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**EVALUATION AND IMPROVEMENT OF MODEL ALGORITHMS FOR
PREDICTING BELOWGROUND CARBON ALLOCATION IN FORESTS**

BY

Kathryn A. Berger

B.S., University of Massachusetts-Amherst, 2006

THESIS

Submitted to the University of New Hampshire

In Partial Fulfillment of the
Requirements for the Degree of

Master of Science

in

Natural Resources

September, 2008

UMI Number: 1459480

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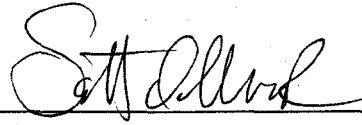
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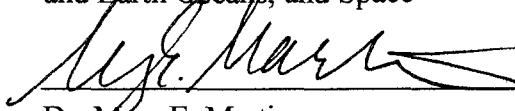
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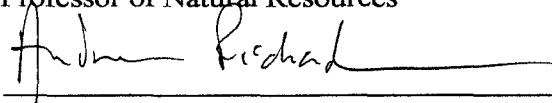
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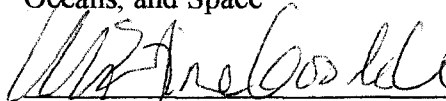
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ACKNOWLEDGEMENTS

It is impossible to thank each person who has helped me over the past two years as I pursued my master's degree at the University of New Hampshire.

To my advisor, Scott Ollinger, and my committee members, Mary Martin, Andrew Richardson, and Christy Goodale, thank you for your time, your support, and your advice as you read and reread my thesis drafts. Your attention to detail and your research expertise were appreciated.

To the University of New Hampshire/ NASA Research and Discover program, thank you for enabling me to pursue my master's work.

To Rita Freuder and Julian Jenkins, thanks for sharing your knowledge of the PnET-CN model.

To my classmates and friends; I couldn't have done it without you. Thanks for your support.

To my family, thanks for believing in me and encouraging me along the way. Without your love and support this would not have been possible.

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ABSTRACT

EVALUATION AND IMPROVEMENT OF MODEL ALGORITHMS FOR PREDICTING BELOWGROUND CARBON ALLOCATION IN FORESTS

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Rapidly rising concentrations of atmospheric carbon dioxide (CO₂) influence forest productivity by stimulating plant growth. It can also modify carbon partitioning patterns, altering the global carbon cycle. Nitrogen and carbon cycles are tightly linked; with changes in nitrogen availability affecting ecosystem carbon allocation by shifting carbon to roots for nitrogen uptake. This paper discusses a modification to the PnET-CN model (Aber et al. 1997) developed to shift plant carbon allocation belowground in response to nitrogen limitation. According to functional equilibrium models of plant carbon allocation, a nitrogen control mechanism alters belowground carbon estimates by increasing carbon allocation to fine roots when nitrogen resources are low. Testing of the modified mechanism with data from three free-air CO₂ enrichment (FACE) forests supported the mechanism by allocating more carbon to fine roots. Application of the model with data from five northeastern forests, under a variety of global climate change scenarios, also supported the modified mechanism with an increase in soil carbon storage.

CHAPTER I

INTRODUCTION

Background

Atmospheric carbon dioxide (CO₂) concentrations have risen 27% since the start of the Industrial Revolution in response to human activities, and they are expected to double by the end of the 21st century (IPCC 2007). Terrestrial ecosystems, particularly forests, play an important role in removing CO₂ from the atmosphere (Canadell et al. 2007). Elevated atmospheric CO₂ stimulates greater net primary productivity (NPP), which can slow the rate of accumulation of CO₂ in the atmosphere (DeLucia et al. 2005; Norby et al. 2005). Reforestation, longer growing seasons, increased nitrogen deposition, climate change, fire suppression, and elevated levels of CO₂ itself have been identified as the most likely factors responsible for this terrestrial carbon sink (Schimel et al. 2001; Bonan 2008).

Although forests comprise a large component of the existing carbon sink (Goodale et al. 2002), the extent to which the sink can be explained by changes in land use as opposed to forest growth enhancement caused by carbon and nitrogen fertilization remains uncertain (Ollinger et al. 2002; Houghton, 2003; DeLucia et al. 2005). Understanding the locations and underlying mechanisms behind these carbon sinks is important because different mechanisms can have very different implications for future CO₂ trajectories (Houghton 2002).

Additionally, field studies have also shown that growth stimulation from elevated CO₂ causes an increase in nitrogen limitation (Oren et al. 2001; Luo et al. 2006). As a result, there is uncertainty as to whether the growth enhancements observed in these experiments will continue over long periods of time. Two experimental forest studies performed by Oren et al. (2001) suggest that estimates of increased carbon sequestration in wood under elevated atmospheric CO₂ are unreasonably optimistic. CO₂-induced woody tissue growth was undetectable on a nutrient poor pine plantation and demonstrated only a transient response on a moderately fertile site after three years. Increased wood growth observed in the first year of the experiment was consistent for both sites, but responses were short-lived. Oren et al. (2001) suggested that the decrease in response to elevated CO₂ might be due to nutrient limitations that can develop quickly in a moderate fertility stand. CO₂-induced wood growth resumed when nitrogen fertilization treatments were applied to the nutrient limited pine stands. The synergistic effects of elevated CO₂ and nitrogen fertilization treatments provided a large gain in woody tissue, more than three times the sum of the separate treatment responses (Oren et al. 2001). This gain was largest at the nutrient poor site, suggesting that site fertility can restrain the response of carbon sequestration in wood tissue under atmospheric CO₂.

The term progressive nitrogen limitation (PNL) was introduced to describe nitrogen limitation induced by elevated atmospheric CO₂. PNL is based upon the concept that increased carbon sequestration in long-lived plant tissues and soil storage under elevated CO₂ progressively limits the amount of available nitrogen for plant uptake (Luo et al. 2004). Elevated CO₂ can only promote additional plant nitrogen uptake by allocating increased carbon to fine roots and mycorrhizal fungi (van Groenigen et al.

2006). Functional equilibrium models have been used to explain plant carbon partitioning trends (Thornley and Johnson 1990). Considered teleonomic models, carbon allocation is optimized depending on growth requirements. Plants allocate additional carbon to the shoot when the supply of carbon is reduced, and shifts carbon partitioning to roots when the supply of water and nutrient resources (predominantly nitrogen) are reduced (Thornley and Johnson 1990). The partitioning of carbon between the root and shoot is allocated in such a way that the relative growth rate of the plant is maximized.

Forests allocate carbon belowground in order to produce roots, root respiration, exudates and mycorrhizae (Raich and Nadelhoffer 1989). Although a considerable amount of the carbon absorbed annually by forests is allocated to fine roots (Gower et al. 1996), the factors that control fine root allocation are still poorly understood. Although explicit validation of predicted carbon allocation to roots is frequently infeasible, observed changes in root production in elevated CO₂ experiments combined with an understanding of basic function plant carbon allocation theory (Thornley 1972; Thornley and Johnson 1990; Coder 1998) suggests a shift in carbon partitioning belowground with rising CO₂.

TBCA: Challenges and Uncertainties

The carbon allocated belowground has a substantial impact on the carbon cycle in terrestrial ecosystems, and it is among the largest biologically mediated carbon fluxes globally (Giardina et al. 2005). The term total belowground carbon allocation (TBCA) represents the sum of all carbon allocated belowground for root and mycorrhizal respiration, turnover, and root exudates (Raich and Nadelhoffer 1989; Giardina et al. 2005). TBCA provides a constant flow of carbon from the CO₂ fixed by photosynthesis

to the soil. Despite the magnitude and importance of belowground carbon allocation, it remains one of the least understood and most difficult to predict carbon fluxes in terrestrial ecosystems (Giardina et al. 2005).

In the absence of direct measurements, Raich and Nadelhoffer (1989) used a mass-balance approach to predict TBCA based upon a global scale relationship between soil respiration measurements and aboveground litterfall. Using a soil respiration and aboveground litterfall dataset from forests around the world, the authors showed a positive linear relationship between the two variables. Based upon the assumption that soil carbon pools are at or near steady state (e.g. in older stands), the authors surmised that the difference between annual losses from soil respiration and annual inputs from aboveground litter represented contributions to belowground allocation. This is expressed by equation 1, where aboveground detritus production (P_a) is subtracted from measured soil respiration (R_s) and is approximately equal to the sum of total annual carbon allocation belowground (P_b belowground detritus production [identified by Raich and Nadelhoffer as fine root production] plus R_r root respiration).

$$\text{Eq. 1. } R_s - P_a \approx P_b + R_r$$

From this equation, the terms can be rearranged to show that TBCA to roots ($P_b + R_r$) can be predicted from annual measurements of soil respiration (R_s) and aboveground litterfall (P_a).

$$\text{Eq. 2. TBCA} = \text{Soil Respiration} - \text{Aboveground Litterfall Carbon}$$

Changes in soil carbon pools are difficult to measure from one year to the next because the changes are small relative to the overall size of the soil carbon pool. Therefore, the mass balance approach can only be used when steady-state conditions

apply, or where annual variation in carbon storage are negligible compared to annual fluxes (Raich and Nadelhoffer 1989; Davidson et al. 2002). This assumption is reasonable for mature, generally undisturbed forests which are no longer accruing large amounts of carbon, but is not supported in young, fertilized or irrigated stands (Gower et al. 1996). The approach also does not provide a means of quantifying critical, individual components of the carbon cycle that are otherwise difficult to estimate because it combines multiple individual belowground fluxes into a single calculation. This equation is used to identify upper and lower limits of TBCA estimates in forest ecosystems (Raich and Nadelhoffer 1989; Davidson et al. 2002; Giardina and Ryan 2002). The use of the globally derived TBCA equation with single forest stands and young forest plantations has yielded poor results and statistically insignificant relationships; although, estimates have improved as sampling methods have been refined, more forest sites have been introduced, and a greater number of mature stands have been included (Davidson et al. 2002; Giardina & Ryan 2002).

The development of the Raich and Nadelhoffer (1989) relationship effectively shifts the challenge of predicting TBCA from estimates of belowground plant biomass and root respiration to estimates of aboveground litter production and soil respiration. Measurements of aboveground litterfall (P_a) and soil respiration (R_s) are common ecosystem observations. Raich and Nadelhoffer (1989) reported significant relationships between these two common measurements ($r^2 = 0.71$) and between TBCA and litterfall ($r^2 = 0.52$). Based upon the relationship between TBCA and litterfall, Raich and Nadelhoffer (1989) developed a statistical model used to predict carbon allocation to roots.

$$\text{Eq. 3. TBCA (g C)} = 1.30 + 1.92 * \text{Litterfall-Carbon (g C)}$$

This relationship allows for the estimation of TBCA based solely on the estimation of aboveground litterfall. According to Raich and Nadelhoffer (1989) the algorithm can be used to place upper bounds on the amount of carbon allocated to roots for tissue production and respiration.

TBCA Dynamics under Elevated CO₂

Experimental sites were designed to study the effects of elevated CO₂ on terrestrial productivity and carbon storage. The development of Free-Air CO₂ Enrichment (FACE) experiments have contributed to a better understanding of the consequences of elevated atmospheric CO₂ on intact ecosystems (Karnosky 2003; Nowak et al. 2004). Fifteen years of FACE experimental data have provided reasonable predictions of plant response to future atmospheric CO₂ concentrations. An analysis of four FACE forests by Norby et al. (2005) demonstrated median NPP enhancement of 23±2%, which was highly conserved across a broad range of productivity. This short-term response to elevated CO₂ suggested a modest increase in the carbon allocated to woody tissue and a large accumulation in belowground carbon, resulting in limited soil carbon storage (Schlesinger and Lichter 2001; Norby et al. 2002). The observed growth response of young FACE forest stands under elevated CO₂ may represent an upper limit for carbon sequestration if the demand for nutrients exceeds nutrient mineralization rates in the soil. A decline in initial stem growth enhancement observed in FACE forests under elevated CO₂ supports this hypothesis (Oren et al. 2001).

While elevated CO₂ enhanced NPP at all FACE forest stands, carbon partitioning strategies differed across sites. CO₂ enrichment of a loblolly pine plantation at Duke

FACE increased annual basal area increment (BAI) of individual canopy pine trees by 13 to 27% during the first eight years of the experiment and accounted for the majority of NPP enhancement at the site (Schlesinger et al. 2006). In contrast, 65% of the pool of additional carbon was allocated to fine roots at the sweetgum plantation of the Oak Ridge National Laboratory (ORNL) FACE site after six years of elevated CO₂ treatments.

Carbon partitioning strategies among forest sites may be influenced by nutrient availability and site-specific resource requirements. FACE experiments provide the opportunity to examine forest responses to elevated CO₂ in an open-air environment without the restricted root development imposed by pots or container walls. This allows exploration of soil nutrients under elevated CO₂. Evidence from FACE site experiments has demonstrated an increase in the carbon allocated to fine roots under elevated CO₂ (King et al. 2004; Palmroth et al. 2006) and has demonstrated stimulation of soil carbon in deeper soil layers (Jastrow et al. 2005; Lichter et al. 2005).

In addition, labeling of roots with ¹⁴CO₂ at a Swiss FACE experimental grassland confirmed that plants grown under elevated CO₂ allocate proportionately more photosynthate belowground when nutrient resources are limited (Hill et al. 2006). Nitrogen fertilization treatments at this grassland FACE site decreased carbon allocated to roots and increased root growth when nitrogen supplies were reduced. The results suggest a fluctuating mechanism for carbon allocation based upon resource availability.

Dynamic carbon partitioning models, which replicate forest responses to elevated CO₂, are important to understanding the effects of climate change on the global carbon cycle. Better knowledge of ecosystem processes under elevated CO₂ allows for the development of ecosystem models with higher confidence projections of the effects of

future global climate change. This study was designed to better simulate belowground carbon allocation to roots in the PnET-CN model (Aber et al. 1997). Global TBCA data sets were used to develop the mechanism, which was tested using published measurements of NPP from three forest FACE experiments. The modification of the model was based upon the hypothesis that variability around the Raich and Nadelhoffer (1989) relationship is due to variation in nitrogen availability; therefore, the simulation of this response would improve the model's ability to represent shifting carbon allocation patterns in response to nitrogen limitation. The primary objectives were: (1) to evaluate the performance of the current PnET-CN model in predicting TBCA under elevated CO₂, and (2) to develop an approach to capture variable TBCA dynamics under the nitrogen limitation induced by elevated CO₂.

CHAPTER II

METHODS

The goal of this investigation was to evaluate the capacity of the PnET-CN model to simulate the effects of rising CO₂ on the proportional allocation of carbon to above versus below-ground tissues.. This analysis included the validation of model estimates against published field measurements of forest NPP at three experimental FACE sites in the eastern U.S. The first objective was to seek the best agreement possible between modeled and observed productivity under ambient conditions. The identification of the specific factors causing variability between sites was beyond the scope of this investigation. The results of the initial analysis led to a second phase of this investigation, which included the development of an alternative mechanism for predicting TBCA based upon allocation theory and the extant literature.

PnET-CN

The PnET-CN model is a daily-to-monthly time step model of carbon, nitrogen, and water fluxes in forest ecosystems, which uses the Raich and Nadelhoffer (1989) approach to estimate TBCA (Aber and Federer 1992; Aber et al. 1997; Ollinger et al. 2002). The model makes use of the relationships between maximum photosynthetic rates and foliar nitrogen concentrations and between the realized rate of photosynthesis and stomatal conductance (Aber and Federer 1992; Reich et al. 1995; Aber et al. 1997). These relationships provide a dynamic link between the simulated cycles of carbon, water and nitrogen. The model's input parameters were designed to capture the dominant carbon,

nitrogen, and water cycling mechanisms, while retaining enough simplicity to be run on relatively few input parameters, and minimal reliance on calibration. This allows model outputs to be tested against independent forest site measurements (e.g. Goodale et al. 1998).

The PnET-CN model (Aber et al. 1997) simulates carbon and nitrogen dynamics through a tightly linked series of pools and fluxes. Unlike earlier versions, PnET-CN does not use a fixed foliar nitrogen concentration. The values vary year-to-year, and are dependent on the relative availability of carbon and nitrogen to the plant. Changes in the nitrogen concentrations are due primarily to differences in climate and site history (Aber et al. 1997). An increase in the foliar nitrogen concentration increases net photosynthesis (in the absence water stress), which increases an internal Plant C pool. As the Plant C pool increases, the need for nitrogen in the plant tissue increases and the available nitrogen pool is reduced. An internal variable (NRatio) determines both the nitrogen concentrations in plant tissues, and the extent of nitrification which occurs within the model (Aber et al. 1997).

The model's internal Plant C pool divides carbon acquired through photosynthesis into biomass pools (foliage, wood, and fine roots) and carbon fluxes (growth and maintenance respiration) (Figure 2). The timing of foliar and wood production is determined by an accrual of growing degree days. Foliar growth respiration is a fixed fraction (25%) of carbon allocated to foliage production (Aber et al. 1995). A similar calculation occurs for respiration during wood production.

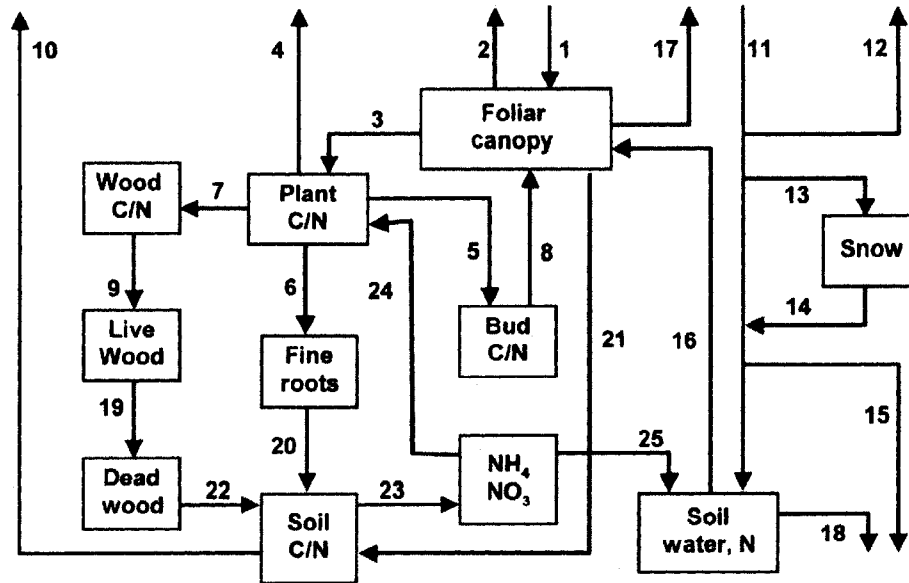


Figure 1. A conceptual diagram of the PnET-CN model. Boxes represent pools and numbered arrows indicate fluxes as follows: (1) Gross photosynthesis and ozone uptake (2) Foliar respiration (3) Transfer to mobile pools (4) Growth and maintenance respiration (5) Allocation to buds (6) Allocation to fine roots (7) Allocation to wood (8) Foliar production (9) Wood production (10) Soil respiration (11) Precipitation and nitrogen deposition (12) Canopy interception and evaporation (13) Snow-rain partitioning (14) Snowmelt (15) Macro-pore flow (16) Plant uptake (17) Transpiration (18) Water drainage (19) Woody litter (20) Root litter decay (21) Foliar litterfall (22) Wood decay (23) Nitrogen mineralization and nitrification (24) Plant nitrogen uptake (25) Nitrogen transfer to soil solution (Ollinger et al. 2002).

Carbon allocated to fine roots is determined using a linear function of foliar production based upon the statistical model developed by Raich and Nadelhoffer's (1989) carbon mass balance approach for TBCA:

$$\text{Eq. 4. Fine Root Carbon (g C)} = 130 + 1.92 * \text{Leaf Carbon (g C)}$$

The carbon allocated belowground is drawn from the Plant C pool and is converted to biomass production by removing growth (25%) and maintenance respiration (equal to root growth) (Aber and Federer 1992; Aber et al. 1995). While fine roots are only one component of all carbon allocated belowground (see Introduction, TBCA: Challenges and Uncertainties), the Raich and Nadelhoffer (1989) approach was selected for use in PnET-CN because it stems from a more consistent and widely distributed set of

observations than are available for fine root growth itself. In the model, the link between TBCA and fine root growth is facilitated by parameters defining the proportion of TBCA that is lost to growth and maintenance respiration (Table 2). The model does not distinguish between fine roots and mycorrhizae, which are effectively treated as an extension of the root system. As such, comparisons against measured fine root growth may have a tendency to show over prediction by the model.

The comparisons completed in this analysis evaluated rates of fine root production between model output and recorded FACE site measurements. Initial comparisons of the degree to which elevated CO₂ stimulated belowground versus aboveground production led to the modification of the model's belowground carbon allocation mechanism. The new mechanism for fine root production was developed by modifying the predictive relationship of TBCA as a function of the nitrogen status of vegetation, based on evidence from FACE experiments that point to N limitation as the driver of altered C allocation patterns.

Model Validations

The PnET models have been validated at a number of northeastern U.S. forest sites (Aber et al. 1997), as well as in a variety of temperate forest systems (Goodale et al. 1998; Ollinger et al. 1998; Ollinger and Smith 2005; Goodale et al. 2002). Predicted NPP and NO₃⁻ runoff have been validated against recorded measurements of two New England forests (Aber et al. 1995, 1997). Although there are currently no standards to evaluate successful model validation, prior PnET investigations have demonstrated a high level of agreement between predicted and observed fluxes (Ollinger et al. 2008). Sources of error in model simulations are generally due to incorrect input parameters or a failure of the

model to imitate important ecological processes. Sensitivity analyses and review of alternative data sources can quantify and occasionally correct errors affiliated with input parameters. Errors associated with poorly understood ecological processes are more difficult to correct and frequently require additional research.

The application of the PnET-CN model to independent measures of NPP at three U.S. FACE sites was used to test the current model's ability to predict proportional changes in fine root growth under elevated CO₂. Results from the CO₂ enrichment experiments demonstrated that under varying degrees of CO₂ fertilization, leaf photosynthetic rates increase along a stable A-C_i curve (Nowak et al. 2004). PnET-CN captures that pattern by using a Michaelis-Menten equation fit to normalize A-C_i curves (Ollinger et al. 2002). Stomatal conductance changes as a function of both CO₂ and foliar percent nitrogen in such a way that allows stable C_a/C_i ratios to be maintained (Ollinger et al. 2002). Results from FACE experiments have shown a consistent enhancement of total NPP under elevated CO₂ (Norby et al. 2005), but have demonstrated variable partitioning patterns of the additional photosynthate between wood and fine roots (DeLucia et al. 2005).

This analysis uses the independent observations of fine root production from three U.S. FACE sites to test the PnET-CN model's ability to estimate fine root production under elevated CO₂. Varying methods for belowground field measurements and inconsistent terminology for fine root turnover and production limit cross-site evaluations (Giardina et al. 2005), and should be considered a limitation of this study. For example, a variety of methods were used to determine fine root production across the three FACE sites that were analyzed. Minirhizotron tubes, video imaging and in-growth soil cores

were used to determine fine root production at ORNL FACE (Norby et al. 2004). Minirhizotron tubes allow observation of fine root production over frequent sampling intervals without the disturbance effects associated with sequential soil coring techniques. A compartment flow model for estimating fine root production based on sequential soil core measurements was employed for the Duke FACE estimates (Matamala and Schlesinger 2000), while a sequential soil coring method was used at the Aspen FACE site (King et al. 2001).

Site Descriptions

Three U.S. forest FACE sites were chosen to examine PnET-CN's simulations of belowground carbon dynamics (Table 1). Sites used for model simulations included: Duke FACE in Durham, NC; Oak Ridge National Laboratory (ORNL) FACE in Oak Ridge, TN; and Aspen FACE in Rhinelander, WI. These forests sites are dominated by young, relatively shade-intolerant fast-growing species (Palmroth et al. 2006).

The application of the PnET-CN model to three FACE sites allowed for comparison of both deciduous (Aspen and ORNL FACE) and coniferous (Duke FACE) forests. Both the Duke and ORNL FACE forests initiated CO₂ enrichment treatments when the forest had reached closed-canopy status approximately ten years after planting. The Aspen FACE site is unique in that CO₂ enrichment was initiated shortly after planting, allowing for the study of seedling growth under elevated CO₂. Additionally, the Aspen FACE site investigates the interactive effects of elevated CO₂ and ozone (O₃), individually and simultaneously, in a three species forest stand divided by vegetation type. This study focused exclusively on the effect of elevated CO₂ on aspen forest growth, using only closed canopy NPP measurements.

Table 1. Characteristics of the three FACE site experiments

FACE Site	Duke FACE	ORNL FACE	Aspen FACE
Location	Durham, NC	Oak Ridge, TN	Rhineland, WI
Latitude	(35°58'N, 79°05'W)	(35°54'N, 84°20'W)	(45°40'N, 89°37'W)
Elevation (m)	150	230	490
Mean Annual Temperature (°C)	15.5	14.2	4.9
Mean Annual Precipitation (mm)	1,140	1,390	810
Growing Season* (days)	200	190	150
Dominant Overstory Vegetation	<i>Pinus taeda</i>	<i>Liquidambar styraciflua</i>	<i>Populus tremuloides</i> , <i>Acer saccharum</i> , <i>Betula papyrifera</i>
Elevated CO₂ Treatment (ppm)	Ambient +200	550	Ambient + 200
Number of Treatment/Control Plots	4 Treatment Plots; 3 Control Plots	2 Treatment Plots; 3 Control Plots	12 Rings: Factorial Treatments of Both CO ₂ and O ₃
Year Planted	1983	1988	1997
Year Treatment Initiated	1996	1997	1998

**Growing season in deciduous stands is the duration that the tree has leaves, in evergreen species systems growing season is period of active stem growth. Periods of active stem wood were estimated using site-specific allometric equations to periodic measurements of tree diameter.*

Source: FACE Site Locations and Contacts 2004; Finzi et al. 2007; Karnosky and Pregitzer 2006; Norby et al. 2006; Norby et al. 2005; McCarthy et al. 2006; Schlesinger et al. 2006.

Model Parameterization

Three classes of parameter inputs are required to run PnET-CN: (1) physiological parameters held constant among all forest types (Table 2), (2) physiological parameters that vary with vegetation type (Table 3), and (3) site-specific parameters that vary by location. Site files include values for climate, soil water holding capacity (WHC), and land use history/agriculture (Tables 4-6). Values for parameters held constant among all vegetation types are described in prior PnET publications (Aber and Federer 1992; Aber et al. 1995, 1996, 1997). The majority of vegetation and site-specific parameter values were derived from the literature or from communication with FACE scientists (Table 3). When site-specific parameter values were not available, mean values for dominant forest functional groups were used.

Table 2. Input parameters required by the PnET-CN model. Asterisks denote values that vary with vegetation type and are described in Table 3.

Name	Definition and units	Value
<i>Canopy variables</i>		
K	Canopy light attenuation constant (no units)	*
FolNCon	Foliar nitrogen content ($\text{g}_\text{N} \text{g}_\text{leaf}^{-1}$)	*
FolReten	Foliage retention time (yr)	*
FolMsMax	Foliar mass maximum (g m^{-2})	*
FolMsMin	Foliar mass minimum (g m^{-2})	*
SenesCstart	First day of year when leaf drop could potentially start	*
SLWMax	Specific leaf weight at top of canopy (g m^{-2})	*
SLWDel	Change in SLW with increasing foliar mass above leaf layer ($\text{g m}^{-2} \text{g}^{-1}$)	*
GDDFolStart	Growing degree days at which foliar production begins	*
GDDFolEnd	Growing degree days at which foliar production ends	*
GDDWoodStart	Growing degree days at which wood production begins	*
GDDWoodEnd	Growing degree days at which wood production ends	*
FolRelGrowMax	Maximum relative growth rate for foliage (yr^{-1})	0.3
<i>Photosynthesis variables</i>		
AmaxA	Intercept of relationship between foliar N% and maximum photosynthesis rate ($\text{nmol CO}_2 \text{g}_\text{leaf}^{-1} \text{s}^{-1}$)	*
AmaxB	Slope of relationship between foliar N% and maximum photosynthesis rate ($\text{nmol CO}_2 \text{g}_\text{leaf}^{-1} \text{s}^{-1}$)	0.1
BaseFolRespFrac	Respiration as a fraction of maximum photosynthesis	200
HalfSat	Half saturation light level ($\text{mmol PAR m}^{-2} \text{s}^{-1}$)	0.76
AmaxFrac	Daily Amax as a fraction of early morning instantaneous rate	*
PsnTOpt	Optimum temperature for photosynthesis ($^{\circ}\text{C}$)	*
PsnTMin	Minimum temperature for photosynthesis ($^{\circ}\text{C}$)	*

Table 2 Continued. Input parameters required by the PnET-CN model. Asterisks denote values that vary with vegetation type and are described in Table 3.

Name	Definition and units	Value
RespQ10	Q ₁₀ value for foliar respiration (factor of respiration increase per 10°C temperature change)	2.0
<i>Water balance variables</i>		
DVPDA	Coefficient for determining DVPD, a photosynthesis multiplier ranging from 0 to 1. $DVPD = 1 - DVPDA * VPD^{DVPDB}$	*
DVPDB	Coefficient for determining DVPD, a photosynthesis multiplier ranging from 0 to 1. $DVPD = 1 - DVPDA * VPD^{DVPDB}$	*
PrecIntFrac	Fraction of precipitation intercepted and evaporated	*
WUEConst	Constant value for water use efficiency (WUE) as a function of vapor pressure deficit (VPD): $WUEConst (mg CO_2 g^{-1} H_2O kPa) = WUE * VPD$	10.9
FastFlowFrac	Fraction of water input lost directly to drainage	0.1
<i>f</i>	Soil water release parameter (d ⁻¹)	0.4
<i>Carbon allocation variables</i>		
CFracBiomass	Carbon as a fraction of foliage mass	*
RootAllocA	Intercept of the relationship between foliar and root allocation	0
RootAllocB	Slope of the relationship between foliar and root allocation	2
GRespFrac	Growth respiration, as a fraction of allocation	0.25
RootMRespFrac	Ratio of fine root maintenance respiration to biomass production	1
WoodRespA	Wood maintenance respiration as a fraction of gross photosynthesis	0.07
PlantCReserveFrac	Fraction of plant C held in reserve after allocation to bud C	0.75
MinWoodFolRatio	Minimum ratio of carbon allocation to wood and foliage	*
<i>Biomass turnover and nitrogen concentration variables</i>		
WoodTrn	Fraction mortality of live wood per year (wood/yr)	0.025
RtTrnA	Coefficients for fine root turnover as a function of annual nitrogen mineralization	0.789
RtTrnB	Coefficients for fine root turnover as a function of annual nitrogen mineralization	0.191

Table 2 Continued. Input parameters required by the PnET-CN model. Asterisks denote values that vary with vegetation type and are described in Table 3.

Name	Definition and units	Value
RtTrnC	Coefficients for fine root turn over as a function of annual nitrogen mineralization	0.0211
WoodLitLS	Fraction of transfer from dead wood to SOM per year	0.1
WoodCLoss	Fractional loss of mass in wood decomposition	0.8
Kho	Decomposition constant for SOM pool yr ⁻¹	0.075
NImmobA	Linear coefficients for fraction of mineralized nitrogen	151
NImmobB	reimmobilized as a function of SOM carbon to nitrogen ratio	-35
FLPCtn	Minimum % nitrogen concentration in foliar litter	*
RLPCtn	Minimum % nitrogen concentration in wood litter	0.012
WLPCtn	Minimum % nitrogen in root litter	0.002
FoINConR	Maximum fractional increase in nitrogen concetration	*
FoINRet	Fraction of foliage nitrogen retranslocated before leaf falls	0.5
MaxNStore	Max nitrogen content in PlantN pool (g m ⁻²)	20
<i>Soil respiration variables</i>		
SoilRespA	Intercept of relationship between mean monthly temperature and soil respiration (g C *m ⁻² *mo ⁻¹)	27.46
SoilRespB	Slope of relationship between mean monthly temperature and soil respiration (g C *m ⁻² *mo ⁻¹)	0.0684
SoilMoistFact	Saturation ratio of the soil	-1

Table 3. Vegetation and site specific variable input parameters required by the PnET-CN model.

Name	Duke FACE	Reference	Aspen FACE	Reference	ORNL FACE	Reference
<i>Canopy variables</i>						
k	0.333	C. Goodale, pers. comm..	0.5	PnET standard for NHWDS	0.35	Avg. from Norby et al. 2003
FolNCon	1.05	CDIAC FACE database	2.23	CDIAC FACE database	1.61	CDIAC FACE database
FolReten	2	McNulty et al. 2000	1	Deciduous	1	Deciduous
FolMsMax	771	Roberts et al. (SRS-071)	300	PnET standard for NHWDS	300	PnET standard for NHWDS
FolMsMin	347	Roberts et al. (SRS-071)	0	PnET standard for NHWDS	0	PnET standard for NHWDS
SenesCstart	300	Estimated by flux tower data	270	PnET standard for NHWDS	270	PnET standard for NHWDS
SLWMax	210	Sun et al. 2000	82	Ryu et al. 2006	75	Herrick and Thomas, 1999
SLWDel	0	Normal for conifers	0.2	PnET standard for NHWDS	0.2	PnET standard for NHWDS
GDDFolStart	900	Sun et al. 2000	900	PnET standard for NHWDS	750	Estimated by flux tower data
GDDFolEnd	3000	Sun et al. 2000	1600	PnET standard for NHWDS	1400	Estimated by flux tower data
GDDWoodStart	900	Sun et al. 2000	900	PnET standard for NHWDS	750	Estimated by flux tower data
GDDWoodEnd	3000	Sun et al. 2000	1600	PnET standard for NHWDS	1400	Estimated by flux tower data

Table 3 Continued. Vegetation and site specific variable input parameters required by the PnET-CN model.

Name	Duke FACE	Reference	Aspen FACE	Reference	ORNL FACE	Reference
<i>Photosynthesis variables</i>						
AmaxA	1.92	McNulty et al. 2000	-46	PnET standard for NHWDS	19.2	Gunderson et al. 2002
AmaxB	39.64	McNulty et al. 2000	71.9	PnET standard for NHWDS	75.2	Franklin et al. 200
PsnTOpt	28	McNulty et al. 2000	20	Hogg 2001	24	PnET standard for NHWD
PsnTMin	4	PnET standard for pine	4	PnET standard for NHWDS	4	PnET standard for NHWD
<i>Water balance variables</i>						
DVPDA	0.05	PnET standard for pine	0.05	PnET standard for NHWDS	0.05	PnET standard for NHWD
DVPDB	2	PnET standard for pine	2	PnET standard for NHWDS	2	PnET standard for NHWD
PrecIntFrac	0.15	PnET standard for pine	0.2	Hogg et al. 2001	0.11	PnET standard for NHWD
<i>Carbon allocation variables</i>						
CFracBiomass	0.47	Hamilton et al. 2001, 2002	0.45	PnET standard for NHWDS	0.45	PnET standard for NHWD
MinWoodFolR atio	1.25	PnET standard for pine	1.5	PnET standard for NHWDS	1.5	PnET standard for NHWD
<i>Biomass turnover and nitrogen concentration variables</i>						
FLPCtn	0.012	PnET standard for pine	0.00899	PnET standard for NHWDS	0.00899	PnET standard for NHWD
FolNConR	0.7	PnET standard for pine	0.6	PnET standard for NHWDS	0.6	PnET standard for NHWD

Site files were compiled for each FACE site based upon land use history and disturbance regimes associated with the site. Vegetation was cleared and burned at all three FACE sites prior to launching the experimental forest program. The Aspen FACE site had a history of agriculture and poplar genetic trials (Karnosky and Pregitzer 2006), while the Duke FACE site had been covered predominantly by a sweetgum forest prior to the initiation of the FACE experiment (Schlesinger et al. 2006). Occasional logging also took place at both of these forest sites. Additional, site-specific information on water holding capacity (WHC) was obtained from the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) (Kittel et al. 2005).

Table 4. PnET-CN model site file parameters for Aspen FACE in Rhinelander, Wisconsin.

Parameter Value	Aspen FACE
Latitude	25.6
WHC (cm)	17.35
Agriculture	1920-1972
Fraction Removed	0.1
Number of Harvests	1
<i>1997 Harvest</i>	
Intensity Fraction	0.9
Fraction Removed	0.9
Soil Loss Fraction	0

Table 5. PnET-CN model site file parameters for Duke FACE in Durham, North Carolina.

Parameter Value	Duke FACE
Latitude	36
WHC (cm)	13.7
Agriculture	None
Fraction Removed	None
Number of Harvests	3
<i>1967 Harvest</i>	
Intensity Fraction	0.25
Fraction Removed	0.25
Soil Loss Fraction	
<i>1979 Harvest</i>	
Intensity Fraction	0.4
Fraction Removed	0.4
Soil Loss Fraction	0
<i>1982 Harvest</i>	
Intensity Fraction	1.0
Fraction Removed	1.0
Soil Loss Fraction	0.1

Table 6. PnET-CN model site file parameters for ORNL FACE in Oak Ridge, Tennessee.

Parameter Value	ORNL FACE
Latitude	35.5
WHC (cm)	15.85
Agriculture	None
Fraction Removed	None
Number of Harvests	1
<i>1987 Harvest</i>	
Intensity Fraction	1.0
Fraction Removed	1.0
Soil Loss Fraction	0.1

Climate Data

Climate files for each FACE experimental forest included monthly average temperature, precipitation, photosynthetically active radiation (PAR), and nitrogen deposition. Monthly average temperature and precipitation data were obtained from the Historic Climate Network (HCN). Wet and dry nitrogen deposition values were obtained from the National Atmospheric Deposition Program (NADP) and the Clean Air Status & Trends Network (CASTNET). PAR measurements are less commonly available, and were obtained from individual FACE site datasets. When access to FACE site PAR data was unobtainable (Aspen FACE), hourly data from the National Solar Radiation Database (NSRD) were converted into monthly averages. When climate file information was not available for a specific site, the nearest measurement collection site of similar vegetation type and elevation was used. (See Appendix A for database references).

Modeling Protocol

Initial PnET-CN simulations under ambient CO₂ were run and compared with independent field measurements of FACE site NPP. This tested the model's ability to simulate forest productivity under ambient conditions. The results of early simulations were used as a benchmark for comparison of model simulations with elevated CO₂. The model's ability to simulate fine root production dynamics under elevated CO₂ was evaluated by re-creating FACE site conditions. A single-step increase to 550ppm of CO₂ was incorporated into the model's simulations at the initiation of each FACE site experiment (Table 1). See Appendix B for changes to PnET-CN's Visual Basic code.

Model Development

Initial PnET-CN model simulations under elevated CO₂ demonstrated that most of the enhanced growth was allocated to the wood biomass pool, with little change in root growth. The model simulations differed from published experimental FACE site results, which had more dynamic carbon partitioning patterns under elevated CO₂ (DeLucia et al. 2005). A modified mechanism was therefore developed to improve PnET-CN model simulations for belowground carbon allocation to fine roots under elevated CO₂.

Based upon the functional equilibrium theory of root to shoot carbon partitioning dynamics (Thornley and Johnson 1990), the internal variable for vegetation nitrogen status was linked to the TBCA mechanism for fine root production. The link allowed fine root production to vary according to nitrogen availability. Plants allocate additional carbon to roots in order to maximize relative growth rates as they become progressively nitrogen limited. When plant nitrogen status is low, additional carbon is allocated to fine root production. Conversely, when nitrogen status is high, fine root production is decreased. Simulations were performed to explore carbon allocation shifts under elevated CO₂ as a function of vegetation nitrogen status. If belowground carbon allocation to roots is a function of nitrogen status, then an anticipated NPP allocation shift will occur in response to elevated CO₂ across FACE site simulations. Model runs with the modified mechanism were compared to independent field measurements of NPP from the three FACE sites.

Given the scarcity of reliable measurements that could be used to explicitly determine how TBCA changes over varying degrees of nitrogen limitation, we instead used an expanded data set that added litterfall and soil respiration measurements from

Davidson et al. 2002 to the original data from Raich and Nadelhoffer (1989). We used the variability around the new regression line to set upper and lower bounds for the steepness of the trend used in the model, under the assumption that greater N limitation would yield higher TBCA for a given rate of aboveground production. Figure 2 illustrates the new relationship. The center line represents the established TBCA relationship derived from the expanded dataset. The lines to either side denote the upper and lower bounds (3.2; 2) of the 95% confidence interval (± 0.6) of a linear regression, on the combined dataset of soil respiration and litterfall measurements from mature (≥ 45 years) forest stands (Raich and Nadelhoffer 1989; Davidson et al. 2002). The forced zero y-intercept value prevents carbon from being allocated belowground when there are no aboveground litterfall inputs. In the model, the modified mechanism varies the slope within this defined range as a function of predicted nitrogen limitation.

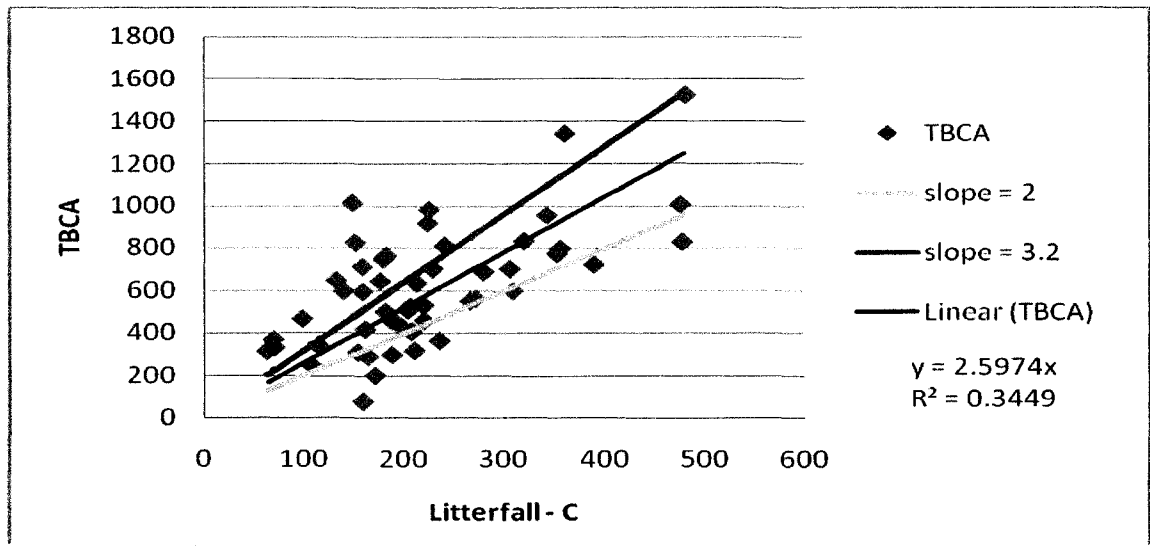


Figure 2. Predicted TBCA (g C) vs. Litterfall-carbon (g C) derived from combined datasets (Davidson et al. 2002; Raich and Nadelhoffer 1989), with a y-intercept value of zero. Linear regression results in a slope of 2.59, produced by the Raich and Nadelhoffer relationship. A fixed linear relationship does not account for much of the variability around the mean. The upper (2) and lower (3.2) slopes provide the bounds of TBCA estimates produced by combined dataset's 95% confidence interval, allows for greater variability in TBCA estimates from litterfall-C measurements.

In the existing PnET-CN model, the NRatio is dependent on the fraction of available nitrogen multiplied by the parameter (FolNConRange) allowing foliar nitrogen concentrations to vary within given boundaries for a specific species or plant functional group. Nitrogen limitation in the new mechanism is represented by a variable identified as NStatus. This was developed using the existing PnET-CN variables: NRatio (a calculated variable expressing the degree of nitrogen limitation on plant function), and FolNConRange (an input parameter value indicating the maximum fractional increase in foliar nitrogen concentration).

In the original PnET-CN model, deciduous trees have a FolNConRange input parameter of 0.6, while conifers have a value of 0.7 (Aber et al. 1997). The plant nitrogen (Plant N) pool is constrained by the fixed input parameter (MaxNStore) for maximum nitrogen storage, which allows NRatio to vary from 1 (low nitrogen availability) to 1.6 (high nitrogen availability) in deciduous tree species. With a higher FolNConRange parameter of 0.7, the conifer species NRatio varies from 1 to 1.7. Modifications to the model are based upon the development of a ratio drawn from the original NRatio and FolNConRange parameters to create a degree of nitrogen availability calculated to include species-specific input parameters. Therefore, they do not require independent calculations of TBCA for each species (Equation 5). NStatus is equal to 0 when the NRatio is at its minimum (1.0), and equal to 1 when the NRatio is at its maximum (1.6 or 1.7 respectively).

$$\text{Eq. 5. } \text{NStatus} = \text{PlantN} / \text{MaxNStore}$$

An NStatus-dependent derived slope replaces the static TBCA relationship used in the current model. This allows the RootAllocB input parameter (the slope of the

relationship between foliar and root allocation) to vary between 2 and 3.2 according to an internally calculated vegetation nitrogen status value. Changes in PnET-CN code are found in Appendix C. The implicit assumption of this approach is that variation observed within the combined global dataset (Figure 2) was caused by differing degrees of nitrogen limitation at the study sites. Although we cannot verify the validity of this assumption, the approach does offer a means of adding a more realistic plasticity to belowground allocation estimates using a robust set of observations to constrain the predictions.

Model Application

Results of simulations runs of FACE site data using the modified mechanism were compared to baseline model runs of PnET-CN to determine a measure of change (expressed as a percent) in fine root stimulation under elevated CO₂. Additionally, new simulations were run using data from five northeastern U.S. forest sites under a variety of projected climate change scenarios to evaluate the impact of carbon partitioning shifts on baseline PnET-CN estimates of forest productivity and carbon storage over longer time scales than can be evaluated at the FACE experiments. The original simulations of these sites using the PnET-CN model were run by Ollinger et al. (2008).

The five northeastern forests used in the model application were: (1) Biscuit Brook, Catskills, NY; (2) Hubbard Brook, White Mountains, NH; (3) Huntington Forest, Adirondacks, NY; (4) Howland Forest, Howland, ME; and (5) Harvard Forest, Petersham, MA (Table 7). Long-term future climate projections (2000 to 2099) at each of the sites were originally generated by Hayhoe et al. (2006) using the Parallel Climate Model (PCM) and HadCM3 (Hadley Centre Coupled Model, version 3) general

circulation models. A1 scenarios project a higher level of greenhouse gas emissions; while B1 scenarios simulate reduced emissions. A degree of global warming has been incorporated into each scenario. These ranged from HADA1, with the highest degree of warming (6.3 °C) to PCMB1, with the lowest degree of warming (1.5 °C) predicted to occur by the time period of 2070-2099. Nitrogen deposition remained a constant 20% of current levels prior to 1930, with a linear increase to present day values.

These analyses were used to evaluate the degree to which the modified algorithm of TBCA to roots altered the earlier estimates of forest productivity run with PnET-CN. The effect of increased carbon allocation to root growth on net ecosystem production (NEP) under future climate scenarios was also examined. NEP is the difference between

Table 7. Site and disturbance history parameters for the five northeastern forest study sites used in model application analysis. (Adapted from Ollinger et al. 2008).

Parameter	Biscuit Brook, NY	Hubbard Brook, NH	Huntington Forest, NY	Howland Forest, ME	Harvard Forest, MA
Location (latitude, longitude)	41.99, -74.50	43.94, -71.75	43.98, -74.50	45.25, -68.73	42.5, -72.2
Forest type	Red oak, red maple	Northern hardwood	Northern hardwood	Spruce	Red oak, red maple
WHC (cm)	12	12	12	18	18
Annual Average Nitrogen deposition (g N m ⁻² y ⁻¹)	0.96	0.64	0.61	0.39	0.80
Disturbance history	Harvest 1859: Mortality: 90% Removed: 80%	Harvest 1904: Mortality: 20% Removed: 80%	Harvest 1859: Mortality: 90% Removed: 80%	Uncut and unmanaged	Agriculture 1750-1850: Mortality: 100% Removed: 5%/yr
	Harvest 1916: Mortality: 90% Removed: 80%	Harvest 1919: Mortality: 80% Removed: 80%	Harvest 1916: Mortality: 90% Removed: 80%		

carbon uptake through photosynthesis and carbon lost through respiration from both live plant tissue and decomposing organic matter. Positive NEP values imply forest carbon sinks; while, negative values suggest a carbon source.

In the Ollinger et al. (2008) simulations, the model would have allocated the majority of newly photosynthesized carbon under elevated CO₂ to the wood carbon pool. Simulations were run with the modified NStatus mechanism to evaluate the effect of dynamic carbon partitioning on carbon storage potential.

CHAPTER III

RESULTS

Baseline PnET-CN Simulations

Baseline runs of the original PnET-CN model, using data from the three FACE forests under ambient atmospheric CO₂, resulted in a 47% overestimation of total NPP at the Aspen FACE site, and an underestimation at both the Duke (36%) and ORNL (37%) FACE sites (Table 8). While some overestimation of modeled NPP is expected to result from components of actual NPP that are subsumed in the model estimates, but typically omitted from field measurements (e.g. woody roots, fruit and flower production, VOC emissions, etc.; Clark et al. 2001) these sources alone are not likely to be the sole source of disagreement between predicted and observed values (additional potential sources of error are provided in the discussion). However, because this study is focused on predicting proportional changes in allocation under elevated CO₂, rather than on capturing the absolute magnitude of NPP at a small number of sites, the results of these model runs provided benchmark values that were used for comparison to enriched CO₂ model simulations.

Despite the poor agreement between predicted versus observed NPP across the sites, the predicted average CO₂ fertilization response was 21% (Table 9), which is similar to the published median value of 23% (± 2) (Norby et al. 2005). As expected, increased carbon accumulation produced by the model was predominantly allocated to

the wood biomass pool (Table 9). Based on the field data, the ORNL FACE site appears to have the highest rate of fine root production, as well as the greatest degree of enhancement, under elevated CO₂ (Norby et al. 2004). Baseline PnET-CN predictions, however, have indicated that the ORNL FACE site had the lowest rate of fine root production, while also displaying the greatest enhancement of fine roots, under elevated CO₂ (Table 9).

PnET-CN:NStatus Simulations

PnET-CN:NStatus simulations increased the total percent of belowground carbon allocation under elevated CO₂ across all of the FACE sites (Table 9). The NStatus modification allowed the slope of the litterfall to TBCA equation to vary as a function of NStatus, which increased carbon allocation to fine roots under elevated CO₂ in response to decreased nitrogen availability. This resulted in a range of higher estimates of fine root stimulation under elevated CO₂, when compared to baseline PnET-CN predictions. However, the predicted results for fine root stimulation remained lower than FACE site published values. The improvement in predicted fine root stimulation was particularly evident at the ORNL FACE site where NStatus simulations doubled baseline estimates produced by the current PnET-CN model (Table 9).

Estimates of total NPP under elevated CO₂ from the modified model (which will subsequently be referred to as PnET-CN:Nstatus) differed to only a small extent (-2.48 to +8.33%) from original model simulations (Table 8). New estimates of NPP in individual biomass pools were largely a result of decreased carbon to the wood pool and increased allocation belowground. The Duke forest site demonstrated the largest difference

between PnET-CN and PnET-CN:Nstatus simulations, with an 8% increase in total estimated NPP.

Table 8. Summary of mean NPP ($\text{g C m}^{-2} \text{ y}^{-1}$) predictions under ambient and elevated CO_2 at three FACE forests, generated by both the PnET-CN and PnET-CN:Nstatus models. Published values are mean NPP gathered by field measurements at each FACE site.

FACE Forest Site	CO_2	Foliage ($\text{g C m}^{-2} \text{ y}^{-1}$)	Wood ($\text{g C m}^{-2} \text{ y}^{-1}$)	Fine Root Production ($\text{g C m}^{-2} \text{ y}^{-1}$)	Total NPP ($\text{g C m}^{-2} \text{ y}^{-1}$)
<i>Duke FACE</i>					
PnET-CN					
	<i>Ambient</i>	73.74	257.05	64.51	395.31
	<i>Elevated</i>	80.08	316.87	69.98	466.95
PnET-CN:Nstatus					
	<i>Ambient</i>	73.74	245.13	78.91	397.79
	<i>Elevated</i>	76.84	346.77	85.82	509.43
Published Values					
	<i>Ambient</i>	217.02	367.40	22.16	606.58
	<i>Elevated</i>	272.30	434.25	36.40	724.95
<i>ORNL FACE</i>					
PnET-CN					
	<i>Ambient</i>	61.69	414.27	54.95	530.91
	<i>Elevated</i>	70.24	602.05	62.32	734.61
PnET-CN:Nstatus					
	<i>Ambient</i>	63.36	397.85	65.88	527.09
	<i>Elevated</i>	73.93	576.09	85.09	735.11
Published Values					
	<i>Ambient</i>	204.60	539.08	94.37	838.05
	<i>Elevated</i>	219.04	592.60	212.43	1024.07
<i>Aspen FACE†</i>					
PnET-CN					
	<i>Ambient</i>	91.8	272.55	71.25	455.60
	<i>Elevated</i>	96.45	410.10	74.10	580.65
PnET-CN:Nstatus					
	<i>Ambient</i>	89.55	261.00	75.15	425.70
	<i>Elevated</i>	94.20	393.60	78.75	566.55
Published Values					
	<i>Ambient</i>	108.16	177.83	15.38	241.37
	<i>Elevated</i>	153.90	314.80	25.27	493.97
†Aspen FACE NPP (predicted) are only for years 2001-2003 where closed-canopy data were available All other NPP values (predicted and observed) are for the full record of the study site.					

Table 9. Summary of percent predicted biomass stimulation (%) under elevated CO₂ at three FACE forests, generated by both the PnET-CN and PnET-CN:NStatus models.

FACE Forest Site	Percent Foliage Stimulation (%)	Percent Wood Stimulation (%)	Percent Fine Root Production Stimulation (%)	Percent Total NPP Stimulation (%)
<i>Duke FACE</i>				
PnET-CN	7.91	18.87	7.81	15.34
PnET-N:NStatus	4.03	29.31	8.05	21.91
Published	20.30	15.39	39.12	16.32
<i>ORNL FACE</i>				
PnET-CN	11.74	31.19	11.82	27.72
PnET-N:NStatus	14.29	30.93	22.57	28.29
Published	6.59	9.03	55.57	18.45
<i>Aspen FACE†</i>				
PnET-CN	4.82	33.54	3.84	21.53
PnET-N:NStatus	4.93	33.68	4.57	24.86
Published	29.72	43.51	39.13	51.13

Source: Published values were made available through the Carbon Dioxide Information Analysis Center (CDIAC) FACE Data Management System (CDIAC 2008).

Altered Patterns of Carbon Partitioning

Because changes in carbon partitioning within plants have the potential to alter patterns of productivity and whole ecosystem carbon balances, additional analyses were performed to determine the mechanism's influence on model projections over longer time scales. Model simulations for the five northeastern forests examined by Ollinger et al. 2008 were run using both the PnET-CN and PnET-CN:NStatus models under a variety of projected climate scenarios (Table 10). NEP estimates from PnET-CN and PnET-CN:NStatus were evaluated to identify altered patterns of carbon storage due to shifts in carbon partitioning. The NStatus simulations exhibited a moderate increase (< 10%) in NEP at Biscuit Brook, and more substantial increases (21%) at both the Harvard Forest and Hubbard Brook, when compared to baseline PnET-CN model projections (Ollinger et al. 2008). Simulations using the NStatus mechanism at the Howland Forest demonstrated

a moderate decrease (13%) in NEP over baseline PnET-CN estimates. There was little change noted at the Huntington Forest (Table 10).

Table 10. Summary of predicted NEP ($\text{g C m}^{-2} \text{ y}^{-1}$) under current and future climate and CO_2 at five study sites (originally introduced in Ollinger et al. 2008) generated by both the PnET-CN and PnET-CN:NStatus models.

Year	CO_2	Biscuit Brook	Hubbard Brook	Huntington Forest	Howland Forest	Harvard Forest
<i>PnET-CN</i>						
1990-2000	Ambient	73.82	39.47	44.40	19.35	88.97
2070-2099	Elevated	207.3	164.58	170.22	52.13	169.90
<i>PnET-CN:NStatus</i>						
1990-2000	Ambient	75.60	47.14	31.21	13.16	113.80
2070-2099	Elevated	226.1	209.09	169.14	46.09	215.59

Values are averages ($\text{g C m}^{-2} \text{ y}^{-1}$) of four climate scenarios over time period indicated. Elevated CO_2 is a scalar from a preindustrial value of 280 ppm to a projected 600 ppm by the year 2100.

The PnET-CN and PnET-CN:NStatus model simulations exhibited minor differences in estimated total NPP (Figures 3 and 6; predicted patterns were similar for all four hardwood sites. For simplicity, Harvard Forest is the only hardwood site shown here). However, the PnET-CN:NStatus model simulations altered carbon allocation patterns by increasing fine root production and decreasing carbon allocation to wood under elevated CO_2 . This reflects the effects of rising CO_2 on predicted nitrogen limitation. Decreased carbon allocation to wood reduced total aboveground NPP (ANPP) when compared to simulations published by Ollinger et al. (2008) (Figures 4 and 7). With the exception of the Howland forest (the only site dominated by spruce, which was predicted to decline under the warmest scenarios), NStatus simulations resulted in greater average NEP over a variety of climate scenarios and elevated CO_2 .

Figures 3 through 5 display carbon allocation trends of a broadleaf forest (Harvard Forest) in Massachusetts. Predictions of total NPP at the Harvard Forest were

similar from both models (Figure 3); while estimates of ANPP decreases (Figure 4) and belowground NPP (BNPP) increases (Figure 5) with the modified NStatus mechanism.

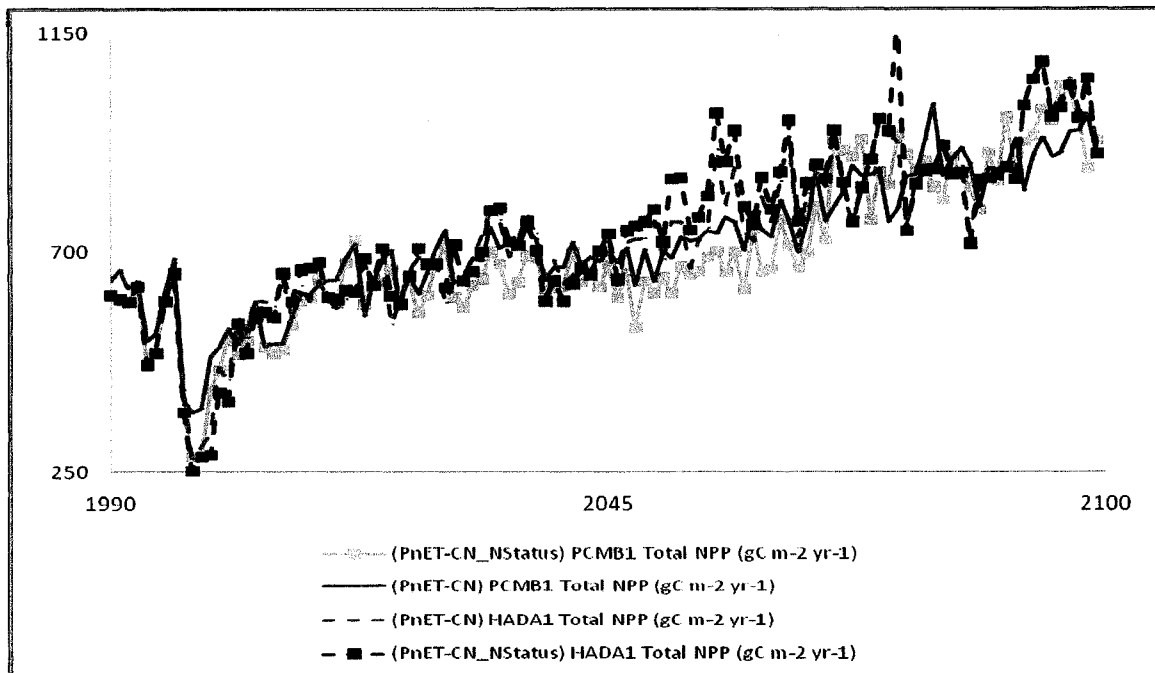


Figure 3. Predicted total NPP at Harvest Forest ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the period from 1990 to 2100 under both the HADA1 and PCMB1 climate scenarios, simulated by both PnET-CN and PnET-CN:NStatus models. Dashed lines represent HADA1 climate scenarios while solid lines indicate PCMB1 scenarios. Square markers signify PnET-CN:NStatus model simulations.

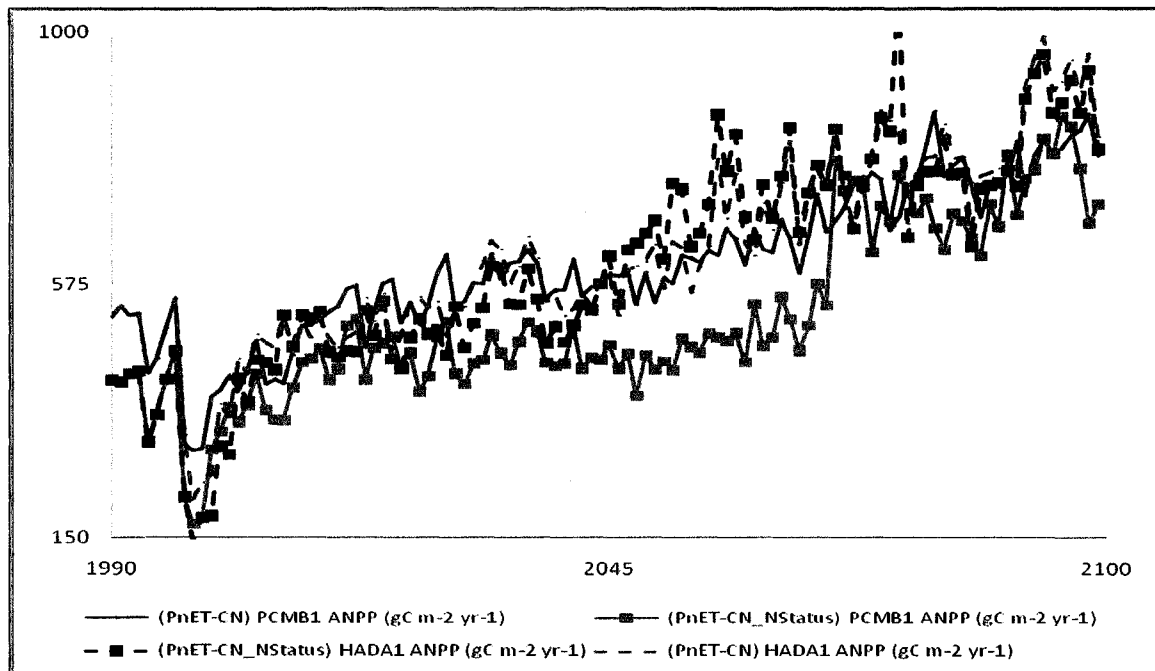


Figure 4. Predicted ANPP at Harvest Forest ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the period from 1990 to 2100 under both the HADA1 and PCMB1 climate scenarios, simulated by both PnET-CN and PnET-CN:NStatus models. Dashed lines represent HADA1 climate scenarios while solid lines indicate PCMB1 scenarios. Square markers signify PnET-CN:NStatus model simulations.

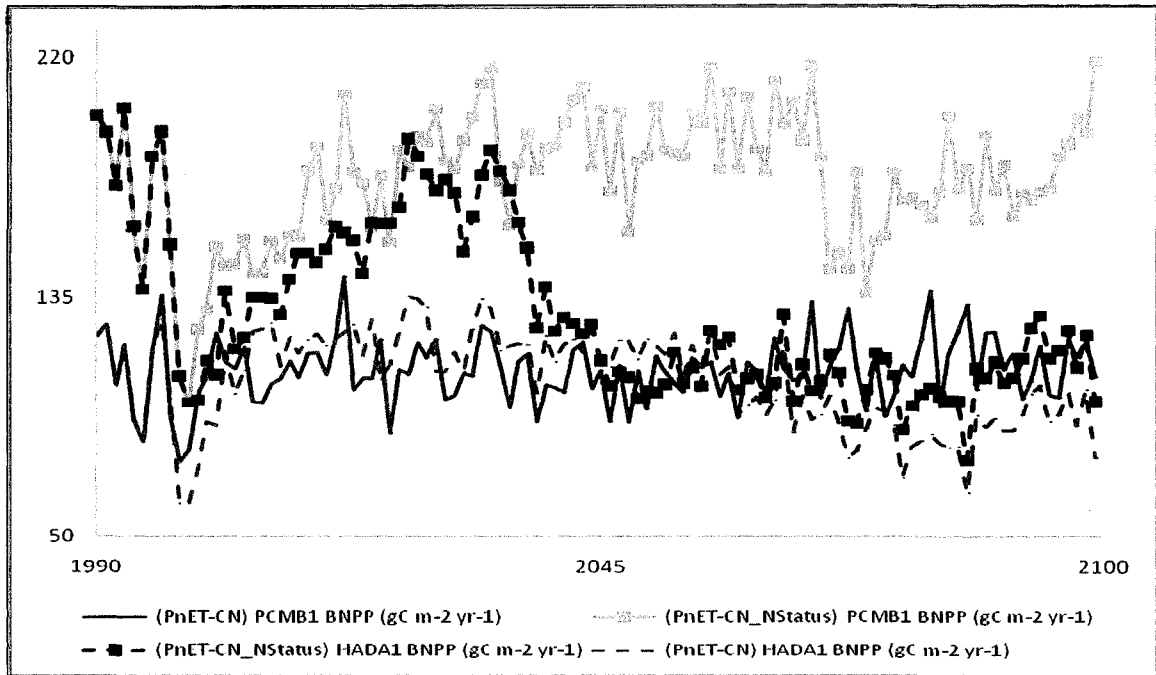


Figure 5. Predicted BNPP at Harvest Forest ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the period from 1990 to 2100 under both the HADA1 and PCMB1 climate scenarios, simulated by both PnET-CN and PnET-CN:NStatus models. Dashed lines represent HADA1 climate scenarios while solid lines indicate PCMB1 scenarios. Square markers signify PnET-CN:NStatus model simulations.

Figures 6 through 8 demonstrate altered patterns of carbon allocation in a spruce stand at the Howland Forest. Predicted NEP decreased in simulations run with the NStatus mechanism. Predicted estimates of total NPP are similar for both the baseline and PnET-CN:NStatus model simulations; however, decreased aboveground growth and increased BNPP were identified in the NStatus runs.

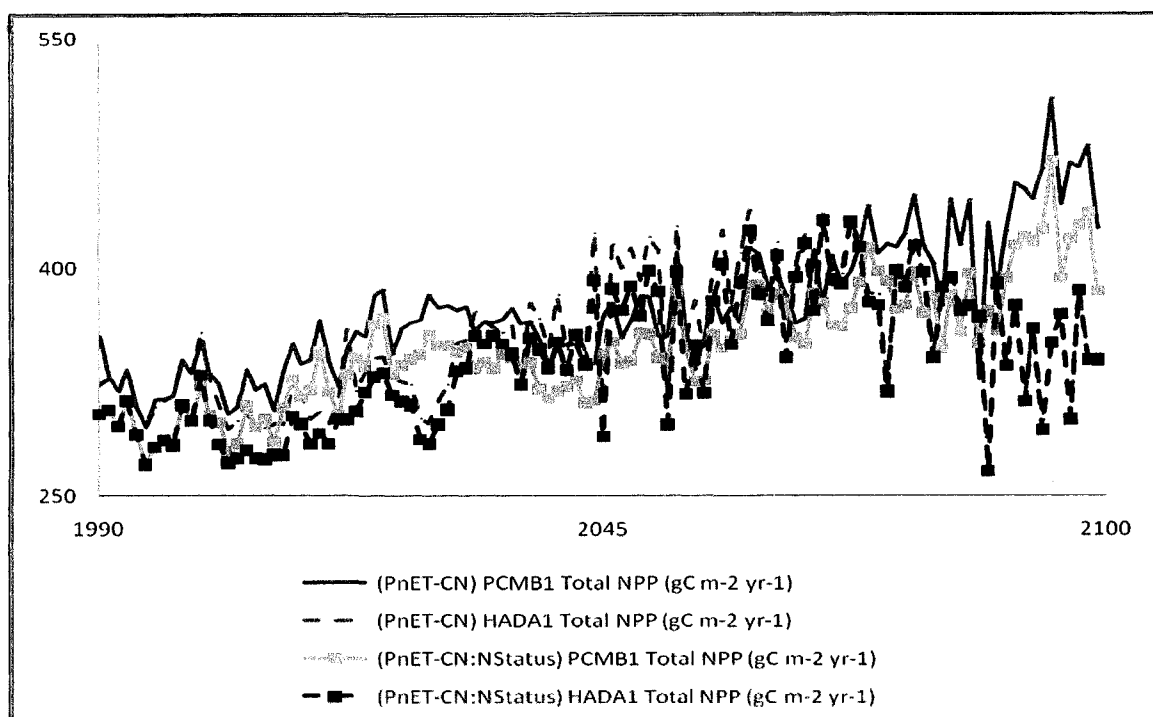


Figure 6. Predicted total NPP at Howland Forest ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the period from 1990 to 2100 under both the HADA1 and PCMB1 climate scenarios, simulated by both PnET-CN and PnET-CN:NStatus models. Dashed lines represent HADA1 climate scenarios while solid lines indicate PCMB1 scenarios. Square markers signify PnET-CN:NStatus model simulations.

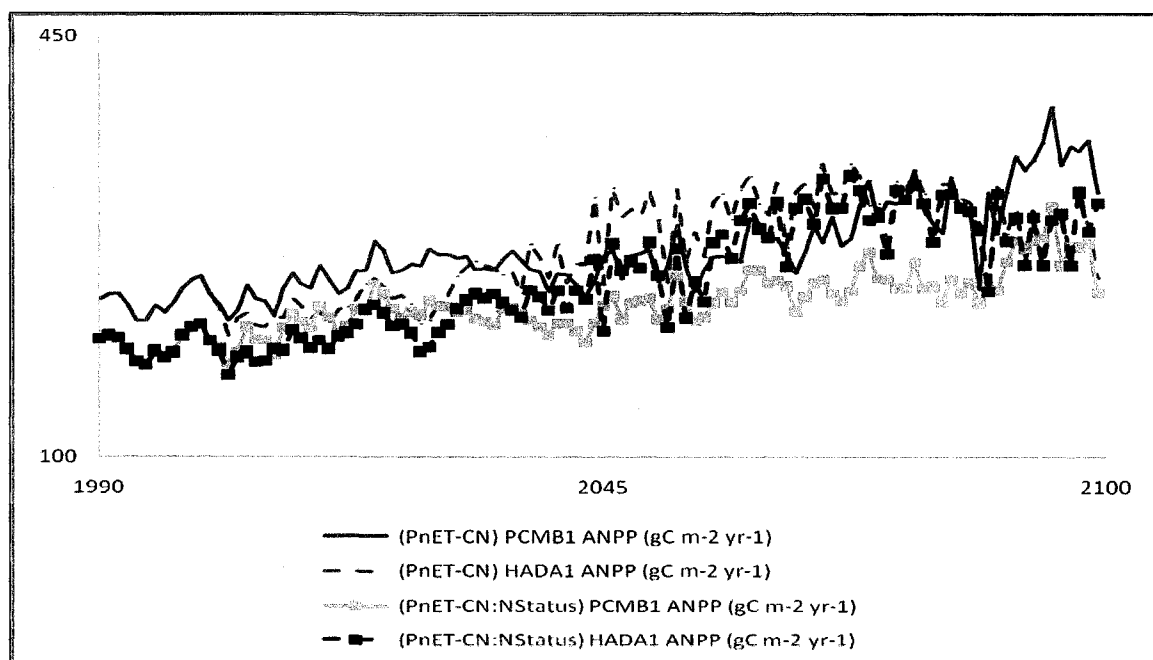


Figure 7. Predicted ANPP at Howland Forest ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the period from 1990 to 2100 under both the HADA1 and PCMB1 climate scenarios, simulated by both PnET-CN and PnET-CN:NStatus models. Dashed lines represent HADA1 climate scenarios while solid lines indicate PCMB1 scenarios. Square markers signify PnET-CN:NStatus model simulations.

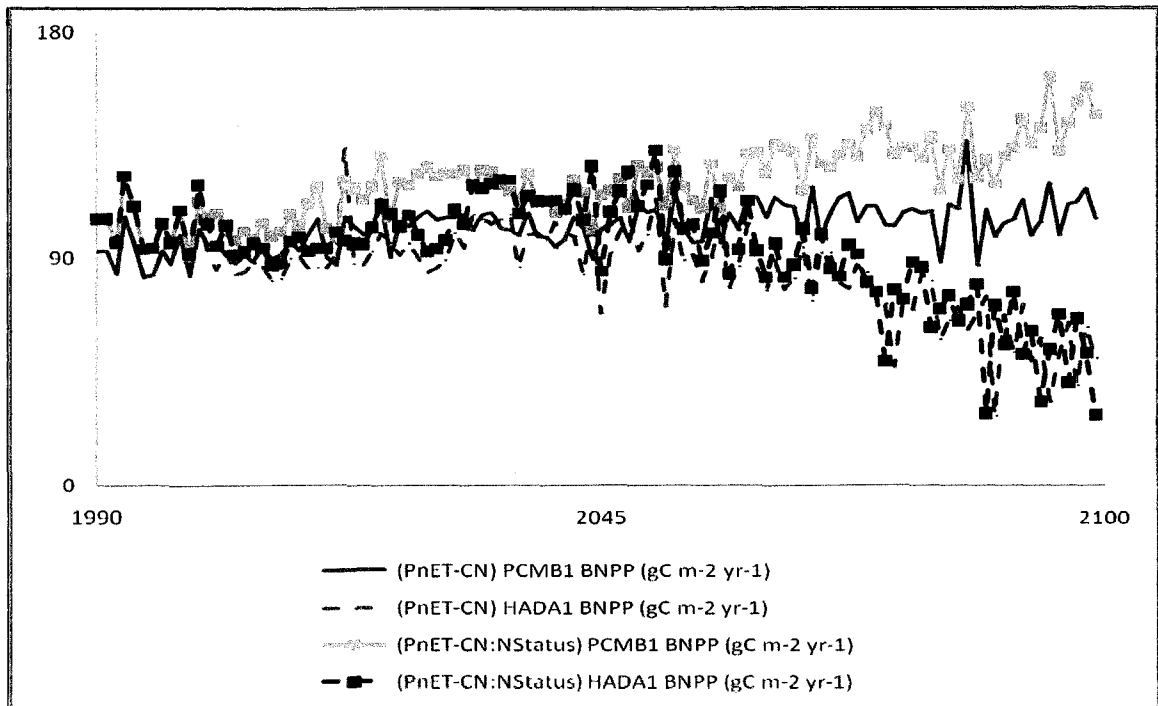


Figure 8. Predicted BNPP at Howland Forest ($\text{g C m}^{-2} \text{y}^{-1}$) for the period from 1990 to 2100 under both the HADA1 and PCMB1 climate scenarios, simulated by both PnET-CN and PnET-CN:NStatus models. Dashed lines represent HADA1 climate scenario while solid lines indicate PCMB1 scenarios. Square markers signify PnET-CN:NStatus model simulations.

CHAPTER IV

DISCUSSION

The primary aim of this study was the evaluation of the PnET-CN model's capacity to simulate the shifts in aboveground versus belowground carbon allocation under elevated CO₂ that have been observed in experiments. The analysis included model validation against published field measurements of NPP and carbon allocation at three U.S. experimental FACE sites. An alternative mechanism for estimating TBCA to roots as a function of variable nitrogen availability was developed. Predictions using the modified PnET-CN:NStatus model included CO₂-induced increases in N limitation to vegetation and subsequent increases in fine root production. NStatus simulations exhibited only small differences in predicted total NPP when compared to current PnET-CN model estimates, despite altered patterns of carbon allocation under elevated CO₂.

Challenges in FACE Model Simulation

Multiple factors may have contributed to the discrepancies found between baseline PnET-CN model simulations and field measurements of forest productivity under ambient CO₂ at both the ORNL and Duke FACE sites. Sources of error in model simulations are often related to incorrect input parameters and/or a failure of the model to capture important mechanisms. At the ORNL FACE site, topography may have contributed to model error in that the model simulated substantial mid-summer water stress at the site, which was not observed in field measurements. The absence of observed water stress may have been related to increased water uptake by tap roots from a nearby

river (R.J. Norby personal communication February 2008). Because the model does not account for this, an overestimation of water stress at the ORNL FACE site may explain lower initial NPP estimates.

Another factor that may have influenced initial model estimates under ambient CO₂ is the simulation of FACE site land use history. Although the dates and magnitudes of disturbances to vegetation were included in the simulations, the effects of these events on soil C and N pools is difficult to capture. This is true for both the immediate disturbances that occurred prior to onset of the experiments as well as those that took place as part of each site's longer-term history. As a result, the degree of N availability predicted by the model may be substantially greater than or less than that which actually occurs at each site. Additionally, most prior studies with the PnET models involved mature, naturally regenerated ecosystems rather than the young plantations that exist at the FACE sites.

Simulations of Observed Carbon Allocation Dynamics

Given the substantial uncertainties in measured fine root growth rates and large differences obtained by different measurement methods, it is difficult to assess whether the Nstatus mechanism developed in this study improved estimates of fine root production under elevated CO₂. The new mechanism did, however, add a more dynamic approach to estimating root allocation that is consistent with observed CO₂ responses. Despite the large discrepancies between the absolute magnitude of predicted and observed growth rates, the new predictions demonstrate a degree of increased fine root production that corresponds to internally modeled nitrogen availability. Consistent with

the published literature, the NStatus mechanism allocates more carbon to roots when nitrogen is limited.

According to Norby et al. (2005), all three FACE forests demonstrated a consistent trend of increasing photosynthesis and NPP, with the proportional enhancement of NPP less than that of photosynthesis, and a greater fraction of carbon allocated belowground. Of the FACE sites studied, the ORNL FACE displayed the largest increase in carbon allocated belowground under elevated CO₂. Annual measurements of fine root production almost tripled in elevated CO₂ treatment plots, which accounted for nearly all of the site's sustained 22% increase in NPP (Norby et al. 2004). At the Duke FACE carbon allocation in loblolly pine was allotted primarily to long-lived woody tissues.

The varying carbon partitioning responses of forest FACE ecosystems under elevated CO₂ have been explained by nitrogen imbalances (DeLucia et al. 2005). Recent studies of nitrogen fertilization experiments under elevated CO₂ at the ORNL FACE demonstrated a shift in carbon allocation from fine root production to wood growth, which provides evidence that nitrogen limitation are a major contributor to increased carbon allocated to fine root production (Iverson and Norby 2008). Differences in carbon allocation under elevated CO₂ at Duke FACE may be the result of more available nitrogen or differences in species requirements.

Consistent with the observed patterns across the sites, simulations run with the NStatus mechanism predicted the highest degree of nitrogen limitation at the ORNL FACE site, which exhibited the largest increase in fine root production. Model runs of the Duke and Aspen FACE sites predicted a lesser degree of nitrogen limitation, and

therefore a lesser amount of stimulation of fine root production under elevated CO₂. The increases in fine root production identified in PnET-CN:NStatus simulations correlated with the published field observations, supporting the theory that increased carbon sequestration under elevated CO₂ will be limited by nutrient supply, particularly nitrogen.

FACE site experiments are designed to replicate realistic conditions; however, there are a number of limitations. The oldest U.S. FACE forest experiment (Duke FACE) has been in existence since 1996, limiting available data to a twelve year period. Prior to FACE studies, one to two year open-top chamber (OTC) studies of seedlings under elevated CO₂ were conducted. These data are not easily scaled-up to longer periods of time (Norby et al. 1999; Schneider et al. 2004, as cited in Nösberger and Long 2006).

A critical question regarding results from FACE experiments is whether exposing a forest stand to a large single-step increase in CO₂ concentrations (ambient to approximately 550ppm) will produce the same results that forests undergo with a natural, more gradual increase in CO₂ over several decades (Nösberger and Long 2006). This is particularly important when studying the impact of microbial processes, which may be altered by a single abrupt increase in CO₂.

Finally, FACE experiments have generally been conducted with young forest plantations. It is unknown whether the dynamics of older forest systems under elevated CO₂ would respond in a similar manner. Despite these limitations, FACE forest studies supply the best available dataset for studying the effects of elevated CO₂ on belowground carbon allocation dynamics.

Significance of Altered Carbon Partitioning

Forest soils are among the largest terrestrial pools of carbon globally, and with the longest average residence times, they account for the storage of approximately three times more carbon than aboveground plant biomass (Canadell et al. 1996; Rasse et al. 2005). Composed of both fast-cycling and recalcitrant substances, the destination of carbon inputs into the belowground soil pool is critically important in determining long-term carbon storage potential. Carbon allocation to roots and mycorrhizal fungi will result in either a short- or long-term carbon sink depending on whether carbon is allocated into stable aggregates, or decomposed and respired quickly after root death (Davidson and Hirsch 2001).

PnET-CN:NStatus simulations produced estimates of total NPP that were consistent with current PnET-CN model estimates, while shifting patterns of carbon partitioning under elevated CO₂. The carbon allocated to wood growth decreased, while fine root production increased. An exception to this pattern was the Duke site, where both wood and fine root production increased under elevated CO₂ (as did total NPP under the new Nstatus mechanism).

In order to investigate the effects of altered carbon partitioning on earlier PnET-CN model runs, five northeastern forest climate change simulations (see previous analysis by Ollinger et al. 2008) were re-run with the modified NStatus mechanism. Model simulations of NPP and NEP indicated an increase in carbon storage (mean for the period of 2070-2100). Increased carbon allocation to fine roots at the four deciduous sites resulted in increased carbon storage under all projected climate scenarios. A decrease in carbon accumulation observed in the spruce forests of Howland, Maine can be explained

by a decline of total NPP under long-term climate projections. This decrease in predicted NPP was caused by simulated temperature stress in that several of the climate scenarios included temperatures rising above the optimal conditions for spruce. Note, however, that PnET-CN does not simulate replacement of spruce by other species that would likely increase in abundance following its decline.

Evidence remains strong that increased belowground carbon inputs under elevated CO₂ result in additional carbon storage. For example, a meta-analysis of enriched forest and grassland CO₂ experiments (at concentrations of 550ppm and 750ppm, respectively) by Jastrow et al. (2005), revealed a 5.6% increase in soil carbon over a range of two to nine years, with a median accrual rate of 19 g C m⁻² y⁻¹. Over half of this carbon was integrated into stable, protective, soil microaggregates, suggesting the potential for long-term carbon sequestration (Jastrow et al. 2005). While a six year study of CO₂ enrichment at the Duke FACE loblolly pine plantation demonstrated an additional soil carbon sink of 52 ± 16 g C m⁻² y⁻¹ (Lichter et al. 2005). The increase in carbon in this study, however, was attributed to greater inputs of litterfall and fine root turnover that accumulated more organic matter into deeper layers of the soil, rather than an accrual of physically protected soil organic matter (SOM) (Lichter et al. 2005). Finally, a meta-analysis by Rasse et al. (2005) reported that the mean residence time of root-derived soil carbon is 2.4 times greater than shoot-derived soil carbon, signifying that increased fine root production is responsible for greater allocation (and storage) of carbon belowground.

Forest ecosystem models used to simulate the effects of global climate change will benefit from an improved belowground carbon allocation mechanism. Models

featured in the *Third Assessment Report of the Intergovernmental Panel on Climate Change* (IPPC 2001) proposed that an increase in CO₂ alone would result in a 350 to 890 Pg carbon accrual in terrestrial ecosystems by the year 2100 (Hungate et al. 2003); while, coupled carbon-climate models suggested carbon accumulation of 260 to 530 Pg (Hungate et al. 2003). These estimates are substantial; however, they do not consider nutrient limitation constraints, and may overestimate the ability of terrestrial ecosystems to sequester carbon from the atmosphere (Thornton et al. 2007). A model that successfully simulates carbon allocation trends coupled with nitrogen constraints under elevated CO₂ will improve projected carbon sequestration estimates for terrestrial ecosystems.

Future Research

The modified NStatus mechanism increased estimates of fine root stimulation under elevated CO₂ and is a first step in improving model simulations. There are still several areas that require further study. Increased fine root production in the current PnET-CN:NStatus model does not cause a simultaneous increase in nitrogen uptake, which has been documented in field observations of forest productivity under elevated CO₂ (Finzi et al. 2007). Examination of the original PnET-CN code suggests the need for a feedback mechanism between increased root growth and a correlated increase in nitrogen uptake. This issue is currently under investigation and should result in an improved and coupled relationship.

Ideally, a global dataset of TBCA and of nitrogen availability (e.g. measurements of foliar nitrogen concentration and/or nitrogen mineralization rates) should be used to develop an improved carbon allocation mechanism. At the present time, the lack of

available datasets and standardized field measurements prevents this. Standardized experimental methods in field and laboratory measurements would improve cross-site comparisons (Pendall et al. 2004). TBCA dynamics could be evaluated more accurately by applying isotope pulse labeling or employing uniform methods in long-term (decadal scale) multifactor experiments. Quantification of precise labile and recalcitrant carbon pool turnover rates is also essential to resolving uncertainty in belowground carbon storage. The development and validation of enhanced models will improve the understanding of the response of longer-lived carbon pools to climate change.

In conclusion, a modified TBCA mechanism based on nitrogen availability improved carbon allocation trends under conditions of enriched atmospheric CO₂. The new mechanism allowed for adaptability of the TBCA to the litter relationship first developed by Raich and Nadelhoffer (1989), according to a simulated level of nitrogen availability. The NStatus mechanism provides an explanation for the variability observed around the mean of the original data collected from three FACE experimental forest sites. While many questions still exist about belowground carbon allocation, each study advances our understanding of forest ecosystem function, particularly underground carbon allocation.

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FACE Site Acknowledgements

The DukeFACE, ORNL-FACE, and AspenFACE experiments are supported by the U.S. Department of Energy Office of Science, Biological and Environmental Research (BER).

Aspen FACE: The site is principally supported by the Office of Science (BER), U.S. Department of Energy, Grant No. DE-FG02-95ER62125 to Michigan Technological University, and Contract No. DE-AC02-98CH10886 to Brookhaven National Laboratory, the U.S. Forest Service Northern Global Change Program and North Central Research Station, Michigan Technological University, and Natural Resources Canada – Canadian Forest Service.

Duke FACE: The site is supported by the Office of Science (BER), U.S. Department of Energy, Grant No. DE-FG02-95ER62083.

ORNL FACE: The site is managed by UT-Battelle, LLC, for the U.S. Department of Energy under Contract DE-AC05-00OR22725.

APPENDICES

APPENDIX A

DATABASES CITED

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APPENDIX B

```

*****Calculate CO2 effect on photosynthesis and conductance*****
Calculate atmospheric CO2 concentration (Ca) lowered to 280 base 11-29-99
If SC.CCRamp = 1 Then
  If RealYear < 1801 Then
    Ca = 280
  'CO2 concentration = 280 at 1800
  ElseIf RealYear > 1800 And RealYear < 2101 Then
    Ca = 280 + (0.0188 * (RealYear - 1800)) ^ 3.35
  ' Ramp up to 600 by 2100
  Else
    Ca = 600
  End If
Else
  Ca = SC.FixedCO2
'Ca at run CO2 level (user input)
End If

```

Figure B1. Original PnET code representing CO₂ rise from preindustrial atmospheric concentrations (280ppm) to a projected 600ppm by 2100.

```

*****Calculate CO2 effect on photosynthesis and conductance*****
' Calculate atmospheric CO2 concentration (Ca) lowered to 280 base 11-29-99
If SC.CCRamp = 1 Then
  If RealYear < 1801 Then
    Ca = 280
  'CO2 concentration = 280 at 1800
  ElseIf RealYear > 1800 And RealYear < 1996 Then
    Ca = 280 + (0.0188 * (RealYear - 1800)) ^ 3.35
  ' Ramp up to 600 by 2100
  Else
    Ca = 550
  End If
Else
  Ca = SC.FixedCO2
'Ca at run CO2 level (user input)
End If

```

Figure B2. Adjusted PnET code simulating a single-step increase in CO₂, representative of the same single-step increase observed in FACE experimental forests. In this scenarios, a single-step increase to 550ppm at the Duke FACE site, at the initiation of the CO₂ treatment (year = 1996).

APPENDIX C

```

TMult = (Exp(0.1 * (Tave - 7.1)) * 0.68) * 1
RootCAdd = RootAllocA * (DaySpan / 365) + RootAllocB * FolProdCMo
RootC = RootC + RootCAdd
RootAllocCMo = ZMin(1, ((1 / 12) * TMult)) * RootC 'averages 1/12 per month
RootC = RootC - RootAllocCMo

```

Figure C1. The original code found in the AllocateMo subroutine of the PnET model, used to predict TBCA according to the Raich and Nadelhoffer (1989) relationship between TBCA and litterfall-carbon.

```

If PlantN > MaxNStore Then PlantN = MaxNStore
  NRatio = 1 + (PlantN / MaxNStore) * FolNConRange
  If NRatio < 1 Then NRatio = 1
  If NRatio > 1 + FolNConRange Then NRatio = 1 + FolNConRange

NStatus = (NRatio - 1) / FolNConRange

TMult = (Exp(0.1 * (Tave - 7.1)) * 0.68) * 1

'Increase root allocation vs N availability mechanism:
RootCAdd = RootAllocA * (DaySpan / 365) + ((3.2 - (1.2 * NStatus)) *
FolProdCMo)

RootC = RootC + RootCAdd
RootAllocCMo = ZMin(1, ((1 / 12) * TMult)) * RootC 'averages 1/12 per
month
RootC = RootC - RootAllocCMo

```

Figure C2. New code implemented into the AllocateMo subroutine of the PnET-CN model, used to predict TBCA according to a new nitrogen availability variable (NStatus) that varies around the Raich and Nadelhoffer (1989) mean slope with a range developed by the dataset's 95% confidence interval.