Comparison of boreal ecosystem model sensitivity to variability in climate and forest site parameters

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Abstract. Ecosystem models are useful tools for evaluating environmental controls on carbon and water cycles under past or future conditions. In this paper we compare annual carbon and water fluxes from nine boreal spruce forest ecosystem models in a series of sensitivity simulations. For each comparison, a single climate driver or forest site parameter was altered in a separate sensitivity run. Driver and parameter changes were prescribed principally to be large enough to identify and isolate any major differences in model responses, while also remaining within the range of variability that the boreal forest biome may be exposed to over a time period of several decades. The models simulated plant production, autotrophic and heterotrophic respiration, and evapotranspiration (ET) for a black spruce site in the boreal forest of central Canada (56°N). Results revealed that there were common model responses in gross primary production, plant respiration, and ET fluxes to prescribed changes in air temperature or surface irradiance and to decreased precipitation amounts. The models were also similar in their responses to variations in canopy leaf area, leaf nitrogen content, and surface organic layer thickness. The models had different sensitivities to certain parameters, namely the net primary production response to increased CO_2 levels, and the response of soil microbial respiration to precipitation inputs and soil wetness. These differences can be explained by the type (or absence) of photosynthesis-CO_2 response curves in the models and by response algorithms of litter and humus decomposition to drying effects in organic soils of the boreal spruce ecosystem. Differences in the couplings of photosynthesis and soil respiration to nitrogen availability may also explain divergent model responses. Sensitivity comparisons imply that past conditions of the ecosystem represented in the models' initial standing wood and soil carbon pools, including historical climate patterns and the time since the last major disturbance, can be as important as potential climatic changes to prediction of the annual ecosystem carbon balance in this boreal spruce forest.

1. Introduction

The Boreal Ecosystem-Atmosphere Study (BOREAS) was conducted to better understand controls on carbon and water cycles in the boreal forest biome under changing climate conditions [*Hall et al.*, 1996; *Sellers et al.*, 1997]. Field measurements of both physical and biological characteristics of the boreal spruce forest were made over the course of several years to help determine ecosystem responses to interannual variability in climate. Continuing studies of net ecosystem exchange of carbon at BOREAS sites, together with regional remote sensing of ecosystem properties, should aid in determining the potential for a substantial terrestrial sink for atmospheric carbon dioxide in high-latitude forest areas [*Ciais et al*, 1995; *Keeling et al.*, 1996; *Fan et al.*, 1998; *Potter and Klooster*, 1999]

To complement field measurements, simulation modeling is a necessary component of any integrated ecological study of responses to climate change and variability, particularly in the case of a region as vast and spatially heterogeneous as the global boreal forest. A primary objective of BOREAS was to collect the data required to improve computer simulation models of the important ecosystem processes controlling carbon and water fluxes over timescales of hours to years [*Sellers et al.*, 1997]. Climate models indicate that the greatest warming engendered by increasing atmospheric CO_2 will occur at high (45° to 65°N) latitudes [*Kattenberg et al.*, 1996], with the most marked effects within the continental interiors. Use of ecosystem models, which represent a synthesis of process-level understanding about major controls on carbon and water cycles, can uniquely improve understanding of the potential effects of global environmental change, principally altered temperature and precipitation patterns, on the boreal forest region.

The extensive BOREAS database of forest site attributes and meteorology now offers a unique opportunity to evaluate ecosystem modeling predictions for boreal spruce forest carbon and water cycles [*Amthor et al*, this issue]. The research questions that motivate analyses presented in this

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paper arise from the fact that sensitivity testing can help identify important commonalities or differences among ecosystem model predictions, as well as quantify the general variability in modeled responses to potential changes in climate and in other model drivers [Kittel et al., 1995; Ryan et al., 1996; Cramer et al., 1999; Clein et al., 2000]. Where ecosystem models differ in their responses to a range of input values, systematic comparisons may suggest hypotheses to test in future field research.

We report here on the first multimodel sensitivity study for BOREAS carbon cycling studies in old black spruce (OBS) stands at the northern study area (NSA). The main objective of this study is to determine whether ecosystem models with different levels of detail (e.g., hourly ecophysiological controls versus daily-to-monthly ecosystem processes) have similar and strong sensitivities to variability in the local climatology and to measured parameters of the BOREAS forest site. A companion paper [Amthor et al, this issue] describes the ecosystem models in detail and compares hourly, daily, monthly, and annual simulation results from these models with measured eddy covariance fluxes of evapotranspiration (ET) and CO_2 at the NSA OBS tower site for the period 1994-1996.

We note that although eddy covariance measurements are important to help evaluate short-term responses of ecosystem models (seasonal and interannual variability), comparisons to tower fluxes alone cannot address potentially longer-term responses to climate, ambient CO_2 levels, and changes in forest stand characteristics, which may also vary greatly over regional extents. As stated by Medlyn et al. [1999], the only practical approach to deal with the mismatch of experimental (tower flux) and the natural timescales of forest development is to build computer models, which can be used to extrapolate responses to the long-term and large scale. Therefore the unique combination of sensitivity simulations reported here with ecosystem model evaluations at the eddy covariance tower footprint scale [Amthor et al, this issue] should lay an important groundwork for a BOREAS regional comparison of spatially explicit models of boreal forests, several of which are included in the present analysis. Our rationale for selecting sensitivity tests of climate, CO_2 levels, and forest stand characteristics was mainly to identify and isolate any major differences in carbon model responses, while also remaining within the range of long-term variability which the boreal forest ecosystem of Canada may experience.

2. Site Description

The NSA-OBS tower site (55.88°N, 98.48°W, elevation 259 m) near Thompson, Manitoba, is dominated by black spruce (Picea mariana) trees. The topography is generally flat with abundant wetland areas, such that drainage of much of the area is poor. Overstory vegetation is about 150 years old. The higher ground has dense stands of black spruce trees, reaching a height of approximately 10 m, and a continuous ground cover of feathermoss (e.g., Pleurozium schreberi); lower elevations in the stand had 1-6 m spruce trees and a Sphagnum ground cover [Goulden et al., 1997; Harden et al., 1997]. Canopy leaf cover is clumped, meaning that leaves are grouped into shoots, branches, whorls, and crowns [Chen, 1996]. Soils at the NSA are predominantly derived from glacial Lake Agassiz sediments and consist of clays, organics, and some sandy deposits (H. Veldhuis,

unpublished data, 1995). The stand was instrumented with an eddy covariance flux tower from 1994-1996, measuring near-continuous exchanges of CO_2, water, and energy between the ecosystem and the lower atmosphere, as well as a basic suite of micrometeorological variables [Goulden et al., 1997]. Continuous soil respiration and moss photosynthesis measurements were made with automated clear chambers during the fall of 1995 and the 1996 growing season [Goulden and Crill, 1997].

3. Ecosystem Model Comparison Approach

Our study approach consists of three main steps: (1) Generate and distribute a common data set of hourly NSA-OBS meteorological variables for the 1996 test (see Amthor et al. [this issue], for methods and results); (2) define a common set of site input parameter values (over storey, ground cover, soils) from published sources on the NSA-OBS tower site (Table 1); and (3) compare the sensitivity of ecosystem models to perturbations in climate drivers and site parameter values, using a common set of diagnostic variables for latent heat fluxes (LE) and ecosystem carbon fluxes.

The models selected by NASA peer review for BOREAS follow-on model analysis and, subsequently, compared in this study were BEPS [Liu et al., 1997; Chen et al., 1999], BGC [Kimball et al., 1997a], CLASS [Verseghy, 1991, 1993; Wang, 2000], Ecosys [Grant et al., 1999], FORFLUX [Nikolov, 1997; Zeller and Nikolov, 2000], LoTEC [King et al., 1997; Post et al., 1997], NASA-CASA [Potter, 1997; Potter et al., 2001], SPAM [Frolking et al., 1996; Frolking, 1997], and TEM [McGuire et al., 1997, 2000]. A detailed description, levels of detail, and documentation of the nine models is provided in a companion paper by Amthor et al. [this issue; Table 1]. The most relevant model attributes for our sensitivity simulations can be summarized in terms of plant production algorithms, soil algorithms, methods of parameterization, and time step. Specifically, one group of models (BEPS, BGC, CLASS, Ecosys, FORFLUX, and LoTEC) uses the Farquhar photosynthesis algorithm for leaf-level carbon assimilation [Farquhar and von Caemmerer, 1982], whereas another group of models (NASA-CASA, SPAM, and TEM) uses calibrated scalar functions simulating effects of solar irradiance, air temperature, atmospheric CO_2 concentration (TEM only), moisture availability, and nitrogen supply to adjust plant production rates. Several models (CLASS, Ecosys, NASA-CASA, and SPAM) include separate components for moss ground cover production. With respect to soil decomposition, all nine models account for effects of temperature and moisture on soil CO_2 production, and a subset of models (CLASS, Ecosys, NASA-CASA, and TEM) include soil nitrogen cycling. One group (BEPS, BGC, CLASS, LoTEC, FORFLUX, NASA-CASA, SPAM, and TEM) uses first-order (i.e., carbon substrate-limited) rate dynamics, whereas FORFLUX uses zero-order rate dynamics, and Ecosys uses microbial kinetics algorithms. Another major distinction in terms of parameterization is between models which compute seasonal plant phenology based on internal climate-based algorithms (CLASS, Ecosys), compared to NASA-CASA, which uses the satellite measured "greenness index" from the advanced very high resolution radiometer (AVHRR), compared to those that use a prescribed phenology for the site (all others). A subset of models (BEPS, BGC, CLASS, LoTEC, NASA-CASA, and

Table 1. Baseline Parameter Values for NSA-OBS Simulations

Parameter	Value	Units	Reference
Overstory - black spruce			
leaf nitrogen	0 7	%	*Middleton et al.* [1997]
leaf lignin	28.2	%	
maximum stomatal conductance	1 0	mm s^{-1}	*Saugier et al.* [1997], *Dang et al.* [1997]
maximum C fixation efficiency	0.4	g C MJ^{-1}	*Goetz and Prince* [1996, 1998]
maximum LAI	4.0	m^2 m^{-2}	*Chen et al.* [1997]
total clumping index	0 5		*Chen et al.* [1997]
specific leaf area	0.01	m^2 g^{-1} C	*Middleton et al.* [1997]
rooting depth	0.5	m	*Steele et al* [1997]
Ground cover – feather moss			
nitrogen content	2.2	%	*Harden et al* [1997]
thickness	0.03	m	*Harden et al.* [1997]
bulk density	0.03	g cm^{-3}	*Harden et al.* [1997]
Organic horizon			
thickness	0.3	m	*Harden et al.* [1997]
bulk density	0 1	g cm^{-3}	*Harden et al.* [1997]
water holding capacity	3.5	g g^{-1} dry	*Frolking et al.* [1996]
Mineral soil			
bulk density	0.8	g cm^{-3}	*Burke et al.* [1997]
sand silt:clay	26:29:45	%	*Burke et al.* [1997]
minimum water content	22	cm^3 cm^{-3}	*Frolking et al.* [1996]
field capacity water content	36	cm^3 cm^{-3}	*Frolking et al.* [1996]
porosity	45	cm^3 cm^{-3}	*Frolking et al.* [1996]
depth to permafrost	0 5	m	*Trumbore and Harden* [1997]
C:N ratio	25		*Harden et al.* [1997]

TEM) are designed to be run on extensive regional grids, whereas the other models are site-specific. In terms of model time steps, CLASS uses 30 min., Ecosys, FORFLUX, and LoTEC (canopy) are hourly models, BEPS, BGC, LoTEC (biomass and soil), NASA-CASA, and SPAM are daily models, and TEM is monthly.

A series of sensitivity simulations was performed with each ecosystem model by changing a single driver or site parameter value in separate model runs. Table 2 lists the perturbations (in percent) used for each input parameter. Models were initialized with values for standing plant biomass and soil organic matter [*Amthor et al*, this issue], and each was run for 1 year with the same set of NSA-OBS climate drivers starting January 1, 1996. Individual model adjustments were made for inputs to match the required simulation time step of an hour, a day, or a month.

Results from all models were compared using annual estimates of a set of standardized diagnostic variables. These diagnostic variables included gross primary production (GPP), net primary production (NPP), autotrophic respiration (Raut), heterotrophic respiration (Rh), and evapotranspiration (ET) (including LE flux from overstory and understory plants). Net ecosystem production (NEP) was computed as a secondary diagnostic variable, from the difference of either GPP-(Raut+Rh) or NPP-Rh. We note that GPP is defined as gross photosynthesis (excluding plant "dark" respiration). Plant maintenance respiration was included as part of total Raut estimates.

It is important to note that the individual sensitivity runs were not intended to be modeling scenario studies, which may be defined as using physically consistent, simultaneous change or variation in all driver or site parameters. For example, we did not attempt to link changes in a certain driver

parameter (e.g., incoming solar radiation) to changes in a potentially related parameter (e.g., air surface temperature). Results from these types of actual climate runs are instead reported in a companion modeling paper with eddy covariance measurements [*Amthor et al.*, this issue], which focuses on understanding and comparing interannual variability in model responses using physically consistent (measured) driver data sets.

For this paper the variations in single model drivers in our sensitivity runs were prescribed principally to be large enough to identify and isolate any major differences in model responses, while also remaining within the range of long-term variability that the boreal forest ecosystem may be exposed to over a time period of about 50 to 100 years [*Kattenberg et al.*, 1996; *Kirschbaum et al.*, 1996]. For example, in prescribing the variability in climate driver values for these sensitivity

Table 2. Settings for Sensitivity Simulations

Parameter and Abbreviation	Value Change
Drivers	
mean air temperature (*Ta*)	±2°C
precipitation rate (*Pt*)	±50%
incoming solar radiation (Srad)	±10%
dew point temperature (*Td*)	±2°C
atmospheric CO_2 concentration (CO_2)	±100 ppm
Site parameters	
leaf area index (LAI)	±50%
leaf clumping (Ω)	-40%, +100%
max. stomatal conductance (*Gs*)	-50%, +100%
leaf nitrogen content (*Ln*)	±50%
sap wood nitrogen content (*Wn*)	±50%
organic horizon thickness and C content (*Oc*)	±50%

simulations (Table 2), we reviewed the range of 1975-1995 data from the Canadian Atmospheric Environment Service (AES) weather station at the Thompson, Manitoba, airport (55.48°N latitude, 97.52°W longitude, 215 m).

Similarly, changes in OBS site parameters for the models were made independently of changes in climate driver parameters and were presumed to be large enough to illustrate major model differences. Variability of site parameters for these sensitivity simulations was determined in part from observed variability in wet conifer stand characteristics across regional transects of boreal forest sites [e.g., *Halliwell et al.,* 1995]. Plant and soil site parameters for sensitivity simulations were chosen to represent important structural and functional attributes of the NSA-OBS stand, which in certain ecosystem models are set as constant values to include as physical controls over carbon and water fluxes in the plants and soil.

For example, one of the important site parameters selected for evaluation was leaf area index (LAI). LAI is a common measure of vegetation leaf density, defined as one half of the total (all sided) area of foliage projected over a unit area of ground. LAI is recognized as a critical structural parameter of terrestrial vegetation regulating the exchange of trace gases and energy between land surface and the atmosphere [*Leverenz and Hinckley,* 1990]. Remote sensing methods have been evaluated extensively to determine LAI from satellite imagery over the entire NSA [*Chen et al.,* 1997], making this a valuable measurement for extrapolation of model results to regional scales.

A related parameter, the leaf clumping index (Ω) [*Chen et al.,* 1997], is a measure of the spatial aggregation of foliage in the canopy. Assumptions of random foliage distributions in boreal forests are invalid and could yield erroneous values of LAI measured by indirect techniques and false characterizations of atmosphere–biosphere interactions [*Kucharik et al.,* 1999]. This clumping index equals unity for uniformly distributed leaves, while $\Omega < 1.0$ for clumped canopies. Thus at the NSA-OBS site, Ω was measured to be 0.5 using an optical instrument based on a gap size distribution theory [*Chen,* 1996]. Assessment of Ω is important because clumping strongly affects the canopy absorption of light and the distribution of the captured light among sunlit and shaded leaves. Foliage clustering is an important feature of boreal spruce forests controlling PAR absorption due to the low Sun angles and frequent cloudiness which increase the proportion of diffuse radiation penetrating the canopy [*Wang and Jarvis,* 1990].

The model setting for maximum stomatal conductance (*Gs*) is another key parameter controlling the potential rate of carbon assimilation and transpiration from vegetation. Stomatal conductance is typically calculated from transpiration rates and the water vapor gradient between the leaf intercellular space and the surrounding air. In the commonly used Ball-Berry approach for leaf conductance, *Gs* is related functionally to CO_2 assimilation rate, CO_2 concentration, and humidity at the leaf surface [*Ball et al.,* 1987]. Plant parameters closely associated with *Gs* include leaf and sap wood nitrogen contents (*Ln* and *Wn*), which can play important roles in regulating potential rates of photosynthesis [*Field and Mooney,* 1986; *Dang et al.,* 1997], and may also affect plant respiration rates and decomposition of plant litter [*Gower et al.,* 1996]. Compared to other forest types, boreal spruce forests are generally described as being chronically N-deficient in terms of slow release of N for plant uptake from cold, waterlogged *soils* [*Mahli et al.,* 1999].

To further assess the coupling of soil parameters to predicted ecosystem fluxes, we included a sensitivity simulation to alter the thickness of the soil organic horizon and its associated carbon content. Unlike temperate or tropical forest ecosystems, the NSA-OBS site has a highly developed peaty soil horizon that overlies the mineral soil [*Harden et al.,* 1997]. Altering the organic horizon in sensitivity runs permits comparison of model responses to variations in total water holding capacity (related to drainage) of the upper soil layers, potential accumulation rates of soil organic carbon, and the carbon substrate pool available for microbial decomposition leading to annual Rh flux predictions. Because ground cover and the organic soil layer are variable over small spatial distances in boreal spruce forests, a feature found to be related to canopy density at the NSA [*Goulden and Crill,* 1997], it is important to evaluate the sensitivity of model responses to this parameter.

In a related manner we note that the models differed in their reliance on site data for initialization. Some made use of measured values for C pools in vegetation and soils, whereas others generated these pools during long-term simulation runs under historical climate conditions. None of the models were expressly forced to a NEP of zero before starting the 1996 sensitivity runs, mainly because carbon cycle is slow in the boreal forest and contemporary sinks may result from the accumulated effects of long-term climate and atmospheric changes. However, in an attempt to standardize the procedure for a long-term simulation approach to initialization of model conditions, baseline plant and soil carbon contents were established whenever possible by driving models with historical climate data for the NSA location and then cycling through the NSA-OBS 1994-1996 climate driver sequence [see *Amthor et al.,* this issue] prior to baseline simulations for 1996. Where otherwise required, reported literature values (e.g., *Gower et al.* [1997] and others in Table 1) were used to initialize biomass and litter/soil C pools.

We anticipate that these initial model conditions could be an important factor in determining model responses to changing input parameters. Incipient model pools for the plant canopy, standing wood, and soil carbon inherently represent the effects of past conditions of climate and the time since the last major disturbance on baseline simulation results. Each model compared in this paper used a somewhat different method to represent site growth history and any persistent effects of past disturbance on large carbon pools in the ecosystem leading into the sensitivity simulations. Therefore we attempted to evaluate the importance of initial model conditions on annual carbon and water fluxes by conducting an additional set of sensitivity simulations using ± 50% standing wood carbon and soil carbon content, relative to the baseline model settings.

4. Model Sensitivity Results

Simulation results were generated by all models for as many sensitivity parameters (listed in Table 2) as could be altered readily in the individual model structures. In some cases, altering a site parameter for sensitivity simulations could not be accomplished with the simple manipulation of a constant value in the model, because the models internally calculated the parameter value. Consequently, wherever a site

Table 3. Baseline Results for Diagnostic Model Variables in 1996 NSA-OBS Simulations

Model	GPP g C m^{-2} yr^{-1}	NPP g C m^{-2} yr^{-1}	Raut g C m^{-2} yr^{-1}	Rh g C m^{-2} yr^{-1}	Rsoil g C m^{-2} yr^{-1}	NEP g C m^{-2} yr^{-1}	ET mm yr^{-1}
BEPS	713	227	487	211	402	20	221
BGC	741	145	596	137	447	7	203
CLASS	805	201	604	156	383	45	291
Ecosys	775	286	489	226	357	61	344
FORFLUX	654	176	477	142	209	34	380
LoTec	1025	290	735	264	627	26	317
NASA-CASA	NA	226	NA	202	354	24	264
SPAM	645	142	503	130	442	13	254
TEM	880	105	774	116	472	-11	278
Average	780	200	583	176	431	24	280
CV	0.16	0.32	0 20	0 29	0.25	0 87	0.19

From *Amthor et al.* [this issue]. GPP, gross primary production; NPP, net primary production; Raut, total autotrophic respiration; Rh, heterotrophic soil respiration; Rsoil, total soil respiration (Rroots plus Rh); NEP, net ecosystem production; ET, evapotranspiration (overstory plus understory); NA, not applicable to model. CV, coefficient of variation.

parameter was computed in the model internally as a function of other important structural and functional variables, simulation results were not generated for comparison to other models.

Baseline diagnostic results for 1996 are provided in Table 3. The mean predicted ratio of GPP to NPP is about 4, a value generally consistent with the previous measurement-based estimates for coniferous evergreen forests [*Ryan et al.*, 1997; *Amthor*, 2000]. Short growing seasons, nutrient-limited environments, and slow carbon assimilation rates tend to favor slower growth, larger below:above ground allocation, and relatively greater respiration costs, leading to high GPP:NPP ratios.

4.1. Mean Air Temperature (*Ta*)

As a general trend, modeled GPP, Raut, Rh, and ET fluxes commonly increase with 2°C higher *Ta* and decrease with 2°C

lower *Ta* (Figure 1). Changes in growing season length and early season plant carbon gain with temperature variation can explain this trend to some extent. For example, in frozen soils, common model controls will restrict root uptake of water and thereby limit plant carbon uptake, regardless of available solar radiation fluxes to drive photosynthesis. Small changes in evergreen plant phenology (i.e., seasonal leaf cover) in some models (i.e., CLASS, FORFLUX, Ecosys, and SPAM) is also directly affected by changes in *Ta* or photoperiod over the year, although model settings for multiyear spruce needle retention may reduce these effects on the selected diagnostic variables.

Another explanation for the common responses to temperature is that modeled Raut appears to be more sensitive to consistently higher *Ta* than GPP, probably because GPP is generally modeled as a function of other important limiting factors such as water and nutrient availability, whereas the
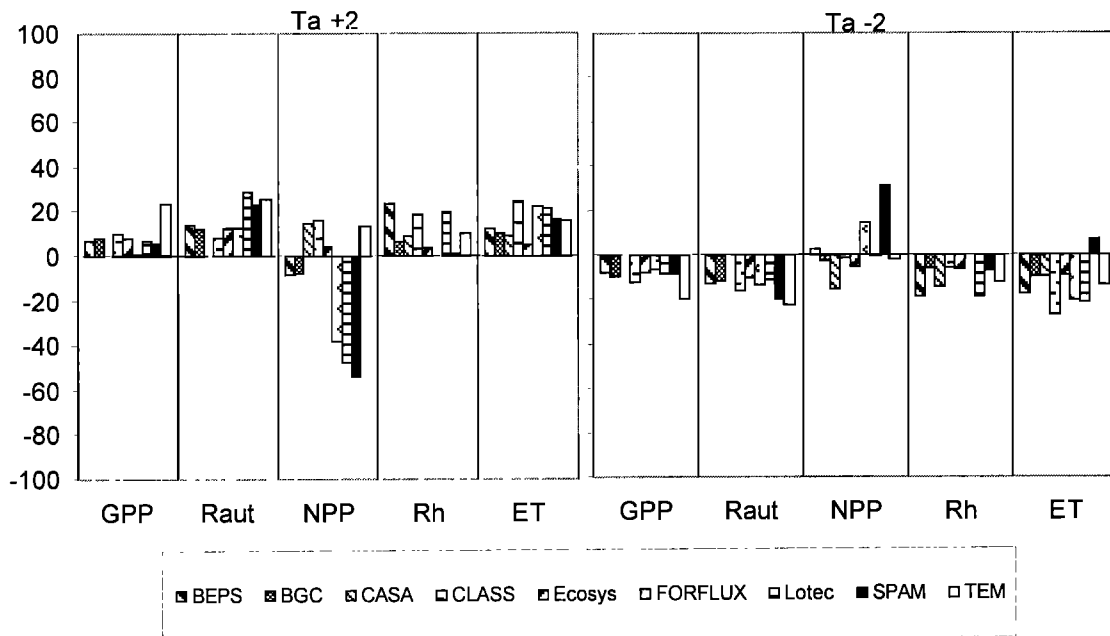
Figure 1. Percent change in model response to climate driver values.

Raut is commonly modeled as being mainly responsive to temperature.

This begins to explain why, among the model diagnostic variables, NPP stands out as one that may increase or decrease with uniformly higher Ta. NPP decreases in model response to higher Ta if Raut sensitivity to temperature is greater than GPP sensitivity (BEPS, BGC, FORFLUX, LoTEC, SPAM). At higher Ta, NPP increases in model responses (i.e., CLASS, Ecosys, and TEM) with higher temperature sensitivity of GPP to increased short-term soil N availability (resulting from faster litter decomposition rates) and elevated plant N uptake.

In NASA-CASA, NPP increases nonlinearly with higher Ta as the result of a greater number of days during the growing season for which the site-calibrated optimal temperature for NPP (23°C) is approached. The SPAM response for NPP is also nonlinear for temperatures between about 5° and 25°C. We expect that these nonlinear model functions would have produced somewhat different results if, for example, Ta were not increased uniformly over the entire year but only during spring months.

It is noteworthy that in BEPS and NASA-CASA, soil-nutrient changes do not affect productivity significantly over a yearly time period. Nitrogen enhancement (increased soil N uptake) effects on modeled NPP, if any, may not be realized until 1-2 years after soil N availability has increased with higher temperatures.

All models show a similar response of predicted higher Rh to the prescribed increase in Ta. However, the magnitude of model Rh responses to Ta vary, for example, according to changes in predicted heat fluxes throughout the soil profile. Responses to changing Ta also depend on how a model simulates snowpack dynamics, or does not include such dynamics (i.e., LoTEC). Results from models that include snow accumulation and melt components generally indicate that the altered timing of snowmelt in spring can have a significant impact on soil temperature profiles and associated changes in annual Rh fluxes. Earlier predicted snowmelt dates with increased Ta result in faster thawing of frozen soils, more rapid changes in soil moisture content, and higher Rh fluxes for the first half of the year.

When increases in predicted Rh with higher Ta are examined on a 3-month seasonal basis, it appears that consistently warmer conditions throughout the year increase soil CO_2 fluxes from microbial activity estimated by some models more during the cold winter (DJF) or the spring (MAM) period than during the summer (JJA) period. The model Rh responses to soil temperature depend on the function used to control microbial activity and the sensitivity of this function at lower temperatures. At low Ta, a 2° increase can significantly boost Rh in relative terms, although its absolute flux rate may remain smaller than estimated during high temperatures of midsummer. However, in Ecosys, for example, this winter and spring temperature effect on soil CO_2 fluxes was constrained by the need to thaw soil before soil temperatures rise.

In most models the ET response to temperature generally follows those of GPP, Raut, and Rh in terms of direction and magnitude. Uniform change in Ta across each time step has a direct effect on predicted annual ET, either through common responses in the Penman-Monteith equation or energy balance calculations for latent heat fluxes. For SPAM, annual ET can increase with lower Ta, which for now remains as a spurious result restricted to winter time calculations.

4.2 Precipitation Rate (Pt)

Most of the ecosystem models are more sensitive to a prescribed 50% decrease in Pt than to a 50% increase in Pt (Figure 2), probably because the NSA-OBS site is not normally affected by severe water limitations in 1996, as suggested in the baseline model results for ET fluxes (Table 3). Models predict a consistent 10-20% reduction in annual water losses from plants and soils in response to 50% lower Pt.
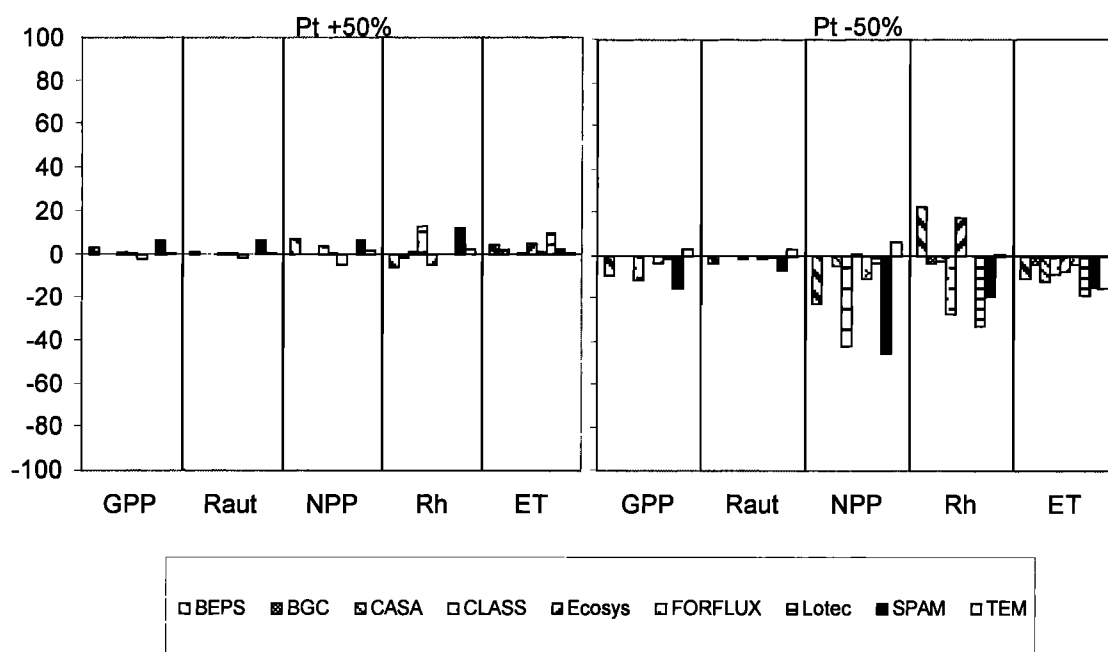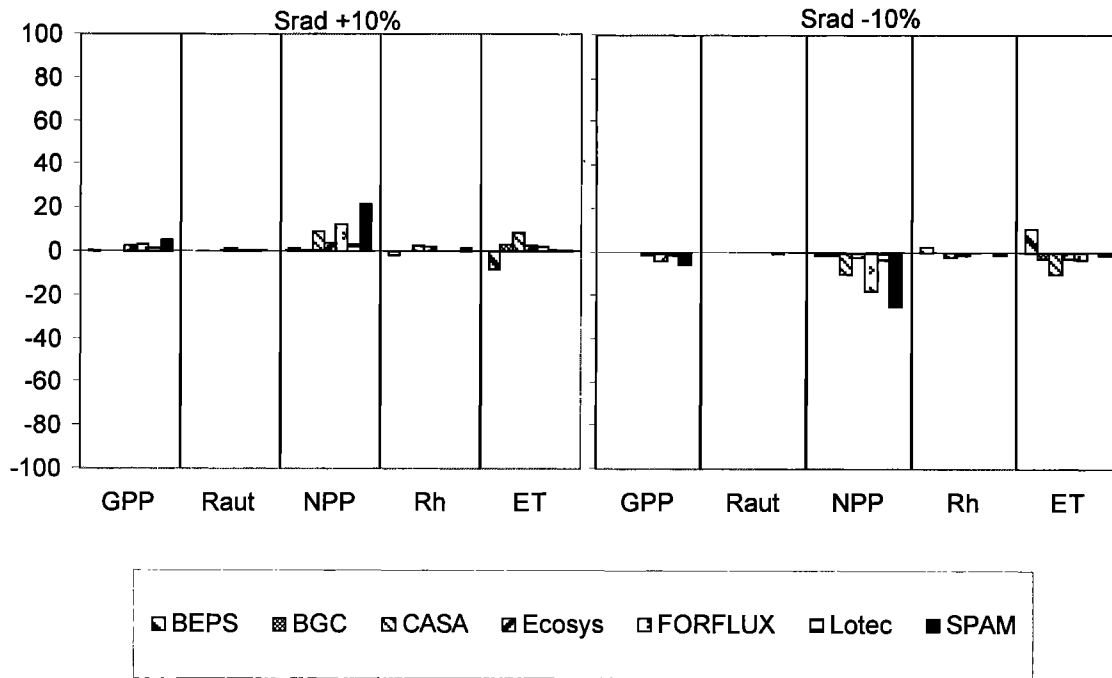

Figure 2. Same as Figure 1.

Figure 3. Same as Figure 1.

Lower *Pt* generally affects annual NPP more strongly than the other diagnostic model variables, with NPP decreasing up to 50%. However, an exception was noted for TEM results, where lower *Pt* (and therefore less snow fall) leads to earlier snowmelt and early onset of the growing season, which increases annual GPP and NPP. Lower soil moisture availability generally reduces plant carbon uptake due to stomatal closure in the models. Reductions in model GPP and NPP with lower *Pt* are also explained on a seasonal basis, showing that consistently drier conditions throughout the year reduce plant carbon gains estimated by the models more during the warm summer months than during the spring.

In SPAM, GPP and Raut responses were more sensitive to higher *Pt* compared to other models. This increase in GPP is due to both an increase in moss GPP occasionally throughout the summer due to generally wetter soil conditions (moss photosynthesis requires adequate moisture), and an occasional increase in spruce GPP during otherwise longer dry spells. Likewise, predicted moss respiration is moisture sensitive, and increases under wetter model conditions. SPAM predicts that the soil surface rarely becomes wet enough to inhibit moss metabolism or dead organic matter decomposition.

Among the selected diagnostic variables, Rh is relatively sensitive to increased *Pt*, because some decomposition response functions in the models (e.g., BEPS and Ecosys) run significantly slower under more saturated soil water conditions when oxygen availability then limits microbial activity. Decomposition response functions run faster as soil water increases in other models (e.g., CLASS and SPAM). The importance of these divergent model responses are discussed further under the section below on comparison of model NEP fluxes.

4.3. Incoming Solar Radiation (Srad)

As a general trend, modeled GPP, NPP, and ET commonly increase with higher Srad and decrease under lower Srad

(Figure 3). Increases in predicted GPP and NPP under higher Srad can be explained on a seasonal basis (comparing results from spring versus summer), showing that consistently sunnier conditions throughout the year increase estimated plant carbon gains by the models more during the spring than during the summer. In models using the Farquhar biochemical equations, the light response curve of photosynthesis is almost linear at low light levels typical of springtime when Srad is presumed to be the limiting factor to photosynthesis. The light response curve becomes saturated at higher light levels when carboxylation capacity (and N concentration) is presumed to be limiting. Therefore a change to higher Srad early in the growing season has a greater effect than during the middle of the growing season.

In general, Raut and Rh are not highly sensitive to Srad. For Ecosys, this is because net carbon fixation (NPP and NEP) is controlled strongly by soil nitrogen availability. In other models (such as NASA-CASA and SPAM), which do not compute full surface energy balance, changes in Srad only affect the response of photosynthesis to light and have no influence on the leaf-surface and ground-surface temperatures.

As with the model responses to higher *Ta*, uniform change in Srad has a direct effect on annual ET, either through common responses in the Penman-Monteith equation or energy balance calculations for latent heat fluxes. However, in BEPS, ET can decrease with higher Srad and increase with the lower Srad prescribed. This is due to a simulated soil water limitation, under conditions when the moss layer is predicted to dry out rapidly and tree roots can no longer obtain enough water to maintain transpiration fluxes.

4.4. Dew Point Temperature (*Td*)

Model responses to changes in *Td* are consistent in direction and magnitude, showing increases in GPP and NPP, and decreases in ET and Rh with higher *Td* (Figure 4).
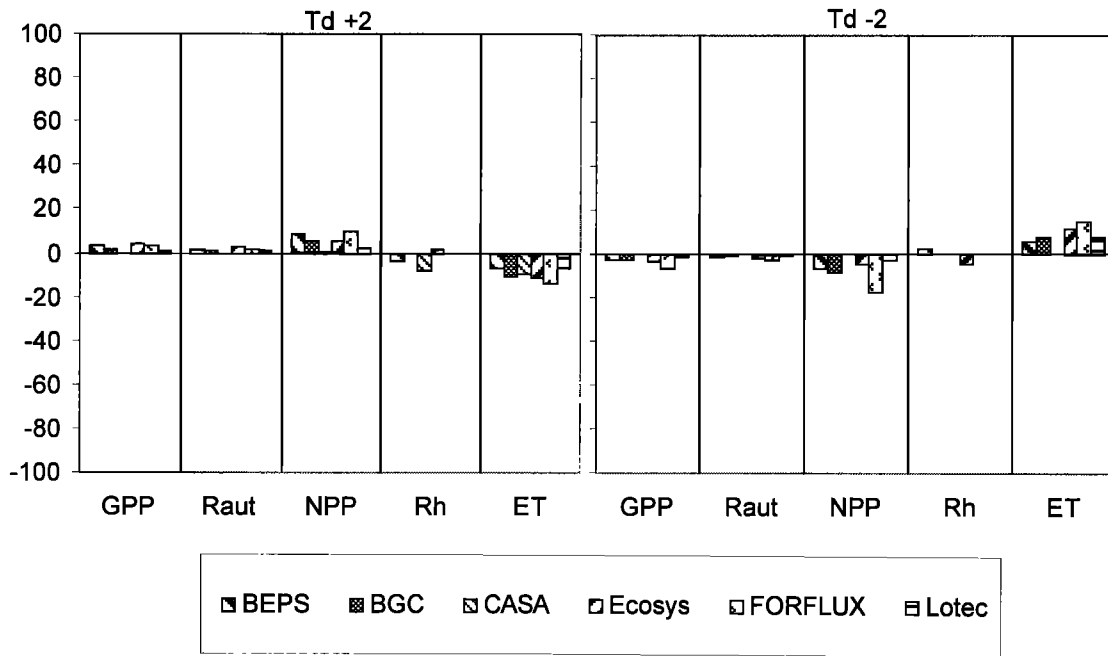
Figure 4. Same as Figure 1.

Conversely, with lower Td, modeled GPP and NPP decrease, whereas ET and Rh fluxes increase. The common explanation appears to be that predicted water stress on plant production is eased somewhat under higher Td and its associated reduction in vapor pressure deficit generated by the modeled leaf physiology. When predicted ET decreases under conditions of higher Td, soil moisture levels can increase slightly, which generally slows soil decomposition and Rh fluxes in the models. On the basis of seasonal patterns of relative humidity actually being lowest in late spring-early summer at this BOREAS site [*Pauwels et al.,*

2001], we would expect the greatest changes in NPP, Rh, and ET due to daily fluctuations in Td to be predicted during the months of April-June.

4.5. Atmospheric CO_2 Concentration (CO_2)

Modeled GPP, Raut, NPP, and Rh commonly increase with 100 ppm higher CO_2 and decrease with 100 ppm lower CO_2 (Figure 5). One explanation is that models that use the Farquhar algorithm (e.g., BEPS, BGC, CLASS, Ecosys, FORFLUX, LoTEC) demonstrate similar sensitivity responses to CO_2. In these models, uniform changes in
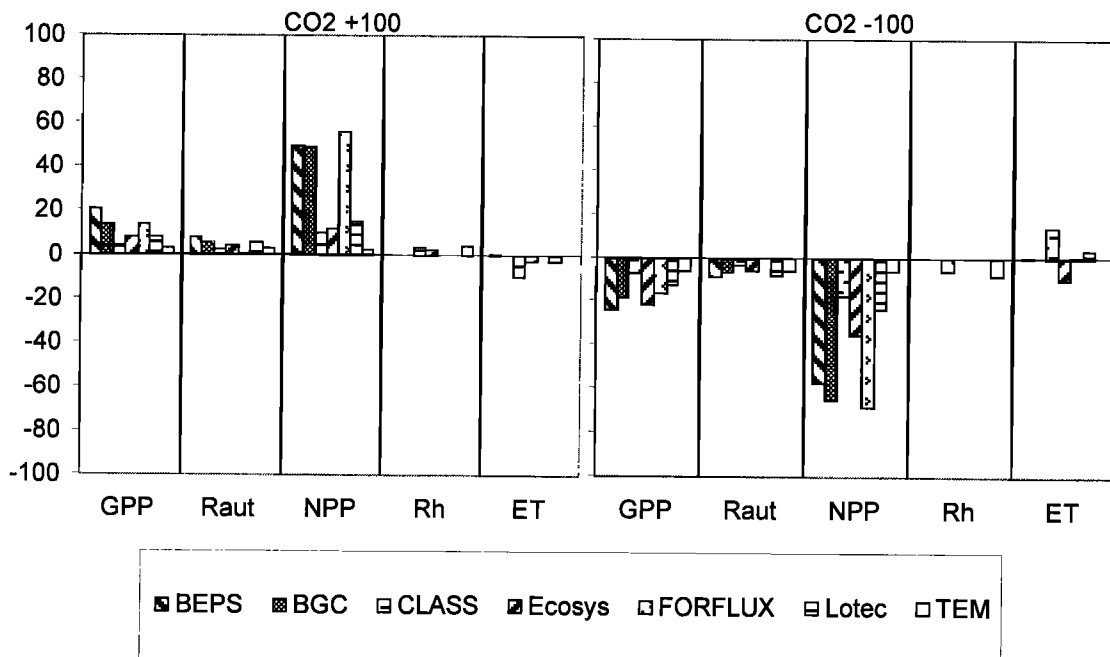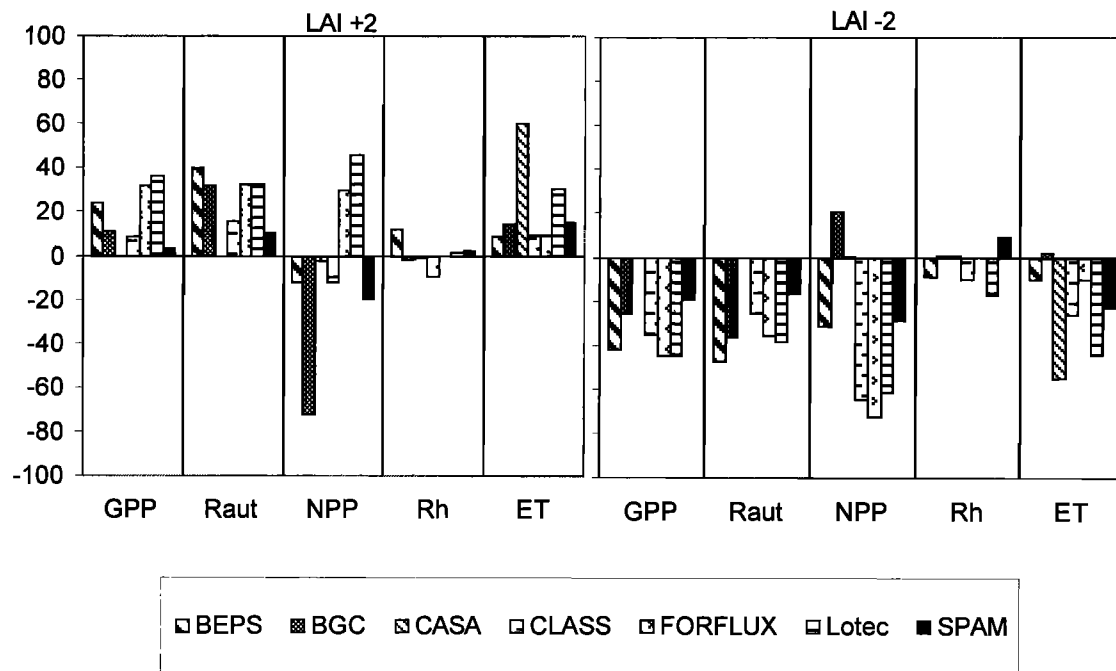

Figure 5. Same as Figure 1.

Figure 6. Percent change in model response to site parameter values.

ambient CO_2 concentration strongly affect GPP through Michaelis-Menten kinetics and Ball-Berry stomatal controls of leaf photosynthesis. A growth response to elevated CO_2 should be reflected in the growth respiration component of Raut [*Penning de Vries et al.*, 1974]. In CLASS, a second-order effect of elevated CO_2 is higher maintenance respiration due to the higher plant biomass from the increased NPP and growth.

By way of further explanation, plant respiration rates are modeled with high sensitivity mainly to temperature and moisture. Thus variations in CO_2 alone can result in large changes in GPP but very little change in respiration rates, resulting in large changes in NPP. This type of strong model response to changing CO_2 is seen clearly in the results for BEPS, BGC, and FORFLUX. ET in most models decreases with higher CO_2 due to stomatal closure, and increases under lower CO_2, due to stomatal opening. Modeled Rh commonly is the least sensitive variable to CO_2 change.

4.6. Leaf Area Index (LAI)

Modeled GPP, Raut, and ET commonly increase with two units higher LAI and decrease with two units lower LAI (Figure 6). NPP is simulated to either increase or decrease under higher LAI. An explanation for this inconsistency among models is that in two models, higher LAI automatically triggers increased sapwood and root respiration rates. This is the case for BEPS and BGC, which use fixed allometric relationships to derive sapwood and root carbon pools from LAI. Changes in LAI therefore result in proportional changes in sapwood and root biomass. Lower LAI results in lower GPP but also lowered maintenance respiration rates because of less root and sapwood biomass. Predicted NPP can increase with lower LAI because reductions in maintenance respiration rates were proportionally larger than reductions in GPP.

In NASA-CASA and SPAM, LAI can be changed independently of root and sapwood biomass. In SPAM the effect is for higher LAI to add needles to the bottom of the canopy, where they have marginal photosynthetic gains and normal respiration costs. These newly added leaves can increase shading of the moss ground cover, reducing its predicted GPP. In contrast, lower LAI can reduce canopy transpiration fluxes, so that the organic soil layers below the living moss are somewhat wetter and predicted heterotrophic respiration is enhanced. SPAM does not take into account increased insolation and resultant drying that might occur with reduced LAI.

In the LoTEC and FORFLUX models, the increase in GPP (canopy photosynthesis) in response to higher LAI is greater than the increase in leaf maintenance respiration. Other components of Raut are largely unaffected by increased LAI; hence the increase in GPP results in an increase in NPP. In LoTEC the relative sensitivity of GPP is relatively large compared to the other models, perhaps as a consequence of this "big leaf" nitrogen form of the model. A big leaf model assumes, as a simplifying approximation, that the entire canopy can be treated as a single extended leaf. The high GPP baseline from LoTEC could be a consequence of a tendency to parameterize the "big leaf" with leaf nitrogen values characteristic of sunlit leaves, and hence the leaf nitrogen parameter that is used to calculate canopy photosynthetic capacity (Vc_{max}) may not be appropriately weighted for the distribution of nitrogen in the canopy. Over the range of LAI tested, canopy GPP from LoTEC scales approximately linearly with LAI. Thus a relatively large increase in LAI yields a relatively large increase in GPP.

In the NASA-CASA model, the ET sensitivity to higher LAI appears to be related to a lateral water routing feature, which should provide a higher water supply potential for ET fluxes than in other models. Water table is simulated by NASA-CASA and maintained near the surface (25 cm depth),
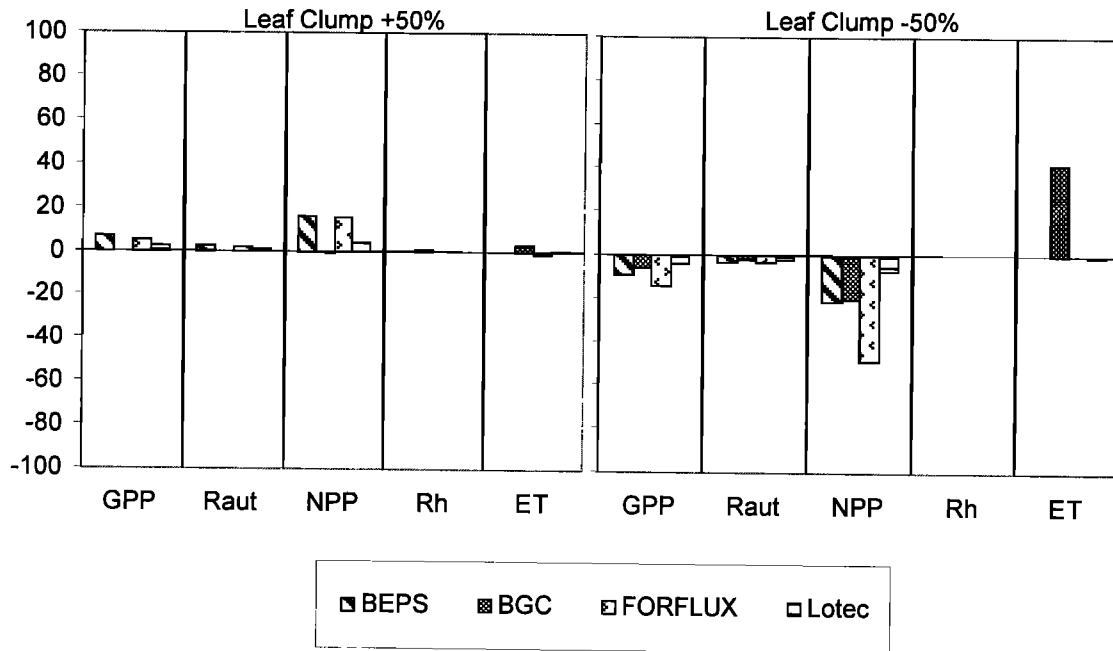
Figure 7. Same as Figure 6.

in agreement with measurements at NSA-OBS site [*Moosavi and Crill,* 1997], by simulating lateral water run-on and runoff from surrounding ecosystem areas. Under conditions of higher LAI for the site, spruce trees are predicted to take advantage of this elevated water table supply of moisture through enhanced ET fluxes.

These tests of uniform changes in LAI on model results for GPP and NPP are particularly relevant to the issue raised in our companion paper, *Amthor et al.* [this issue], concerning the initialization of models with settings that represent some of the most productive areas of the NSA-OBS tower footprint. If instead the models had used a uniform LAI value of 2,

rather than LAI of 4 as their baseline setting, then it appears that many (e.g., BEPS, CLASS, FORFLUX, LoTEC, NASA-CASA, SPAM) would estimate lower NPP for the tower area and some probably would show lower overall errors in matching net carbon exchange measured at the tower on a daily basis.

4.7. Leaf Clumping (Ω)

Models are more sensitive to the prescribed decrease in Ω than to the prescribed increase in Ω (Figure 7), probably because the "baseline" value of 0.5 for Ω (Table 1) is already fairly high within the range of most model response functions.
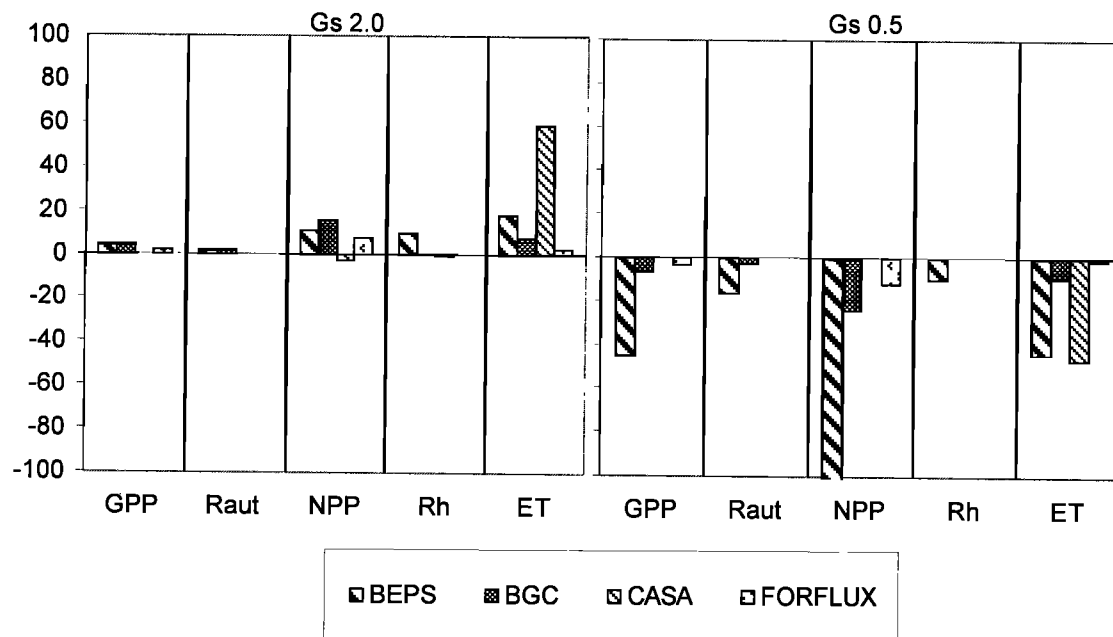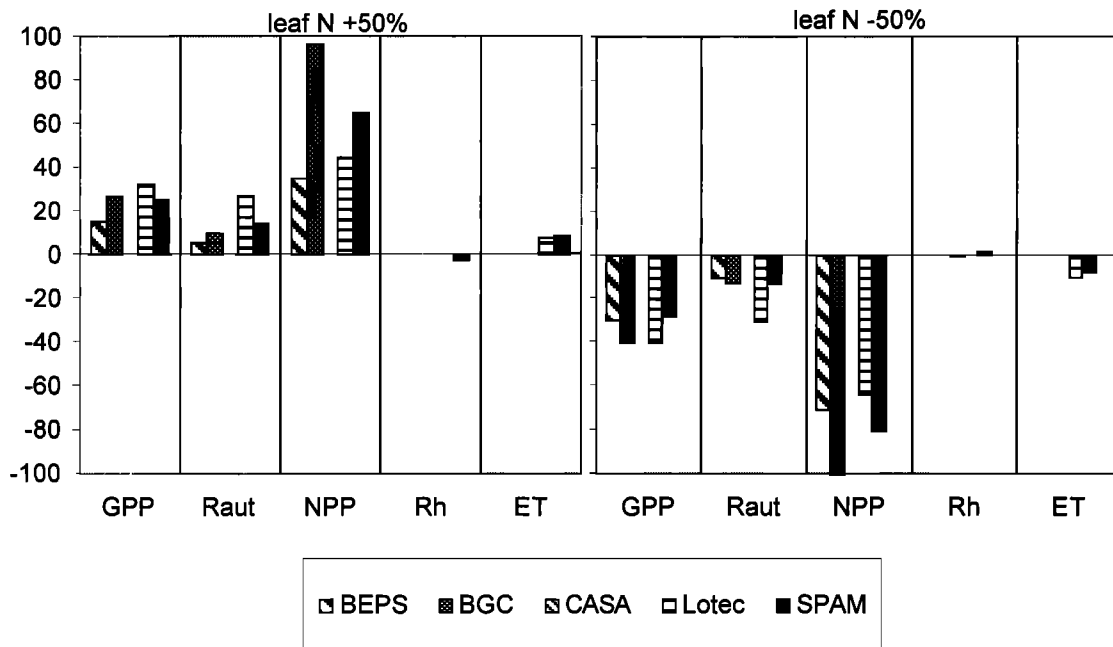

Figure 8. Same as Figure 6.

Figure 9. Same as Figure 6.

Lower Ω commonly results in lower modeled GPP, Raut, NPP, and ET, mainly because the models predict lower light interception rates in the forest canopy. However, none of the models using Ω as an input parameter also simulate moss productivity at the ground surface, which could compensate for reduced canopy production at lower Ω, assuming a higher radiation flux reaches the ground surface.

In BGC and FORFLUX, less canopy interception of radiation with lower Ω means that more radiation is available to evaporate water from the ground cover surface and soil. Moreover, predicted transpiration is typically only about 18-45% of the modeled annual ET flux at this site (Table 3). Hence reduced canopy interception of light due to lower Ω results in a decrease of transpiration flux but a proportionally larger increase in evaporation from the soil surface and therefore a net increase in modeled ET flux. This might be explained by a weaker dependence of transpiration on radiation compared to soil evaporation, because transpiration depends also on humidity levels.

4.8. Maximum Stomatal Conductance (Gs)

Model GPP, Raut, NPP, Rh, and ET commonly increase with higher Gs and decrease with lower Gs (Figure 8). This consistent pattern is explained by most models having strong controls over leaf gas exchange by stomatal opening and closing. BEPS and NASA-CASA are particularly sensitive to changes in Gs. This may be a general attribute of models requiring an external setting of the maximum Gs, rather than an internal calculation based on physiological principles.

4.9. Leaf Nitrogen (Ln) and Sap Wood Nitrogen (Wn) Content

Model GPP, Raut, NPP, and Rh (and ET, to a lesser degree) commonly increase with 50% higher leaf or sap wood N and decrease with lower N (Figure 9). This pattern is explained by the models having important nitrogen limitation functions influencing carbon assimilation rates.

For example, in SPAM, GPP is directly correlated to Ln, and foliar respiration is directly correlated to GPP. However, root and sap wood respiration account for roughly half of total Raut (mostly roots), and since these do not change with Ln, Raut is less sensitive to Ln than GPP. Likewise, in the BGC model, temperature and moisture are the primary controls on Raut, so changes in Ln alone have little effect on plant respiration. GPP, however, is highly sensitive to Ln due to the large response of carboxylation velocities and assimilation rates to Ln in the standard Farquhar equation. These effects give a high overall NPP sensitivity to Ln settings in BGC and SPAM.

We note that in most of the ecosystem models compared here, the distribution of Ln in canopies was assumed to be vertically uniform. If instead the upper (sunlit) canopy leaves are allocated higher Ln than the lower (shaded) leaves in the models, even more nonlinear responses might be expected. This is the case in Ecosys, which remobilizes N continuously from lower canopy leaves to upper canopy leaves.

4.10. Organic Horizon Thickness and C Content (Oc)

Model Rh is the main variable with high sensitivity to changes in the thickness of the surface organic layer (Figure 10). Model Rh (and ET, to a lesser degree) commonly increase with 50% higher organic layer thickness and decrease with 50% lower organic layer thickness. This pattern is explained in BGC, NASA-CASA, and SPAM as having strong primary controls over microbial activity (and hence predicted Rh fluxes) by carbon substrate availability and important secondary controls by water-holding capacity in the surface organic layer.

5. Changes in Net Ecosystem Production (NEP)

We examined the response of NEP separately from that of other diagnostic variables, mainly because NEP is the net result of several primary ecosystem carbon fluxes, and hence
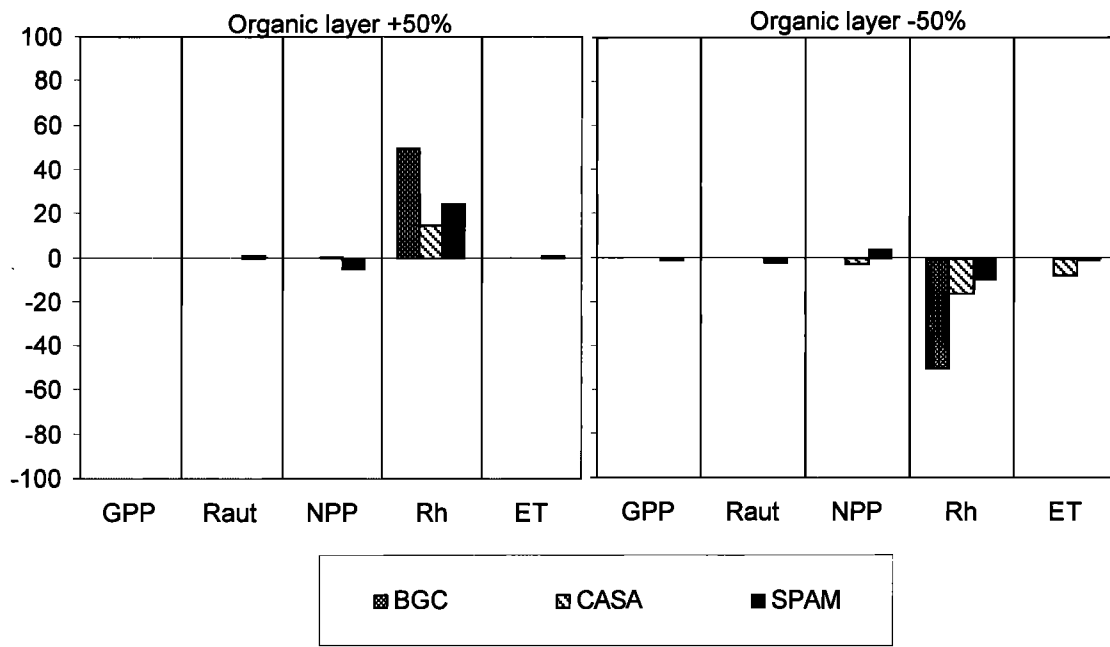
Figure 10. Same as Figure 6.

is more complex to interpret in its causal mechanisms. Excluding destruction by fire or other disturbances leading to widespread mortality of tree stands, NEP by definition represents a small residual of the difference between much larger flux variables (GPP-(Raut+Rh) or NPP-Rh). Any changes in model inputs that result in major changes in a single component of NEP, but not in the other component(s), can result in large shifts in predicted NEP.

All models except TEM predict a positive annual NEP flux (net CO_2 sink) under the baseline climate conditions for 1996 (Table 3). In spite of its potential for large variations, the NEP predictions are fairly consistent among models in response to changes in climate and site parameters. With respect to climate perturbations, modeled NEP generally increases (higher ecosystem C sink) with lower Ta or higher Pt, Td, Srad, and CO_2 (Figure 11a). NEP commonly decreases (higher ecosystem C source) with higher Ta or lower Pt, Td, Srad, and CO_2.

With respect to perturbations in the site parameters, the models commonly predict a NEP increase (greater ecosystem C sink) with higher Ω, Gs, Ln, or with lower Oc values (Figure 11b). Modeled NEP typically decreases (greater ecosystem C source) with higher LAI or Oc, or lower Ω, Gs, and Ln values.

Several sensitivity responses stand out as being informative with respect to major controls on the component fluxes of NEP. For example, all the models (except CLASS and TEM) show a more positive NEP response under consistently cooler Ta of -2°C, mainly as the result of strong relative declines in predicted Rh compared to smaller changes in NPP fluxes. Model responses to the warmer Ta of +2°C are variable and depend mainly on the response of GPP and NPP under consistently higher air temperatures. If predicted NPP declines substantially with higher Ta (as in the results from BEPS, BGC, FORFLUX, LoTEC, and SPAM; see explanation above), then annual NEP can become negative (net C source). Otherwise, if predicted NPP declines

relatively little with higher Ta (as in the results from CLASS, Ecosys, and NASA-CASA), then annual NEP can remain a small positive net C sink, despite higher predicted Rh fluxes.

For instance in LoTEC, the change in Ta is applied to both air temperature and a prescribed soil temperature. The decomposition rates and predicted Rh fluxes from soil organic matter is relatively sensitive in LoTEC to the prescribed increase in soil temperature (even, probably unrealistically, during the winter), and this results in large negative NEP fluxes predicted with higher Ta. Most other models applied the change in Ta to an internally predicted soil temperature with physically based thermal flux algorithms, which probably dampens the overall effect of higher Ta somewhat on annual predicted Rh fluxes.

Under wetter conditions (e.g., 50% higher Pt), BGC, Ecosys, and FORFLUX predict that NEP becomes more positive as the result of strong relative decreases in soil respiration associated with higher moisture inputs, compared to small changes in predicted NPP fluxes. On the other hand, several model NEP responses (BGC, NASA-CASA, CLASS, LoTEC) are sensitive to soil drying effects on predicted Rh. Drier soils in response to reduced Pt can strongly retard modeled Rh flux, causing NEP to increase in a roughly equivalent manner as certain model responses under cooler temperature conditions. Nonetheless, a general functional response to drying may not always be appropriate to the organic soils of the NSA-OBS site, where one might expect a drying of litter and soils to increase decomposition rates. For example, in BEPS, strong negative NEP in response to lower Pt is due mainly to the positive response of predicted Rh to drier soil conditions, as discussed previously.

With respect to changing surface irradiance, the strongly positive NEP response in BGC to 10% higher Srad primarily reflects an increase in predicted GPP, since respiration rates are generally insensitive to changes in Srad. Specifically, BGC calculates maintenance respiration rates using algorithms based on air temperature and moisture. Srad has a
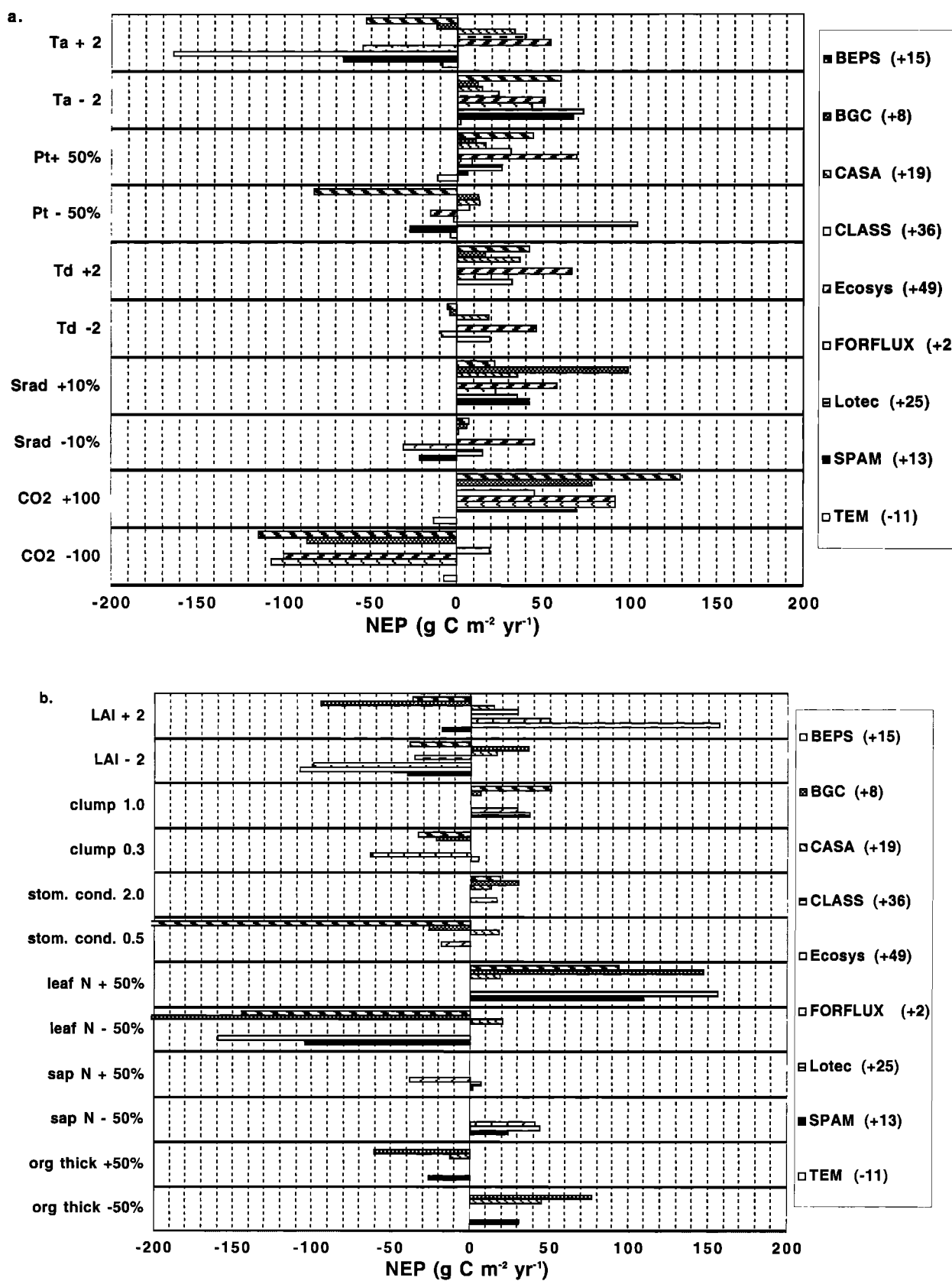
Figure 11. Change in model NEP fluxes in response to (a) climate driver and (b) site parameter values. Numbers in parentheses next each model name are baseline 1996 NEP fluxes in units of g C m^{-2} yr^{-1}.

small effect on growth respiration rates in a model of this type.

Strong sensitivity of predicted NEP to altered CO_2 can be explained in a similar fashion. In BGC, CLASS, Ecosys, FORFLUX, and LoTEC the response of NEP to CO_2 is the same as for the response of GPP and NPP to CO_2. Namely, predicted GPP is strongly affected in these models through Michaelis-Menten kinetics and Ball-Berry stomatal functions, whereas predicted Rh is weakly affected by changes in to CO_2. In BEPS, high sensitivity to CO_2 is explained also by the strong response of GPP from the Farquhar equation, lacking consideration of potential nutrient limitation on plant production over short periods. BEPS also shows a particularly high NEP sensitivity to Gs, which may be due, again, to requiring an external setting of the maximum Gs, rather than an internal calculation based on consistent physiological principles.

High sensitivity of NEP to Ln in most models is generally the result of their estimated Vc_{max} being linearly proportional to leaf nitrogen content in the Farquhar carboxylation equations. Over a 1-year simulation period, it appears that predicted Rh fluxes do not respond rapidly to increased Ln content of the decomposing litter, at least not rapidly enough to offset higher plant carbon gain with higher Ln and begin to balance the increase in predicted annual NEP flux. The same type of lagged effects on Rh, specifically during periods when plant production is increasing rapidly, can also explain selected model responses to the higher LAI and Ω settings.

The predicted changes in NEP resulting from altered organic horizon thickness and C content are explained almost entirely by model Rh fluxes, which increase strongly with higher Oc thickness, and decrease with lower Oc thickness. Hence the amount of soil carbon substrate available for relatively rapid microbial decomposition, a parameter which is sometime set as an initial model condition from reported field measurements or other external data sources, can strongly affect annual NEP estimates. This is a case where uncertainty in a key model setting can result in major changes in a single component of NEP (i.e., microbial CO_2 emission) but not in the other components GPP and Raut.

6. Sensitivity to Initial Conditions

Several models (CLASS, LoTEC, NASA-CASA, SPAM) were evaluated for the influence of initial pools for wood carbon and soil carbon on predicted annual production and respiration fluxes. Each in this group of models could be used in a manner to generate sensitivity simulations readily with the entry of external initialization values. Other models are designed to initialize major carbon pools internally as a built-in function of other important structural and functional variables and therefore were difficult to use for these types of simulations.

Results of sensitivity simulations using +50% initial wood carbon amounts, relative to the baseline model settings, reveal that predicted NPP flux decreases by between 5 and 12% annually. This is the result mainly of additional Raut costs predicted with the higher woody biomass setting. The net effect of this setting is to reduce the predicted carbon sink (computed as a positive annual NEP) by between 50 and 80%. Sensitivity simulations using -50% initial wood carbon amounts show the opposite effects on annual NPP, Raut, and NEP estimates of about the same magnitude.

Results of sensitivity simulations using +50% initial soil carbon pool(s), relative to the baseline model settings, together show that modeled annual Rh fluxes increase between 15 and 40%. This additional flux of soil CO_2 to the atmosphere can potentially change the simulated site from a predicted annual carbon sink to a carbon source (computed as negative NEP) of between 10 and 60 g C m^{-2} yr^{-1}. Sensitivity simulations using -50% initial soil carbon amounts show the opposite effects on Rh of about the same magnitude, potentially more than doubling the predicted carbon sink flux in some cases.

Judging from these results, it appears that past conditions of the boreal spruce ecosystem including climate trends and the time since last major disturbance (e.g., wild fire), as represented in the model's initial standing wood and soil carbon pools, are as important as hypothetical changes in climate variables in determining the model response for a net ecosystem carbon sink. Because NEP in the boreal spruce forest is a small residual of the difference between much larger carbon fluxes, certainty in predictions of a net source or net sink for atmospheric carbon will be strongly dependent on correct assumptions about the antecedent state of wood and soil carbon pools in a model. These assumptions about the sizes of large carbon pools must be based on accurate information from time trends in regional climate warming over the past several decades, changes in length of the growing season, mortality rates of trees in the stand, and whether (repeated) wild fires may have burned away portions of the soil organic layers.

These tests of initial conditions for wood biomass and soil carbon pools on model results for NEP are again relevant to the issue raised in our companion paper [*Amthor et al.*, this issue] concerning the initialization of models with settings that represent some of the most productive areas of the NOBS tower footprint. If the models had used 50% higher initial values of wood biomass or soil carbon pools as their baseline settings, then it appears that models would generally estimate lower sink NEP fluxes for the tower area and probably would show lower overall errors in matching net carbon exchange measured at the tower on a daily basis. Varying the initial pools for wood carbon and soil carbon by ±50% is reasonable, based on measured variability in boreal spruce stands [*Halliwell et al.*, 1995; *Harden et al.*, 1997; *Rapalee et al.*, 1998].

7. Conclusions

Results from this sensitivity analysis reveal that boreal spruce forest models with different levels of detail (e.g., hourly ecophysiological controls versus daily-to-monthly ecosystem processes) can have similar and strong sensitivities to variability in the local climatology and to site parameters. In general, we found that there are common model responses in GPP, Raut, and ET fluxes to uniform changes throughout the year in air temperature or surface irradiance and to decreased precipitation amounts. With practically no exceptions, increase or decrease in air temperature, surface irradiance, or precipitation amounts leads to the same direction of change (increase or decrease) in GPP, Raut, and ET fluxes. Regardless of design, the models also show similar directional (positive or negative) responses (with the exception of NPP sensitivity) to changes in LAI, leaf or sap wood nitrogen content, and soil organic layer thickness or

carbon content. The reason for these patterns of response to stand characteristics is that all the ecosystem models tested here have a strong dependence of predicted carbon fluxes to major structural components of the forest stand, such as foliar density and soil carbon accumulation following a hypothetical disturbance.

The various models have different sensitivities to certain input drivers, namely the NPP response to increased CO_2 levels, and the response of soil microbial activity and Rh fluxes to precipitation inputs and soil wetness near the organic surface. These differences can be explained by the type (or absence) of photosynthesis-CO_2 response curves used in the models, and by response algorithms for litter and humus decomposition to drying in organic soils of the boreal spruce ecosystem. Some of these response functions have dependencies on nitrogen availability, which will require more process-level results from field studies to resolve in terms of relevance and form.

The simulation results presented here raise a series of issues elaborated below that will require long-term field-based research in order to more thoroughly understand and realistically simulate controls on carbon and water cycles in the boreal spruce forest biome under current and future conditions. For example, the response of several ecosystem models presented here suggests that NPP at the NSA OBS site would decrease markedly with consistently higher air temperatures. Hence a key hypothesis to be tested experimentally is that Raut sensitivity to elevated temperatures is greater than GPP sensitivity in boreal spruce forests. An alternative hypothesis suggested by other model responses is that either change in length of growing season or in soil N availability might act as a compensatory mechanism to maintain or increase NPP on an annual basis under consistently higher air temperatures [Gower et al., 1996]. A key issue here will be the long-term response of soil CO_2 fluxes and nutrient mineralization to an increase in air temperature (i.e., dates and rates of thawing with depth in the soil as the spring warming front penetrates the soil profile).

Common model results presented in this study suggest that increases in precipitation amounts would have a small positive effect on black spruce NPP. However, if forest ET fluxes increase at the same time to maintain favorable soil water conditions and minimize effects of slowing soil decomposition and CO_2 emission fluxes, annual NEP may not increase substantially under higher precipitation conditions. As was the case for temperature effects, the long-term response of soil CO_2 fluxes and nutrient mineralization to an increase in soil water conditions must be investigated further in field experiments in order to clarify this issue. Results presented in this modeling study suggest that effects of climate or any other environmental factors leading to drier soil conditions appear to be among the most important and the most poorly understood of any affecting NEP predictions from ecosystem models. If future field research indicates that drier soils in boreal spruce forests can inhibit measured Rh fluxes, then annual NEP may increase in an equivalent manner. However, with so little experimental evidence to rely on, it cannot be said with certainly that a drying of boreal spruce soils will not increase actual short-term decomposition rates, decrease soil C pools, and thereby decrease annual NEP fluxes in the long term.

The models in this study generally predict a significant increase in spruce forest NPP and NEP in response to a 100 ppm rise in ambient CO_2 concentration. This simulation is consistent with short-term results from experimental studies where a step change in CO_2 has been applied. A key question is whether the boreal spruce ecosystems can sustain such an increased C uptake for a long enough period of time to significantly affect the atmospheric CO_2 budget. The answer seems to depend on the availability of soil nutrients (and particularly N) to meet the increased plant nutrient demand caused by accelerated photosynthesis. Since the rise in atmospheric CO_2 is likely to be accompanied by a climatic warming in high latitudes, mineral nutrients may be released at a higher rate due to increased soil organic matter decomposition. This would reduce potential nutrient limitations and help maintain high NPP and NEP rates of the boreal spruce forests. Results from a recent metaanalysis of 500 CO_2-enrichment studies reported by Curtis and Wang [1998], indicate that in open systems there is little evidence of photosynthetic acclimation to elevated CO_2, but that the long-term CO_2 fertilization effect (although reduced) could be significant in sites with low soil nutrient availability. This suggests that current model predictions of CO_2 effects (which do not include photosynthetic down-regulation) may actually provide a realistic scenario for expected long-term changes in boreal spruce productivity under future CO_2 conditions. Medlyn et al. [1999] reached the same conclusion using metaanalysis of the effects of elevated CO_2 on forest physiology (photosynthesis, stomatal conductance, and dark respiration).

Common model results presented here imply that major changes in nitrogen availability have the potential to change both the sign and the magnitude of NEP fluxes in boreal spruce forests. Similar to LAI and leaf-clumping parameters used as modeling inputs, leaf N content in boreal plant species is a variable that requires highly accurate specification over the northern forest region. The relatively large shifts in NEP and other carbon fluxes predicted by the models are roughly proportional to expected variations of leaf N content in these boreal spruce ecosystems.

In summary, this study shows that although forest models are intended to be simplified mathematical representations of real-world ecosystems, the similarities and differences in model responses to changes in climate and forest site parameters can provide clues about which processes require greater understanding and which external model settings require the highest accuracy for regional simulations. It is clearly demonstrated from the results of this modeling study that there can be large sensitivities to certain plant and soil site parameters. In many cases better information regarding the spatial heterogeneity of a few key variables (e.g., leaf N content, stand age distribution, LAI, and land cover class) obtained from new remote sensing or ground sampling techniques could markedly improve model predictions, by facilitating more accurate representation of spatial heterogeneity and sub-grid scale variability in model inputs and estimated processes.

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