics of ^{15}N-labeled NH_4^+ uptake were determined in excised roots, whereas total NH_4^+ uptake and uptake rates were determined in intact root systems following a 48-h labeling of intact seedlings with ^{15}N. In both species, the elevated CO_2 treatment caused a significant down regulation of $^{15}NH_4^+$ uptake capacity in excised roots as a result of a severe inhibition of the maximum rate of root $^{15}NH_4^+$ uptake (V_{max}). Rates of $^{15}NH_4^+$ uptake in intact roots were, however, unaffected by CO_2 treatment and were on average 4-to 10-fold less than the V_{max} in excised roots, suggesting that $^{15}NH_4^+$ absorption from the soil was not limited by the kinetics of root $^{15}NH_4^+$ uptake. Despite the lack of CO_2 effect on intact root absorption rates. $^{15}NH_4^+$ uptake on a per plant basis was enhanced at high CO_2 concentration in both species, with the relative increase being markedly higher in ponderosa pine than in loblolly pine. High CO_2 concentration increased total $^{15}NH_4^+$ uptake and the fraction of total biomass allocated to fine roots (< 2 mm in diameter) to a similar relative extent. We suggest that the increased uptake on per plant basis in response to CO_2 enrichment is largely the result of a compensatory increase in root absorbing surfaces.

We also examined how elevated CO_2 and nitrogen (N) supply affect plant characteristics of loblolly pine (*Pinus taeda* L.) with an emphasis on root morphology (Larigauderie, Reynolds & Strain, 1994). Seedlings were grown in greenhouses from seeds during one growing season at two atmospheric CO_2 concentrations (375 and 710 mL L^{-1}) and two N levels (High and Low). Root morphological characteristics were determined using a scanner and an image analysis program on a Macintosh computer In the high N treatment, elevated CO_2 increased total plant dry weight by 80% and did not modify root to shoot (R/S) dry weight ratio, and leaf and plant N concentration at the end of the growing season. In the low N treatment, elevated CO_2 increased total dry weight by 60%. Plant and leaf N concentration declined and R/S ratio tended to increase. Nitrogen uptake rate on both a root length and a root dry weight basis was greater at elevated CO_2 in the high N treatment and lower in the low N treatment. We argue that N stress resulting from short exposures to nutrients might help explain the lower N concentrations observed at high CO_2 in other experiments. Nitrogen and CO_2 levels modified root morphology. High N increased the number of secondary lateral roots per length of first order lateral root ad high CO_2 increased the length of secondary lateral roots per length of first order lateral root. Number and length of first order lateral roots were not modified by either treatment. Specific root length of main axis, and to a lower degree, of first order laterals, declined at high CO_2 , especially at high N. Basal stem diameter and first order root diameters increased at high CO_2 , especially at high N. Elevated CO_2 increased the proportion of upper lateral roots within the root system.

As a follow up to the above study, Gebauer et al. (1996) grew loblolly pine (*Pinus taeda* L.) seedlings for 138 d at two CO_2 partial pressures (35 and 70 Pa CO_2) and four N solution concentrations (0·5, 1·5, 3·5 and 6·5 mM NH_4NO_3). Allometric regression analysis was used to determine whether patterns of biomass allocation among functionally distinct plant-parts were directly controlled by CO_2 and N availability or whether differences between treatments were the results of size-dependent changes in allocation. Both CO_2 and N availability affected growth of loblolly pine. Growth stimulation by CO_2 at nonlimiting N solution concentrations (3·5 and 6·5 mM NH_4NO_3) was ca. 90^{o}. At the lowest N solution concentration (0·5 mM NH_4NO_3), total plant biomass was still enhanced by $33^{o}{}_{o}$ under elevated CO_2. Relative growth rates were highly correlated with net assimilation rates, whereas leaf mass ratio remained unchanged under the wide range of CO_2 and N solution concentrations. When differences in plant size were adjusted apparent CO_2 effects on biomass allocation among different plant parts disappeared, indicating that CO_2 only indirectly affected allocation through accelerated growth. N availability, by contrast, had a direct effect on biomass allocation, but primarily at the lowest N solution concentration (0·5 mM NH_4NO_3). Loblolly pine compensated for N limitation by increasing specific lateral root length and proportional biomass allocation to the lateral root system. The results emphasize the significance of distinguishing size-dependent effects on biomass allocation from functional adjustments made in direct response to changing resource availability.

In another phytotron experiment, BassiriRad et al. (1997) examined growth and rates of NO_3^- and PO_4^{3-}-uptake in seedlings of two desert C_3 shrubs (*Larrea tridentata* and *Prosopis glandulosa*) and a desert C_4 perennial grass (*Bouteloua eriopoda*) grown under CO_2 partial pressures of 35 or 70 Pa. Plants were grown in soil but uptake studies were conducted on roots of intact seedlings placed in nutrient solutions containing both NO_3^- and PO_4^{3-}. Elevated CO_2 increased total biomass by 69 and 55% in *Larrea* and *Prosopis* seedlings and by 25% in *Bouteloua* $NO_3^-$and PO_4^{3-} uptake rates were more than doubled in *Bouteloua* at high compared to ambient CO_2. In contrast, CO_2 enrichment inhibited root

NO_3^- uptake capacity in *Larrea* by about 55% without a significant effect on PO_4^{3-} absorption rate, rates of NO_3^- and $PO_4^{3-}$and uptake in *Prosopis* were insensitive to CO_2 treatment. Elevated CO_2 enhanced the proportion of biomass allocated to the fine roots in *Bouteloua* but markedly reduced this fraction in *Larrea* and *Prosopis.* Foliar N concentration of both shrubs decreased in response to elevated CO_2, but was unaffected in *Bouteloua.* We suggest that contemporary changes in root size and activity are critical in determining interspecies variation in plant nutrient relations under high CO_2.

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