

Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO₂], temperature and nitrogen input

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[1] The response of plant ecosystems to environmental change will determine whether the terrestrial biosphere will remain a substantial carbon sink or become a source during the next century. We use two ecosystem models, the Generic Decomposition And Yield model (G'DAY) and the daily time step version of the Century model (DAYCENT), to simulate net ecosystem productivity (NEP) for three contrasting ecosystems (shortgrass steppe in Colorado, tallgrass prairie in Kansas, and Norway spruce in Sweden) with varying degrees of water, temperature, and nutrient limitation, to determine responses to gradual increases in atmospheric CO₂ concentration ([CO₂]), temperature, and nitrogen input over 100 years. Using G'DAY, under rising [CO₂], there is evidence of C sink "saturation," defined here as positive NEP reaching an upper limit and then declining toward zero, at all three sites (due largely to increased N immobilization in soil organic matter) but a positive C sink is sustained throughout the 100 years. DAYCENT also predicts a sustained C sink at all three sites under rising [CO₂], with evidence of C sink saturation for the Colorado grassland and the C sink levels off after 80 years for the Kansas grassland. Warming reduces soil C and the C sink in both grassland ecosystems but increases the C sink in the forest. Warming increases decomposition and soil N mineralization, which stimulates net primary productivity (NPP) at all sites except when inducing water limitation. At the forest site some of the enhanced N release is allocated to a woody biomass pool with a low N:C ratio so that warming enhances NEP without increased N input at the forest site, but not at the grassland sites. Responses to combinations of treatments are generally additive for DAYCENT but more interactive for G'DAY, especially under combined rising [CO₂] and warming at the strongly water- and N-limited shortgrass steppe. Increasing N input alleviates C sink saturation and enhances NEP, NPP, and soil C at all sites. At the water-limited grassland sites the effect of rising [CO₂] on growth is greatest during the drier seasons. Key sensitivities in the simulations of NEP are identified and include NPP sensitivity to gradual increase in [CO₂], N immobilization as a long-term feedback, and the presence or not of plant biomass pools with low N:C ratio.

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1. Introduction

[2] In the global carbon budget for the 1980s and 1990s, terrestrial ecosystems constitute a net sink of approximately 0.2 and 1.4 Pg C yr⁻¹, respectively [Schimel, 1995; Houghton *et al.*, 2001]. There is, however, considerable debate over whether the terrestrial carbon (C) sink will be sustained, will saturate, or is about to change from a

substantial net C sink to a net C source as a result of global environmental change [Schimel *et al.*, 1995; Cramer and Canadell, 2000; Houghton *et al.*, 2001]. Some scientists have argued, for instance, that the terrestrial biosphere could become a C source in the next century [Cao and Woodward, 1998; Pearce, 1999; Scholes, 1999; Scholes *et al.*, 1999; Walker *et al.*, 1999; Kirschbaum, 2000]. One of their main arguments is that the balance between respiratory C losses (autotrophic and heterotrophic; plant and soil) and plant C gain will shift because respiration will increase exponentially with rising temperature (T) whereas plant productivity will become more CO₂-saturated with increasing atmospheric CO₂ concentration ([CO₂]). This argument has been criticized because it is based largely upon observations of direct, relatively short-term effects of T and [CO₂] on plant

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and soil processes and therefore ignores potentially important long-term plant-soil feedbacks operating on decadal and longer timescales [e.g., *McMurtrie and Comins*, 1996; *Medlyn et al.*, 2000; *McMurtrie et al.*, 2001].

[3] Using a forest ecosystem model that incorporates both short- and long-term effects, *McMurtrie et al.* [2001] predict that a nitrogen-(N)-limited Norway spruce ecosystem based on that at Flakaliden, Sweden, will remain a C sink throughout the next century. The size of the C sink they predict is, however, sensitive to assumptions about soil-N feedbacks. Their sensitivity analysis identifies soil N immobilization, controlled by varying soil N:C ratios, as a key process in C sink variation under conditions of rising [CO₂] and temperature. Under rising [CO₂] their simulations with flexible soil N:C ratio show evidence of C sink saturation, with net ecosystem production (NEP) increasing to a peak and then declining toward zero NEP.

[4] The mechanisms underlying possible C sink saturation are complex, involving physiological and structural processes at ecosystem and regional scales, and processes affected in direct and/or indirect ways by environmental changes (predicted to result from rising [CO₂] and T). For example, elevated [CO₂] directly stimulates photosynthetic CO₂ uptake, and generally improves both water- and N-use efficiencies but these effects diminish at high CO₂ levels. Elevated temperature stimulates soil heterotrophic respiration but also enhances N-release, which may lead to increased NPP. The mechanisms have been incorporated in numerous modeling studies including that by *McMurtrie et al.* [2001] and one where six dynamic global vegetation models (DGVMs) were forced by the combination of increasing atmospheric CO₂ concentration and climate change [*Cramer et al.*, 2001]. Five of the six DGVMs predict that the current global C sink, in a world without deforestation and land-use by humans, will be sustained or enhanced over the next century. On average, the DGVMs show a sink of 1.6 Gt C yr⁻¹ for the 1990s, rising to approximately 4 Gt C yr⁻¹ by 2050 and then declining to approximately 3.5 Gt C yr⁻¹ by 2100. For all six DGVMs the decline in the global C sink is dominated by the temperature effect; sink saturation is less evident in simulations with rising [CO₂] alone than under both rising [CO₂] and T. The combined effect of increasing [CO₂] and T on water- or nutrient-limited plant productivity cannot yet be accurately predicted [*Bonan and van Cleve*, 1991; *Melillo et al.*, 1993; *Houghton et al.*, 1998] because of inadequate understanding of mechanistic responses to increasing [CO₂] and T, including effects on air humidity, plant water use, soil nutrient availability, species composition, and fire frequency.

[5] In the case of temperature response alone, evidence gathered from a soil-warming experiment on Norway spruce at Flakaliden in Sweden [*Jarvis and Linder*, 2000; *Strömberg and Linder*, 2002] contradicts claims that the projected temperature rise, around 1° to 3.5°C in the next 50–100 years [*Houghton et al.*, 1995] or 1.4° to 5.8°C from 1990 to 2100 [*Houghton et al.*, 2001], is likely to result in conversion of forest C sinks to sources. In this experiment, measured 5 years after commencement of treatments, soil warming increased annual stemwood growth by more than 50%, but CO₂ efflux from the forest floor was less than 10%

higher, which was not significant [*Strömberg and Linder*, 2002]. The large growth response to soil warming was attributed mainly to increased N uptake and partly to earlier snowmelt and longer growing season [*Jarvis and Linder*, 2000]. In spite of low CO₂ efflux from the forest floor after 5 years, forest productivity remained at the high level, raising uncertainties about the effect of future litter input and subsequent N mineralization-immobilization feedbacks to productivity over the long term.

[6] Other recent soil-warming experimental evidence, used in a recent meta-analysis of ecosystem warming experiments in tundra, forest, and grassland ecosystems [*Rustad et al.*, 2001], suggests that the relative magnitude of temperature-induced increases in respiration, production, and nutrient mineralization will be crucial for predicting the carbon sink response to rising temperature. *Rustad et al.* [2001] found that increases in N mineralization (+64%) were larger overall than increases in soil respiration (+20%) and aboveground plant productivity (+27%). They found that forested ecosystems generally had larger soil respiration responses and larger N mineralization responses than tundra or grassland, but smaller productivity responses than tundra. Their results for meta-analysis grouping all ecosystems were significant in spite of large variability among sites and insignificant correlations between ecosystem parameters (N mineralization, soil respiration, and biomass production), and between geographic, climatic, and environmental variables, thus highlighting the likely importance of other site-specific factors [*Rustad et al.*, 2001].

[7] NEP responses to increasing [CO₂], to increasing temperature, and to other associated environmental changes are uncertain for most ecosystems [*Schimel et al.*, 2001] and are likely to differ in contrasting environments over the next century [e.g., *Cao and Woodward*, 1998]. One uncertainty [*Gifford*, 1992, 1994; *Zak et al.*, 1993; *Peñuelas and Estiarte*, 1997] concerns whether enhanced NPP will lead to greater availability of carbon substrate in the soil to support increased populations of atmospheric N₂ fixers [*Vitousek et al.*, 2002]. If so, then factors that directly and indirectly increase NPP could lead to an inflow of N to the ecosystem additional to other N inputs such as atmospheric deposition. *Oren et al.* [2001], for example, demonstrate that forest growth response to elevated [CO₂] may be undetectable on infertile soil, or initially increase and then decrease on sites of intermediate fertility, but increase and stay high with increased N inputs.

[8] Although most field studies involving elevated CO₂ levels have been single factor experiments, rising CO₂ concentrations are likely to be accompanied by increases in temperature and N inputs and increases or decreases in precipitation. In one field study designed to address these interactions, *Shaw et al.* [2002] showed that while elevated [CO₂] increased NPP in a California annual grassland as a single factor manipulation, increased [CO₂] suppressed the positive effects of increased precipitation, temperature, and N deposition on NPP in the multifactor treatments. The extent to which these results apply to other ecosystems is unknown, but they make clear that interactions are important and not easily predictable. Results from various single-factor experiments can be

Table 1. Treatments Applied in Ecosystem Simulations^a

Description	Denoted
Gradual increase in [CO ₂] (350 to 700 ppm)	C
Gradual increase in temperature; T _{max} (1°C), T _{min} (3°C), T _{soil} (2°C)	T
Gradual increase in [CO ₂] and temperature	CT
Gradual increase in [CO ₂] and N input (1 g m ⁻²)	CN
Gradual increase in [CO ₂], temperature and N input	CTN

^aValues in round brackets indicate the rates of increase per century applied gradually, and abbreviations are: T_{max}, air temperature maximum; T_{min}, air temperature minimum; T_{soil}, soil temperature.

used to build, test, and improve ecosystem models. Models can then be used to explore how different factors interact on short as well as long timescales, to identify key sensitivities and generate hypotheses, and as such, they complement observations in the field.

[9] Our goal in this paper is to investigate mechanisms underlying the NEP response to gradual increases in [CO₂], temperature, and N input, using ecosystem response simulations, based on three contrasting ecosystems: a boreal, N-limited coniferous forest (this experimental site includes high [CO₂] and soil-warming treatments) at Flakaliden, Sweden; a temperate, C₄-dominant tallgrass prairie at Kansas, and a C₃/C₄ shortgrass steppe at Colorado (both grassland sites include high [CO₂] treatments). All three ecosystems have been the subject of several years of fieldwork, including CO₂ enrichment experiments at all three and soil warming at Colorado and Flakaliden, that provides valuable, prerequisite data sets for parameterizing models. Thus the three sites were chosen because they represent contrasting vegetation types and had data available for model parameterization. This study therefore advances that by *McMurtrie et al.* [2001] by extending the modeling analysis to forest and grassland sites with different water- and N-limitations, using two process-based models with different formulations of plant and soil processes, and by using realistic meteorological data. Using the process-based plant ecosystem models G'DAY (Generic Decomposition And Yield) [*Comins and McMurtrie*, 1993] and DAYCENT (daily time step version of the CENTURY model) [*Del Grosso et al.*, 2001], we simulate net primary production (NPP), heterotrophic respiration (R_h), the carbon sink (NEP = NPP - R_h), and soil carbon responses to various combinations (Table 1) of the three treatments (rising [CO₂], rising T, and rising N input) over the next century. Our secondary goal is to investigate differences between forest and grass systems, and water- and N-limited sites. Our more general aim is to investigate whether or not there is a strong basis for claims that the terrestrial C sink may soon switch to being a net C source. An important outcome of this work is the identification of key sensitivities in models that affect the future size of predicted C sink/source and how they vary with environmental and nutrient availability gradients. We are also interested in whether responses to perturbations in multiple variables are additive or interactive, and whether the NPP response to rising

[CO₂] is larger in dry years than in wet years as found by *Owensby et al.* [1999] for tallgrass prairie.

2. Modeling

[10] The modeling analysis was done at the stand scale, without vegetation dynamics, to primarily focus on physiological and biogeochemical mechanisms involved in ecosystem responses to the various treatments. One model (G'DAY) was developed primarily for forests and is being extended to grasslands, while the other (DAYCENT) was developed primarily for grasslands and is being extended to forests. This makes them highly suitable for this analysis. Key algorithms and parameters for the two models are described in Appendix A (Table A1).

2.1. G'DAY Model

[11] The Generic Decomposition And Yield model (G'DAY) simulates C and N dynamics in plant-soil ecosystems using a daily time step, and has been used to investigate long-term ecosystem responses to rising [CO₂] and temperature, and management practices. Only a brief outline of G'DAY is given here because G'DAY has been fully described elsewhere [*Comins and McMurtrie*, 1993; *Medlyn et al.*, 2000]. G'DAY consists of plant and soil submodels. The plant submodel simulates net C uptake, C and N contents of foliage, wood (stems, branches, and coarse roots), fine roots, and the litter derived from these plant components. Wood N is divided into an immobile pool (structural compounds) and a mobile pool (nonstructural compounds). The soil submodel simulates C and N contents of four litter pools (structural and metabolic, both aboveground and belowground) and three soil organic matter (SOM) pools (active, slow, and passive, with different decay rates) as in the CENTURY soil model [*Parton et al.*, 1987, 1993]. Thus G'DAY represents a set of physiological processes that include C assimilation, respiration, allocation, tissue senescence, N uptake, N translocation, N inputs from atmospheric deposition and biological fixation, and soil processes that include litter and SOM decomposition, N mineralization and immobilization, and N loss by gaseous emission and leaching.

[12] Productivity in G'DAY is modeled using the plant submodel RESCAP (RESource CAPture), which was originally developed for cereal crops [*Monteith*, 1986; *Monteith et al.*, 1989] but has been modified and applied to a *Pinus radiata* forest plantation [*Dewar*, 1997]. Productivity is assumed to be the minimum of light- and water-limited growth rates. Daily light-limited productivity (G_L) for the forest is calculated using the BEWDY model described by *Medlyn et al.* [2000]. BEWDY incorporates a mechanistic model of C₃ leaf photosynthesis [*Farquhar and von Caemmerer*, 1982] including direct effects of temperature and [CO₂] on photosynthesis, and separation of sunlit and shaded foliage. For the grassland systems, G_L is determined from intercepted light using an equation for light-use efficiency [*McMurtrie et al.*, 1992], without direct effects of [CO₂] on C₄ photosynthesis. In both C₃ and C₄ cases, G_L increases with light absorbed by the canopy as an increasing function of leaf N content to an upper bound of leaf N, after which N uptake by the plant is curtailed. For both forest and

grassland systems, plant respiration is assumed to be a constant fraction of gross photosynthesis [Gifford, 1994, 2003; Waring *et al.*, 1998; Dewar *et al.*, 1999], implying that the temperature dependence of autotrophic respiration is linked to that of photosynthesis.

[13] Water-limited productivity (G_w) is determined by the rate of water extraction by roots [Dewar, 1997], which is evaluated from root mass and available soil moisture. Productivity and transpiration are related through the water-use efficiency (q), which is assumed to vary inversely with daylight mean saturation vapor pressure deficit (D), so that the product qD for the system will be conserved over time [Tanner and Sinclair, 1983]. Dewar [1997] reasoned that the close physiological link between water and CO₂ fluxes, and the conservative natures of light utilization coefficient ϵ and qD , allows ϵ and qD to form the basis of a simple model for plant productivity. Although previous leaf-scale estimates of water-use efficiency indicate a linear dependence on [CO₂] [Morison, 1993; Medlyn *et al.*, 2001], analysis of biomass and soil moisture data at the tallgrass prairie site indicates a power law dependence on [CO₂] (D. A. Pepper, manuscript in preparation, 2004),

$$q = (q_0/D)([CO_2]/350)^a, \quad (1)$$

where the value a is 0.703, obtained by simultaneously fitting G'DAY to both net primary productivity and soil moisture data at 350 and 700 ppm [CO₂], and q_0 is the water-use efficiency at ambient [CO₂] and D of 1 kPa. Estimated values of q_0 are 1.3, 2.2, and 3.6 g C kPa (g H₂O)⁻¹ for Colorado, Kansas, and Flakaliden, respectively. Different q_0 values reflect inherent differences in the hydraulic and carbon uptake designs of different vegetation types.

[14] In G'DAY, following Parton *et al.* [1993], we assume that the N:C ratios of substrate entering active, slow, and passive SOM pools increase linearly between prescribed minimum and maximum values as N_{inorg} increases from zero to a critical value ($N_{crit} = 2 \text{ g m}^{-2}$). Soil inorganic N (N_{inorg}) is therefore represented explicitly as described by McMurtrie *et al.* [2001], including soil N mineralization-immobilization, variable N:C ratio of SOM, and influxes (N input) and effluxes (N loss and plant uptake).

[15] A grazing effect [Halliday *et al.*, 2003] was included in the model for the two grasslands. Half of net primary production is grazed, 30% of C consumed by grazers is returned to the ecosystem via faeces, and 85% of N is returned via faeces and urine. We assumed that faeces has a N:C ratio of 0.04 (C:N ratio of 25) and lignin content of 25%.

[16] The water, temperature, and nitrogen effects on G'DAY are implemented via processes described in Appendix A (Table A1). Briefly, G'DAY assumes that water-limited NPP (G_w) and decomposition rate will increase with plant available water. Mean maximum and minimum air temperatures are inputs that drive the air, soil, and leaf temperatures, and vapor pressure deficit in the model, rather than an energy balance approach being taken. Both NPP and decomposition rate increase with increasing temperature up to an optimum temperature, but their temperature

responses may be constrained by water or nitrogen availability. Nitrogen limits NPP under low soil mineral N supply as diluted leaf N content reduces photosynthesis and light-use efficiency. The N:C ratio of material entering SOM pools is a function of the soil inorganic N pool, and affects soil N availability by determining both soil N immobilization and gross mineralization. High soil N availability indirectly increases leaf area, which leads to increases in the amount of light absorbed and hence, light-limited production. Further details are provided in Appendix A (Table A1) and the literature [Comins and McMurtrie, 1993; Dewar, 1997; Medlyn *et al.*, 2000; McMurtrie *et al.*, 2001].

2.2. DAYCENT Model

[17] DAYCENT [Parton *et al.*, 1998; Kelly *et al.*, 2000; Del Grosso *et al.*, 2001] is the daily time step version of the CENTURY model [Parton *et al.*, 1987, 1993, 1994]. DAYCENT simulates exchanges of carbon, nutrients, and trace gases among the atmosphere, soil, and vegetation, and has been used to investigate impacts of changes in atmospheric CO₂ concentration and N deposition rates, as well as disturbance events and management practices.

[18] DAYCENT includes submodels for plant productivity, decomposition of dead plant material and SOM, soil-water and temperature dynamics, and N-gas fluxes. The amount of C in the various pools, the N concentrations of the pools, abiotic temperature and soil-water factors, and soil physical properties control flows of C and nutrients. Soil texture and current and historical land-use information are needed to parameterize the model for a particular site. In contrast to G'DAY, the DAYCENT submodel for NPP does not explicitly model photosynthesis and light interception. Radiation is, however, accounted for by assuming that maximum NPP is controlled by radiation, which depends on latitude and day of year. Maximum NPP is down-regulated on a weekly time step by equations representing nutrient, water, temperature, and shade limitation [Metherell *et al.*, 1993]. NPP is distributed among leaf, wood (stem, branch, and coarse root), and fine root compartments based on plant type, soil-water content, and mineral N availability. Turnover rates of plant compartments are controlled by soil water, temperature, season, and plant-specific senescence parameters. SOM is divided into three pools based on decomposition rates [Parton *et al.*, 1993, 1994]. Decomposed detrital material that has a high N:C ratio flows to the active SOM pool, which includes microbial biomass and the highly labile byproducts of decomposition that turn over in approximately 1 year or less. The products of detrital decomposition that have a lower N:C ratio flow to the slow SOM pool, which includes the relatively resistant (10- to 50-year turnover rate) byproducts of decomposition. The passive SOM pool consists of humus that is extremely resistant to further decomposition. As soils become finer textured a lower portion of SOM is respired as CO₂ and more SOM is retained in stable form due to physical and chemical protection. Decomposition of SOM and external nutrient additions supply the nutrient pool, which is available for plant growth and microbial processes that result in trace gas fluxes. Nutrients and SOM are concentrated near

the soil surface and decrease exponentially with depth. An N-gas submodel simulates nitrogen emissions in detail [Parton *et al.*, 1996, 2001; Del Grosso *et al.*, 2000]. The land surface submodel of DAYCENT simulates water flow through the plant canopy, litter, and soil profile, as well as soil temperature throughout the profile [Parton *et al.*, 1998; Eitzinger *et al.*, 2000].

[19] DAYCENT assumes that NPP and organic matter decomposition rates increase as soil water content increases until optimum water content is reached, but the optimum is higher for NPP than decomposition. Similarly, both NPP and decomposition are influenced by temperature, and the sensitivity of temperature response is different for the processes. Optimum, minimum, and maximum temperatures for NPP vary with vegetation type whereas no minimum or maximum temperatures for decomposition are assumed, although the rate at which decomposition increases declines as temperature increases (positive first derivative, negative second derivative). Both NPP and decomposition are also limited by mineral N availability. The N effect on decomposition is very similar to G'DAY (Table A1). In most native systems (those not dominated by N fixing vegetation) the primary source of mineral N is from mineralization of soil organic matter via decomposition. When mineral N is in short supply, microbes are assumed to have preferential access to N. The effects of elevated atmospheric CO₂ concentration are manifested in three ways in DAYCENT; maximum NPP can increase, transpiration per unit leaf area can decrease, and plant tissue N:C ratio can decrease (Table A1). DAYCENT assumes a linear increase in maximum NPP with rising CO₂ concentration, but this will only be realized if water, temperature, and nitrogen are nonlimiting. CO₂-induced changes in growth rates and tissue N concentration affect the quantity and quality of litter inputs to soil and hence affect decomposition rates. Increased inputs under elevated [CO₂] tend to increase decomposition rates, but if N is sufficiently limiting, then lower N:C of litter under high [CO₂] can inhibit decomposition rates. Decreased transpiration can lead to higher soil water contents and indirectly influence decomposition rates, especially in arid systems.

[20] Comparisons with field data show that DAYCENT simulates soil organic carbon (SOC) levels and trace gas fluxes reasonably well. The model has been applied to compare the effects of different land uses on crop SOC and trace gas fluxes [Del Grosso *et al.*, 2001, 2002]. DAYCENT and G'DAY used similar assumptions for cycling of C and N from grazing.

2.3. Modeling of Water-Use Efficiency

[21] An important difference (Table A1) between G'DAY and DAYCENT is in how they represent effects of [CO₂] and T on water-use efficiency. DAYCENT assumes that high [CO₂] increases water-use efficiency by reducing transpiration, so that water savings are immediately reflected in soil moisture. Thus soil-moisture limitation to rates of decomposition and soil-N mineralization are alleviated under rising [CO₂]. Increases to NPP under rising [CO₂] using DAYCENT arise from the combined direct effect of [CO₂] on NPP, indirect effects of soil moisture on

NPP, and reduced N-limitation to NPP due to enhanced soil-N mineralization on moister soils.

[22] In G'DAY, on the other hand, the rising [CO₂] treatment increases water-use efficiency (with q increasing by a factor of 1.63 as [CO₂] increases from 350 to 700 ppm (equation (1)), so that transpiration (E) is reduced only under light-limited conditions ($E_L = G_L/q$). Under water limitation, as frequently occurs at Colorado and Kansas sites, water-limited transpiration (E_W) is determined by root mass and available soil moisture. Thus, improvements in water-use efficiency under the rising [CO₂] treatment immediately stimulate water-limited NPP ($G_W = E_W q$) but may not immediately affect soil moisture. Another difference between G'DAY and DAYCENT is that the water reduction factor acting on decomposition rate is a function of moisture content of the topsoil layer in G'DAY whereas in DAYCENT it is a function of water content of the entire root zone.

2.4. Site Characteristics

[23] We parameterized G'DAY and DAYCENT for two grasslands and a forest ecosystem. The two grassland sites represent the xeric and mesic ends of a west-to-east moisture gradient across the large grassland region of the U.S. central plains. Grasslands worldwide are widespread, covering almost one fifth of the global land surface (24×10^6 km² [Lieth, 1972; Hall and Scurlock, 1991]) and contain almost one third of global soil carbon stocks [Anderson, 1991]. Estimated worldwide boreal forest land cover is 13.7×10^6 km² [Dixon *et al.*, 1994]. The forest site represents young boreal conifer forest.

[24] The first grassland ecosystem is a shortgrass steppe site at the Central Plains Experimental Range (CPER) located ~60 km northeast of Fort Collins in northeastern Colorado (40°8'23"N, 104°45'15"W; 1625 m a.s.l.). Mean annual temperature and precipitation are approximately 9.5°C and 320 mm, respectively [Mosier *et al.*, 1996, 1997]. Mean monthly temperature ranges from -4° to 22°C seasonally and has an average daily maximum-minimum range of 17°C. Annual precipitation has ranged between 107 and 588 mm over the last 50 years. The grazing-tolerant C₄ grass blue gramma (*Bouteloua gracilis*) is the dominant vegetation type in this strongly water-limited and N-limited system [e.g., Sims *et al.*, 1978]. The data set present in the literature includes annual NPP, soil moisture contents, and other variables measured in control and CO₂-enhanced open-top chambers beginning in 1997 [Morgan *et al.*, 2001], and daily meteorological data for 30 years (1969–1999). Under high [CO₂], there is evidence of increased productivity, a decline in plant tissue nitrogen concentration, and increased soil moisture [e.g., Morgan *et al.*, 2001, 2004; Mosier *et al.*, 2002]. Under soil warming, there is evidence of increased soil respiration and reduced soil moisture [Rustad *et al.*, 2001, and references therein].

[25] The second grassland system is a tallgrass prairie site north of Manhattan, Kansas (39°7'N, 96°21'W; 324 m a.s.l.). The 30-year mean monthly maximum temperature ranges from -7°C in February to 33°C in early July. The 30-year average annual precipitation is 840 mm, with 520 mm occurring during the growing season. Vegetation,

comprising a mixture of C₃ and C₄ species, is dominated by C₄, warm-season grasses (85% C₄ grasses, 5% C₃ forbs, 5% *Cyperacea*, 3% perennial C₃ grasses, and 2% annual C₃ grasses and forbs), and displays seasonal growth limited by nitrogen and water [Owensby *et al.*, 1994]. Further details about species composition and experimental procedures are given by Owensby *et al.* [1993, 1994, 1999]. Open-top chambers have been used at this site to implement treatments at ambient and twice-ambient CO₂ concentrations. At an ambient CO₂ concentration of 350 ppm, annual productivity is water-limited at this site [Owensby *et al.*, 1999]. The data set in the literature includes annual aboveground and belowground C and N contents of biomass, soil moisture contents, and daily meteorological data for eight consecutive years (1989–1996) [Knapp *et al.*, 1993, 1994, 1996; Owensby *et al.*, 1993, 1994, 1999; Ham *et al.*, 1995; Bremer *et al.*, 1996; Hamerlynck *et al.*, 1997]. There is evidence that the productivity response to elevated [CO₂] is N-limited and is larger in dry than wet years [Owensby *et al.*, 1994], and that soil moisture is enhanced at high [CO₂] [Owensby *et al.*, 1999; Morgan *et al.*, 2004].

[26] The forest system is a plantation of Norway spruce (*Picea abies*, L. Cast) planted in 1963 at the Flakaliden site (64°7′N, 19°27′E; 310 m a.s.l.) approximately 60 km west of Umeå, Sweden, where treatments have included fertilization, irrigation, CO₂ enrichment in whole-tree chambers, and soil warming. Mean monthly temperature ranges from −9°C in February to 14°C in July. Mean annual precipitation is ~600 mm, which generally maintains the nutrient-poor soil at high water content. More than a third of precipitation falls as snow, with snow cover usually persisting from mid-October to mid-May. The site is N-limited but not water-limited [Bergh *et al.*, 1998, 1999]. The data set in the literature includes annual NPP, tree height and diameter, C and N contents of biomass, and daily meteorological data for 13 consecutive years (1990 to present). After 5 years of soil warming (by 5°C at 10 cm depth, through the growing seasons during years 1995–2000), annual volume growth increased by 100% and 50% in irrigated (control) and irrigated-fertilized stands, respectively, that were in a long-term nutrient optimization experiment beginning in 1987 [Jarvis and Linder, 2000; Strömgren and Linder, 2002]. Elevated-[CO₂] effects on productivity at the tree level are positive but small (S. Linder, personal communication, 2004).

2.5. Model Input Requirements

[27] Meteorological data required by G'DAY and DAYCENT are daily maximum and minimum air temperatures, total solar radiation, and precipitation. For the G'DAY model, mean daily saturation vapor pressure deficit (D) was calculated using a sinusoidal pattern of temperature over a 24-hour cycle under an assumption that air is saturated at the daily minimum temperature, following the method of McMurtrie *et al.* [1990]. Simulations below were based on daily meteorological measurements over an 8-year period at each site. Our objective was to run simulations over approximately 1 century, so we opted for a 104-year period at each site, from 1996 to 2100, which we represent by 13 cycles of the 8-year meteorological data file. For the

C₃ forest, G'DAY included both the direct CO₂ effect on NPP and the indirect effect of increased water-use efficiency. For both C₄-dominant grasslands, G'DAY included only the water-use efficiency effect. DAYCENT included direct effect on NPP and transpiration for all three sites (linear CO₂ effects with 10%, 20%, and 25% increases of NPP and 40%, 40%, and 10% reductions of transpiration at twice ambient [CO₂], at Colorado, Kansas, and Flakaliden, respectively).

[28] For the G'DAY model, assumptions about future changes in vapor pressure deficit D are critical at water-limited sites because D determines water-use efficiency. It is common in ecophysiological models to evaluate absolute humidity by assuming that air is saturated at the daily temperature minimum [Running *et al.*, 1987; McMurtrie *et al.*, 1990; Glassy and Running, 1994]. For simulations of rising temperature, values of D may fall between two extremes: (1) absolute humidity may increase so that air is saturated at future T_{\min} ; and (2) absolute humidity may not change in the future (i.e., air is saturated at current T_{\min}). For the G'DAY simulations below, we choose the middle ground and model D under rising temperature (treatment T) by assuming absolute humidity increases by half the increase that would occur if air was saturated at the higher future T_{\min} .

2.6. Climate Change Simulations

[29] The treatments involving gradual increases in [CO₂], T, and N input, at rates per 100 years specified in Table 1, were applied to the data so that daily mean values increased gradually while conserving daily (high frequency) variability [cf. McMurtrie *et al.*, 2001]. These climatic change simulations aimed to investigate gradual (linear) increases at the following rates per 100 years (treatments): a [CO₂] increase from 350 to 700 ppm; daily mean maximum and minimum air temperatures and soil temperature increases of 1°, 3°, and 2°C, respectively; and an additional nitrogen (N) input to the inorganic N pool that increases from 0 to 1 g m⁻² yr⁻¹. When applied together, the increases in [CO₂] and temperature approximate the IPCC climate change scenario IS92a [Houghton *et al.*, 1995].

[30] Simulations were initiated by running long-term simulations under current climate. This procedure was continued until the 8-year sum of NEP was zero under current climate; we denote this as “quasi-equilibrium” although technically it includes daily variability that cancels out over the 8-year period. The G'DAY and DAYCENT models were run to quasi-equilibrium before simulating responses to the treatments. The quasi-equilibrium starting point is probably unrealistic for these sites which are expected to have positive NEP. However, we were most interested in the ecosystem response to the treatments without any influence from a system drifting from a pre-existing nonequilibrium state toward a state closer to equilibrium. Starting at quasi-equilibrium allowed us to attribute ecosystem responses wholly to treatments and thereby avoid any confounding response by a nonequilibrium state. All simulations at Kansas and Colorado included grazing. Fire was not factored into simulations at any site.

[31] We simulated outputs of net primary production (NPP) and heterotrophic respiration (R_h) to calculate the

carbon sink ($NEP = NPP - R_h$) responses to various combinations (Table 1) of the three treatments (rising [CO₂], rising T, and rising N input) over the next century. We also output soil carbon (including aboveground and belowground litter) in order to trace changes in NEP to C storage changes in soil versus biomass.

3. Results

[32] Simulations of annual NPP, NEP, and soil C in response to the treatments are shown in Figures 1, 2, and 3, respectively for the strongly water- and N-limited Colorado shortgrass site, the N-limited and moderately water-limited Kansas tallgrass site, and the cooler N-limited Flakaliden forest site.

3.1. Net Primary Productivity

[33] Increasing [CO₂] (treatment C, Table 1) has a positive impact on NPP at all three sites (Figure 1, open squares) for both models. G'DAY shows an initial rapid response that decelerates, most markedly at the nutrient-poor Flakaliden site. DAYCENT shows a more gradual increase over the century at all three sites, and some deceleration is evident at Colorado. At the end of the 104-year period, using G'DAY and DAYCENT, respectively, NPP has increased by approximately 19% and 25% at Colorado, 11% and 12% at Kansas, and 12% and 6% at Flakaliden (Table 2).

[34] The temperature treatment (treatment T, Table 1) enhances soil net N mineralization, directly affects photosynthesis, and alters vapor pressure deficit. Both models predict that the NPP response to increasing temperature will be negative at Colorado and positive at Kansas and Flakaliden (Figure 1, open triangles), except for DAYCENT's simulation of the final 20 years at Flakaliden; the increase in NPP with temperature is related to increased mineralization with higher temperature, the decrease in NPP at the end is accompanied by increasing soil C, and immobilization of N in SOM is inhibiting NPP. Negative responses result from T-induced increases in water stress simulated by both models. After 104 years, using G'DAY and DAYCENT, respectively, NPP responses reached -4.3% and -1.2% at Colorado, +6.5% and +7.2% at Kansas, and +23.8% and -0.9% at Flakaliden (Table 2).

[35] Under the CT treatment (Figure 1, open diamonds) simulated NPP increases more than under either C or T alone. These increases tend to be greater using G'DAY than DAYCENT. Simulated NPP responses to rising [CO₂] and temperature are approximately additive at all sites using DAYCENT, and at Flakaliden using G'DAY, but not at the grasslands (Figures 1 and 4). The nonadditive or interactive effect of rising [CO₂] and temperature on the simulated NPP

response is positive (synergistic), and is largest for G'DAY at the strongly water- and N-limited Colorado site (Figure 4). This synergistic effect relates to the increasing temperature optimum of photosynthesis at high [CO₂] and the alleviation of soil N constraints on the [CO₂] response when the soil is warmed [Medlyn *et al.*, 2000] under alleviated water stress at higher [CO₂].

[36] Increasing N input (treatments CN and CTN, Table 1) stimulates NPP response over the long term for both models, tending to enhance and prolong the rapid initial increase in NPP with increasing [CO₂]. Comparison of simulations C and CN (Figure 1, open squares and solid squares, respectively) indicates that a small increase in N input is sufficient to overcome the progressive soil-N constraint that occurs under treatment C.

[37] Since the NPP responses to treatments tend to be additive under increasing N input, the largest response is the combined treatment CTN (Figure 1, solid diamonds), except at Colorado where responses to CN are also large for both models. At Kansas and Flakaliden, responses to CTN exceed CN because rising temperature enhances N availability, whereas at Colorado, rising temperature tends to enhance water limitation. The NPP enhancements after 104 years under the CTN treatment, using G'DAY and DAYCENT, respectively, are approximately 59% and 101% at Colorado, 55% and 37% at Kansas, and 67% and 62% at Flakaliden (Table 2).

3.2. Heterotrophic Respiration

[38] Differences between simulated NPP and R_h are small relative to their magnitude, and their trends are fairly similar. Therefore we do not display simulations of R_h . How the pattern for R_h differs from NPP can be inferred from the NEP plots (Figure 2). In general, simulated R_h responses to treatment CT were additive using DAYCENT (data not shown) and interactive using G'DAY to similar extents at each site, as for NPP (Figure 4).

3.3. Net Ecosystem Productivity

[39] Simulated annual net ecosystem production (NEP) shown in Figure 2 is obtained by subtracting heterotrophic respiration (carbon loss; R_h) from net primary production. The NEP response to rising [CO₂] is positive at all sites using both models (Figure 2, open squares) indicating larger NPP responses than R_h responses for both models. Both models show evidence of NEP saturation except for DAYCENT at Kansas and Flakaliden. DAYCENT displays smaller positive NEP than G'DAY at Colorado and Flakaliden because DAYCENT simulates more similar increases in NPP and R_h . Under rising [CO₂] the G'DAY model has a peak NEP of 4.4 g C m⁻² yr⁻¹

Figure 1. Simulations of annual net primary productivity (NPP) in response to the various treatments: gradual increases in [CO₂] (denoted C), temperature (T), and nitrogen (N), and their combinations (CT, CN, and CTN) as specified in Table 1. NPP responses are shown for: the strongly water- and N-limited shortgrass steppe at the Colorado site using (a) G'DAY and (b) DAYCENT, the water-limited tallgrass prairie at the Kansas site using (c) G'DAY and (d) DAYCENT, and nutrient-limited Norway spruce at the Flakaliden site using (e) G'DAY and (f) DAYCENT. All curves are 8-year averages of annual NPP. Both models were run to quasi-equilibrium prior to treatment perturbations. The simulated quasi-equilibrium for two loops of the 8-year meteorological data file (first 16 years) is shown as a baseline.

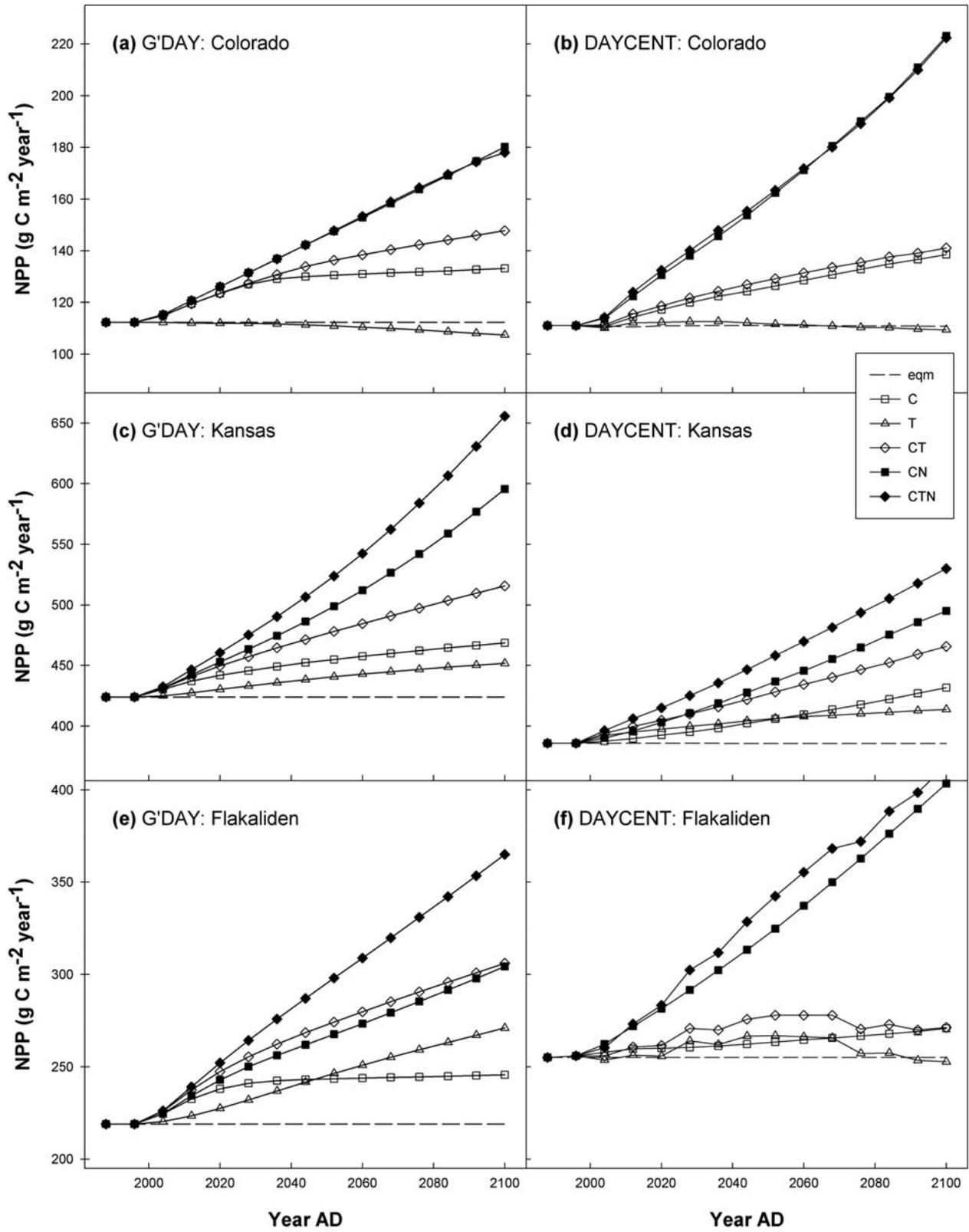


Figure 1

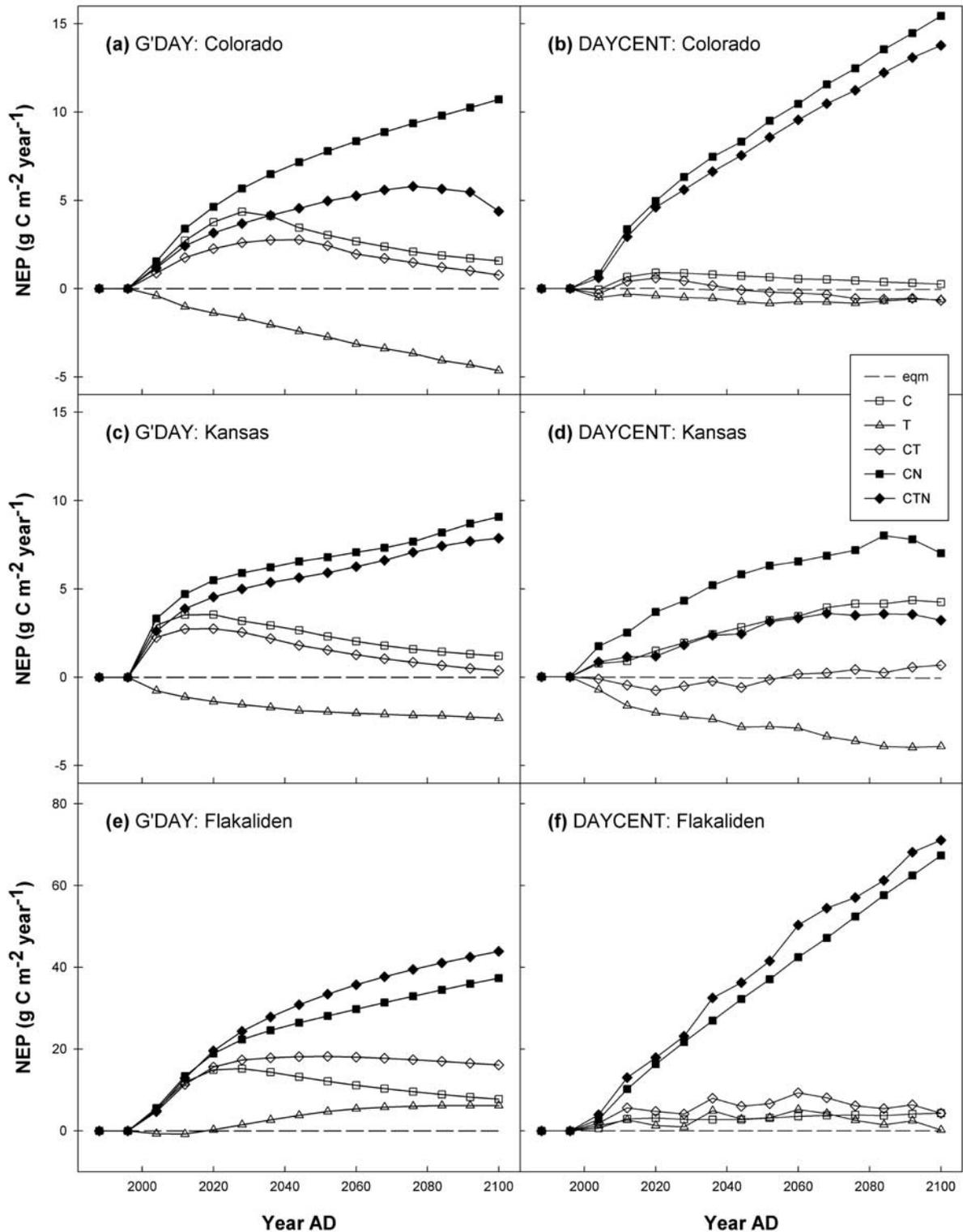


Figure 2. Simulations of annual net ecosystem production (NEP) in response to the various treatments: gradual increases in [CO₂] (denoted C), temperature (T), and nitrogen (N), and their combinations (CT, CN, and CTN), over the 104-year period as specified in Table 1. NEP responses are shown for: the strongly water- and N-limited shortgrass steppe at the Colorado site using (a) G'DAY and (b) DAYCENT, the water-limited tallgrass prairie at the Kansas site using (c) G'DAY and (d) DAYCENT, and nutrient-limited Norway spruce at the Flakaliden site using (e) G'DAY and (f) DAYCENT. All curves are 8-year averages of annual NEP. Both models were run to quasi-equilibrium prior to treatment perturbations. The simulated initial equilibrium (first 16 years) is shown as a baseline.

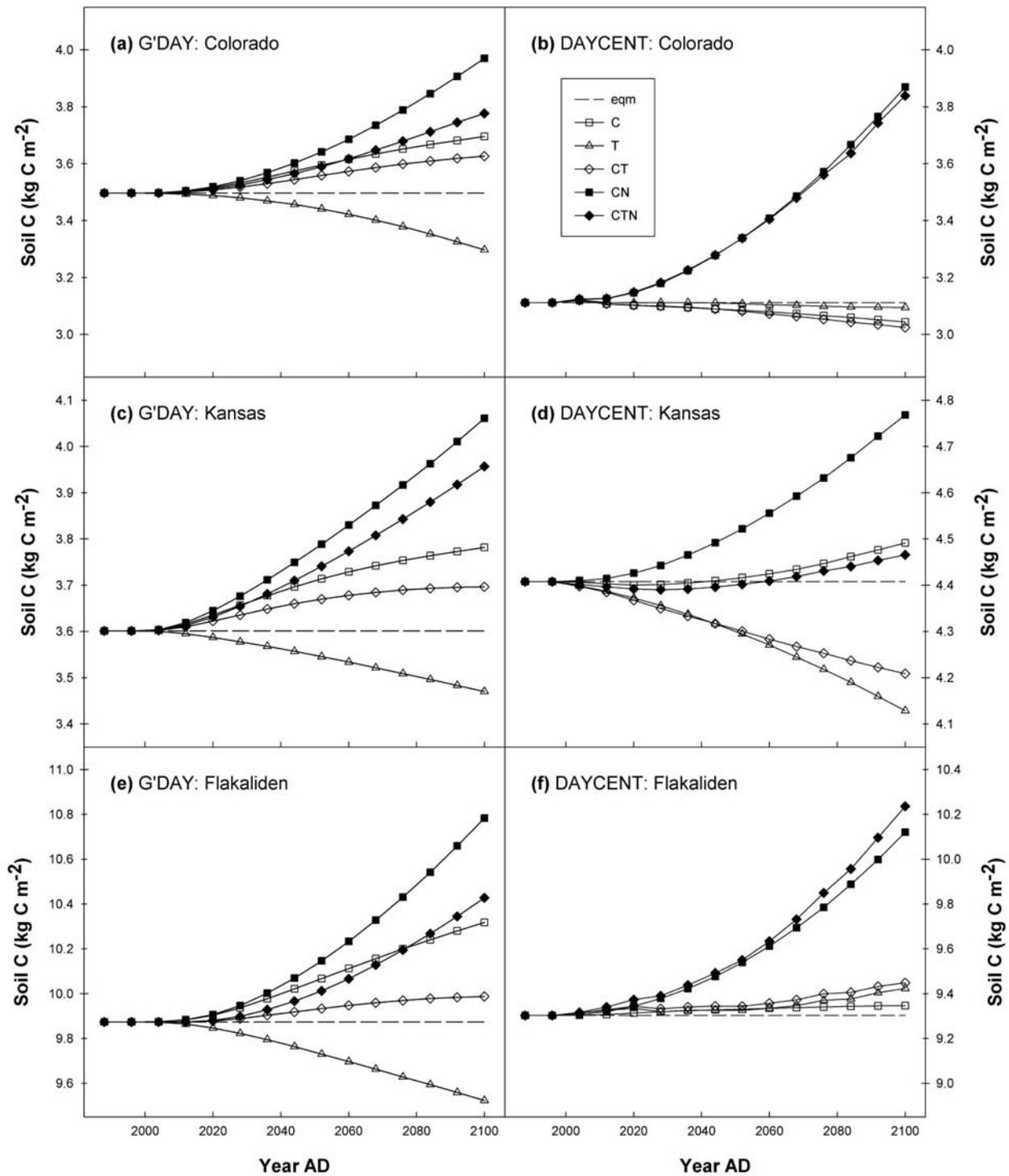


Figure 3. Simulations of soil carbon (soil C) in response to the various treatments: gradual increases in [CO₂] (denoted C), temperature (T), and nitrogen (N), and their combinations (CT, CN, and CTN), over the 104-year period as specified in Table 1. Soil C responses are shown for: the strongly water- and N-limited shortgrass steppe at the Colorado site using (a) G'DAY and (b) DAYCENT, the water-limited tallgrass prairie at the Kansas site using (c) G'DAY and (d) DAYCENT, and nutrient-limited Norway spruce at the Flakaliden site using (e) G'DAY and (f) DAYCENT. All curves are 8-year averages. Both models were run to equilibrium prior to treatment perturbations, and the simulated initial equilibrium (first 16 years) is shown as a baseline.

Table 2. Simulated Treatment Responses of Net Primary Productivity (NPP) and Soil C Expressed as Percent Change After 104 Years Compared to Equilibrium Base Levels^a

	C		T		CT		CN		CTN	
	G'DAY	DAYCENT	G'DAY	DAYCENT	G'DAY	DAYCENT	G'DAY	DAYCENT	G'DAY	DAYCENT
	<i>NPP</i>									
Colorado	18.6	25.1	-4.3	-1.2	31.6	27.3	60.5	101.4	58.5	100.8
Kansas	10.5	11.9	6.5	7.2	21.7	20.7	40.5	28.2	54.7	37.4
Flakaliden	12.2	6.2	23.8	-0.9	39.8	6.4	39.0	58.2	66.8	62.1
	<i>SoilC</i>									
Colorado	5.7	-2.2	-5.7	-0.3	3.7	-2.7	13.6	20.7	8.0	20.0
Kansas	5.0	2.3	-3.6	-6.1	2.6	-4.0	12.8	6.5	9.9	0.0
Flakaliden	4.5	0.5	-3.6	1.1	1.1	1.5	9.2	8.7	5.6	9.8

^aTreatments C, T, CT, CN, and CTN are as per Table 1.

around year 2030 at Colorado, 3.6 g C m⁻² yr⁻¹ around year 2010 at Kansas, and 15.2 g C m⁻² yr⁻¹ around year 2020 at Flakaliden. The post-peak decline is similar at the three sites, but the absolute decline for Flakaliden is more than twice that for Colorado and Kansas. Using DAYCENT, peak NEP is approximately 0.9, 4.4, and 4.3 g C m⁻² yr⁻¹ at Colorado, Kansas, and Flakaliden, respectively.

[40] NEP responses to rising temperature differ qualitatively for forest and grasslands. For the forest, G'DAY predicts an initial transient decrease followed by recovery to a substantial temperature-induced enhancement in NEP that persists over the rest of the century (Figure 2e), whereas DAYCENT predicts a small increase in NEP that declines to approximately zero by 2100 (Figure 2f). For the grassland sites, simulated NEP remains negative over the century under treatment T using both models (Figures 2a–2d).

[41] Increasing N input enhances NEP at all sites for both models. The decline in NEP occurring over the long term under the C treatments does not occur with increasing N input.

[42] As for NPP, the effects of treatments on simulated NEP are approximately additive for DAYCENT at all sites (Table 2) and for G'DAY at Flakaliden (Figure 4). At the grassland sites, G'DAY simulations display greater interactive response to multifactor treatments.

3.4. Soil Carbon

[43] Simulations of soil carbon responses to treatments for the three sites are shown in Figure 3. The effect of increasing [CO₂] is positive at all sites after 104 years, except for DAYCENT at Colorado: +5.7% and -2.2% at Colorado, +5.0% and +2.3% at Kansas, and +4.5% and +0.5% at Flakaliden, for G'DAY and DAYCENT, respectively (Table 2). Soil C responses to [CO₂] and T are smaller for DAYCENT partly because litter C inputs are smaller. Soil C declines under treatment C for DAYCENT at Colorado because decomposition of SOC increases (under wetter soil) more than C inputs to the soil. Note, however, that NEP is positive for treatment C, even though soil C decreases, because NEP also includes C in biomass, and the increase in biomass C exceeds soil C loss.

[44] The positive CO₂ effect on soil C is in contrast to the negative effect of increasing temperature at all sites, except for DAYCENT at Flakaliden: -5.7% and -0.3% after 104 years at Colorado, -3.6% and -6.1% at Kansas, and -3.6%

and +1.1%, at Flakaliden, for G'DAY and DAYCENT, respectively (Table 2 and Figure 3). The temperature response is negative because increasing decomposition exceeds litter C inputs and this leads to reduced soil organic matter. In the case of DAYCENT at Flakaliden, both NPP and NEP increase a small amount under treatment T, and this means the increase in R_h is very small. A small increase in NPP leads to increased litterfall and C flow into SOC pools. Litter C input is greater than C loss from R_h , resulting in net C flux into soil, and soil C accumulates over the century.

[45] Under the CT treatment, G'DAY predicts increased soil C at all sites. For both grasslands the NPP, soil C, and NEP responses are enhanced more under the CT treatment than the summation of separate responses to C and T treatments (Figure 4). DAYCENT, however, predicts that soil C will decrease at the grassland sites under treatment CT but increase at Flakaliden. These differences in soil C response by DAYCENT can be understood from the approximately additive responses to C and T treatments.

[46] Increasing N input increases soil C levels substantially at all sites. Soil C is generally higher under CN than under CTN, except for DAYCENT at Flakaliden, because warming enhances soil decomposition more than NPP.

4. Discussion

[47] We will discuss the above results in the following order: impacts of rising [CO₂], rising temperature, rising [CO₂] and T, and rising N input. We will then discuss new insights into carbon sink saturation and key model sensitivities.

4.1. Under Rising CO₂

[48] Under rising [CO₂] both models predict a sustained C sink (positive NEP) over the next century at all three sites. Generally, NEP (=NPP - R_h) remains positive in the simulations because the predicted net primary productivity NPP response to rising [CO₂] exceeds the predicted response in heterotrophic respiration R_h . However, there are some key similarities and differences between the two models. G'DAY predicts that NEP will increase and peak after 2 to 3 decades, then gradually decline at the grasslands (Figures 2a and 2c) and the forest (Figure 2e). Thus there is a tendency for sink saturation, as previously proposed [Scholes, 1999], as the NPP response decelerates. This is

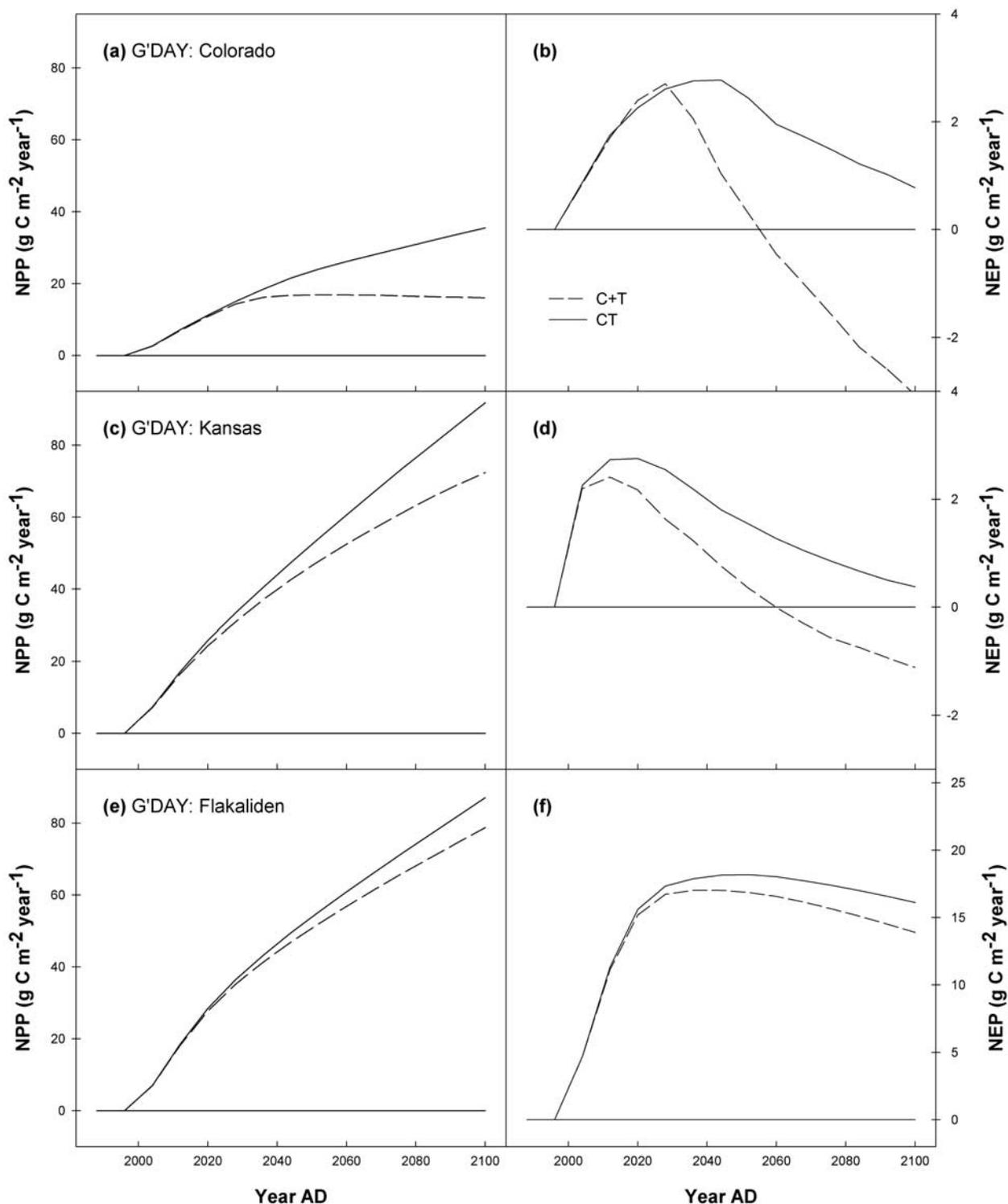


Figure 4. Annual NPP and NEP responses relative to equilibrium levels (shown at the beginning of each simulation in Figures 1 and 2, respectively) using G'DAY. The summation of separate responses to C and T treatments (as specified in Table 1) C + T are shown along with the response to treatment CT for: Colorado (a) NPP and (b) NEP, Kansas (c) NPP and (d) NEP, and Flakaliden (e) NPP and (f) NEP.

consistent with evidence emerging after several years from elevated CO₂ experiments, in which a step increase in [CO₂] is applied, that N feedbacks may progressively limit the NPP response [Luo *et al.*, 2004]. Under rising [CO₂], DAYCENT predicts a small positive NEP response at the shortgrass steppe (Colorado) that peaks and then declines, a small positive response at the forest (Flakaliden), and a strong positive NEP response at the tallgrass prairie (Kansas) that peaks after approximately 8 decades. Thus there is evidence of sink saturation for both models, and this occurs when R_h , although remaining less than NPP for positive NEP, increases at a faster rate than NPP, as NPP becomes progressively N limited. This similarity occurs because the models have similar assumptions about N feedback mechanisms acting on NPP (Table A1). This result highlights the importance of soil nitrogen availability on sink saturation in terrestrial ecosystems.

[49] Differences in simulated NEP between models and sites can be traced to differences in NPP and R_h . Generally, NPP using DAYCENT increases more slowly and takes longer to level off than G'DAY. This difference arises because in DAYCENT, potential NPP and transpiration are linear functions of [CO₂], whereas G'DAY assumes saturating CO₂ functions. A faster rate of increase in NPP leads to greater rates of input of C and N into soil, and of N immobilization into SOM. Another reason why NPP levels off more slowly for DAYCENT is that soil C simulated by DAYCENT increases less than for G'DAY (Figure 3, treatment C), so that N immobilization in SOM is reduced, leading to reduced N-limitation of productivity [Luo *et al.*, 2004]. In spite of these differences, the magnitude of NPP responses to treatment C after 100 years is similar to observations under twice ambient [CO₂] at the grasslands [Morgan *et al.*, 2001; Owensby *et al.*, 1993].

[50] G'DAY predicts that NPP response to rising [CO₂] at the grasslands is larger in relatively dry years (out of the 8-year meteorological data sequence) when water limitation to growth is alleviated more than in wetter years (simulations not shown). This prediction is consistent with experimental results [Owensby *et al.*, 1994, 1999; Morgan *et al.*, 2001, 2004]. At the non-water-limited forest, simulated NPP responses to rising [CO₂] differ little between wet and dry years, implying that alleviation of water limitation to growth is less than at the grassland sites.

[51] Changes in simulated soil C and N:C ratio differ between sites and models. Under rising [CO₂] DAYCENT predicts little change in SOC and soil N:C ratio at Colorado, but a small increase in SOC and little change in N:C ratio at Kansas. At high [CO₂], G'DAY predicts increased soil C at all three sites and reduced N:C ratio of SOM (because of enhanced soil N immobilization leading to decreases in soil inorganic N). Decomposition rates (C outputs) and carbon inputs to soil have been measured for Colorado shortgrass steppe and are both enhanced under high [CO₂] treatments [Pendall *et al.*, 2003, 2004], but experimental measurements of the effect of high [CO₂] on soil C and N:C ratio are not available. The change in soil C over time will depend quantitatively on the balance between these C input and output fluxes. DAYCENT predicts similar changes to NPP and R_h , so there is little change in NEP, which is reflected in

soil C. G'DAY predicts the balance to favor C inputs to soil, derived from an early increase in NPP that exceeds the R_h response. For Kansas tallgrass prairie, however, measured total soil C and N both increased under elevated [CO₂] [Jastrow *et al.*, 2000; Williams *et al.*, 2000, 2004], while soil N:C ratio tended to decrease slightly [Williams *et al.*, 2000]. The increased soil C under elevated [CO₂] was attributed to higher rates of C inputs to soil than decomposition [Williams *et al.*, 2004]. Thus, experimental observations on the tallgrass prairie accord with the predictions of both models for Kansas under gradually increasing [CO₂]. The different soil C results between Colorado and Kansas for DAYCENT are caused by lower N availability at Colorado and greater N constraint to NPP. Experimental measurements of soil C and N:C ratio under high [CO₂] treatments are not available for Norway spruce at Flakaliden. However, for another experimental pine ecosystem (N-limited Loblolly pine at Duke, North Carolina) exposed to high [CO₂] for several years, there is some evidence of increased soil C and N sequestration in SOM [Schlesinger and Lichter, 2001; Finzi *et al.*, 2002]. It is difficult to compare our model results with experimental observations because experiments employ step increases in [CO₂], temperature, or increased N, whereas the model results in this paper assumed gradual increases.

4.2. Under Rising Temperature

[52] At both grassland sites the rising temperature treatment (T) induces declines in NEP and soil C using both models (Figures 2a–2d). Both models predict little change in NPP at Colorado but increasing NPP at Kansas (Figure 1). These results are caused by enhanced water stress at Colorado that constrains NPP (Figures 1a and 1b), and enhanced decomposition at Kansas leading to increased NPP (Figures 1c and 1d) but a larger increase in R_h . At Colorado, decomposition and R_h are constrained by enhanced water stress more for DAYCENT than G'DAY. For DAYCENT, the C sink at Colorado is fairly unresponsive to warming because water stress limits both NPP and decomposition. This contrast between the grassland sites, and between the models, flags the importance of water availability for a C sink response to warming.

[53] At the forest site under rising temperature both models predict positive NEP (Figures 2e and 2f), which is sustained in the long term with G'DAY but declines to zero after 90 years with DAYCENT. According to G'DAY, warming stimulates NPP through a direct effect of elevated temperature on photosynthesis and through enhanced decomposition leading to reduced soil C (Figure 3e) but increased soil N mineralization, whereas DAYCENT predicts small increases in soil N release, NPP, and soil C (Figure 3f). Rising temperature at Flakaliden has little effect on decomposition using DAYCENT because of increased soil moisture limitation, so N limitation to growth is not strongly alleviated. Both models have similar decomposition-temperature relationships, but decomposition in DAYCENT is more sensitive to soil moisture. The G'DAY results agree with data showing a significant warming response on NPP at this site [Strömberg and Linder, 2002]. After 5 years of soil warming treatment at the

Flakaliden site, stemwood production doubled in the irrigated (control) stand and increased by 50% in the irrigated and fertilized stand [Strömngren and Linder, 2002]. This growth response to warming was attributed to the strong effect of increased soil N mineralization on growth (alleviation of growth N limitation was relatively greater in the irrigated unfertilized stand) and increased season length (particularly the effect of increased soil temperature at the beginning of the growing season). Increased total N content in aboveground tree biomass reflected soil N released under soil warming. Measurements of soil-surface CO₂ flux in the Flakaliden soil-warming experiment suggest that R_h acclimated to temperature during the first 5 years [Strömngren and Linder, 2002], partly due to depletion of labile SOM because of enhanced decomposition in warmed soil [Eliasson et al., 2004]. G'DAY simulates positive NEP that levels off in the long term, indicating that the rate of increase in simulated R_h toward the end of the century is similar to that of NPP. Soil C decreases (Figure 3e), which will tend to negatively feedback on R_h .

4.3. Under Rising [CO₂] and T

[54] Under rising [CO₂] and T (treatment CT), G'DAY predicts a substantial positive NEP at all sites whereas DAYCENT predicts a small sustained positive NEP only at Flakaliden. Using G'DAY, both NPP and R_h increase in response to treatment CT at all sites, but the increase in NPP early in the century is larger, so that NEP is substantially positive. On the other hand, DAYCENT predicts positive but similar increases in NPP and R_h at all sites, so that NEP is positive but small at the forest and close to zero at the grasslands. G'DAY predicts larger NPP increases under treatment CT than DAYCENT partly because rising [CO₂] and rising temperature have a pronounced interactive effect using G'DAY but are approximately additive using DAYCENT.

[55] Interactions between rising [CO₂] and temperature can happen in numerous ways, for example, (1) the photosynthetic temperature optimum is higher at elevated [CO₂] [McMurtrie and Wang, 1993]; (2) effects of temperature and [CO₂] on water-use efficiency WUE are nonadditive (equation (1)); (3) effects of temperature and soil moisture on NPP, decomposition, and N mineralization are multiplicative in many models, leading to nonadditive temperature and [CO₂] effects; and (4) NPP and/or decomposition may be water-limited at current [CO₂] and hence less responsive to rising temperature than at elevated [CO₂] where water stress is alleviated owing to improved WUE. Treatments T and C are nonadditive using G'DAY (Figure 4) which incorporates all four interactions above. Nonadditivity is most pronounced at the strongly water-limited Colorado grassland, and is least at the N-limited forest. The C-T interaction is weaker in DAYCENT's simulations. Key differences between the models are that DAYCENT does not incorporate the first and second methods and that they differ in how the third and fourth methods are incorporated (Table A1).

4.4. Under Increasing N Input

[56] NEP responds positively to increasing N input, and C sink saturation is alleviated by a modest increase in N input

(Figure 2). Under increasing N, neither model shows strong evidence of sink saturation or declining NEP. This means that sink saturation is related to soil N limitation. For instance, according to G'DAY, at the strongly water-limited Colorado site, alleviation of water limitation under rising [CO₂] (treatment C) leads to a peak in NEP after ~32 years followed by a decline (Figure 2a), whereas under treatment CN the decline is not evident. The strong N effect on NPP simulated by both models at the forest site agrees with fertilization experiments from this site [Bergh et al., 1999], and the strong NPP response under elevated [CO₂] and N addition at the tallgrass prairie agrees with data showing a significant interaction between these two factors at this site [Owensby et al., 1994].

4.5. Insights Into Carbon Sink Saturation

4.5.1. Grassland Versus Forest

[57] The most striking difference between the grasslands and forest is the NEP response to rising temperature, which is positive over the long term for the forest ecosystem (Figures 2e and 2f) but negative for the grasslands (Figures 2a and 2d). This result highlights the importance of ecosystem structure on C sink response to climate change. An explanation according to G'DAY is that some of the additional NPP in the forest is allocated to woody biomass where carbon can be stored for a long time compared to foliage and fine roots. Even a small allocation of released N to low N:C ratio woody biomass can be sufficient to produce a substantial increase in ecosystem C storage (Figure 2e) [Rastetter et al., 1992; Shaver et al., 2000]. The presence of woody biomass provides a low N:C ratio pool that allows the system to store more carbon under rising temperature for the same total system N content. This mechanism for increased C storage under warming is absent for grasslands, where plant carbon is stored in foliage and roots, which have higher N:C ratios and faster turnover than woody biomass.

4.5.2. Effects of Water Limitation

[58] At the water-limited grasslands, NEP is sensitive to rising [CO₂] because enhanced water-use efficiency at high [CO₂] leads to wetter soils, which enhances both NPP and decomposition. The effect on decomposition is more sensitive for DAYCENT, so that under higher [CO₂], soil moisture limitation to decomposition is alleviated more using DAYCENT than G'DAY. In DAYCENT, transpiration is directly reduced under high [CO₂] so that water savings are immediately reflected in soil moisture. Simulated R_h response to rising [CO₂] is thus greater for DAYCENT than G'DAY at the strongly water-limited Colorado site, which explains why DAYCENT predicts lower NEP than G'DAY at Colorado. Higher water contents under elevated [CO₂] simulated by DAYCENT for the grassland sites agree with data from both sites [Mosier et al., 2002; Morgan et al., 2004]. Increased R_h simulated by both models at the short-grass steppe is also consistent with observations of higher decomposition rates under elevated [CO₂] at this site [Pendall et al., 2003]. Assumptions about the sensitivity of decomposition to water savings under rising [CO₂] between the two models at Colorado have an important influence on the magnitude of simulated NEP. Water sav-

ings occur and soil respiration does respond to experiments at Colorado that use a step increase in [CO₂], but the response to gradually increasing [CO₂] has not received enough attention to resolve this difference between the models.

[59] Care should be taken in extrapolating the results reported in this paper to different systems. For example, observations from the two grasslands considered here have shown significantly higher soil water under elevated [CO₂] whereas observations for a drier grassland in the Mojave Desert, Nevada, showed no increase in soil water content [Morgan *et al.*, 2004]. Thus Morgan *et al.* [2004] argue that a minimum level of water is needed before a CO₂-induced water effect can be observed. In very dry systems, available water may be lost via evaporation and transpiration regardless of high [CO₂], but in moderately dry systems, high [CO₂] can induce a more gradual decline in soil water content after rain events. Morgan *et al.* [2004] conclude, however, that in many situations, indirect moisture effects alone can account for observed increases in grassland biomass under elevated [CO₂].

4.5.3. Effects of N Limitation

[60] Cramer *et al.* [2001] predict negative global terrestrial NEP under rising temperature [see also Schimel *et al.*, 2001]. This prediction is consistent with the T simulations by G'DAY and DAYCENT for the grasslands (Figures 2a–2d) but not for the forest (Figures 2e–2f). Of the six DGVMs considered by Cramer *et al.* [2001], all of which incorporate ecophysiological effects of temperature on NPP, only HYBRID [Friend *et al.*, 1997] and SDGVM [Woodward *et al.*, 1998, 2001] simulate soil C-N interactions in soil and litter decomposition. It is these interactions that underlie our predictions of positive NEP under rising temperature at the forest site [cf. Wullschleger *et al.*, 2001].

[61] The average simulation of DGVMs by Cramer *et al.* [2001] in response to rising [CO₂] shows a large global terrestrial C sink that is dissimilar to the pattern of NEP under our C simulation but is similar to our CN simulations (Figures 2a, 2c, and 2e). Thus the absence of sink saturation in our treatments CN and CTN is consistent with simulations of DGVMs that do not include soil-N limitation feedbacks [Cramer *et al.*, 2001; Houghton *et al.*, 2001]. The contrast with our simulations C and CT, where there is evidence of sink saturation, indicates that controls on soil N availability, and in particular soil N immobilization, are crucial in determining the future of terrestrial C sinks [McMurtrie *et al.*, 2001]. When N limitations are relieved under our CN and CTN treatments, the two models have similar NPP and NEP responses. This result supports previous claims that soil N feedbacks dominate the long-term responses to rising [CO₂] and temperature [McMurtrie and Comins, 1996; Medlyn *et al.*, 2000; McMurtrie *et al.*, 2001].

[62] Experimental evidence indicates that the fraction of mineralized N that is immobilized in soil can be high [Nadelhoffer *et al.*, 1999], but the mechanisms of N immobilization are not well understood. Suggested mechanisms include an increase in microbial population [Aber *et al.*, 1998], abiotic incorporation directly into soil organic matter [Berg and Theander, 1984; Dail *et al.*, 2001],

conversion to organic nitrogen forms by mycorrhizae, and a change in soil N:C ratio without a change in efflux implying a change in microbial populations to ones with different N requirements [McMurtrie *et al.*, 2001]. A modest gradual annual increase in N input (0.01 g m⁻² yr⁻¹) here is enough to override progressive soil N limitation with rising [CO₂]. The additional 0.01 g m⁻² N input per year accumulates over the 104 years to 50 g N m⁻², which is sufficient to support increased ecosystem C storage of 752, 696, and 2728 g C m⁻² at Colorado, Kansas, and Flakaliden, respectively, for the CN treatment using G'DAY, and 950, 585, and 3813 g C m⁻² using DAYCENT. These increases in C storage can be expressed relative to initial NPP. The increase in C storage over 104 years at Colorado, Kansas, and Flakaliden is, respectively, 6.7, 1.6, and 12.5 times initial NPP according to G'DAY, and 8.6, 1.5, and 15 times according to DAYCENT. It is interesting to compare these results with global simulations from Cramer *et al.* [2001]. Their six DGVMs predicted 350 to 890 Pg of carbon (1 Pg = 10¹⁵ g) to accumulate in the terrestrial biosphere by year 2100 under increasing atmospheric [CO₂] alone [Hungate *et al.*, 2003], which represents 6–15 times an initial global terrestrial NPP of 60 Pg C yr⁻¹ [Cramer *et al.*, 2001]. Assuming no change in N:C ratios of trees and soils, this increase in terrestrial C storage requires an additional N input of 7.7 to 37.5 Pg, which is much higher than current estimates of global atmospheric N deposition over the next century [Hungate *et al.*, 2003]. Further modeling analysis and data-model integration focused on C and N cycle responses to elevated [CO₂] and temperature is needed [e.g., Luo *et al.*, 2004]. Increased nitrogen fixation would be expected to alleviate both progressive N limitation and C sink saturation to some extent. Gifford [1992, 1994] argues that there would be a small annual increase in N fixation with increased carbon availability, which would be sufficient over periods of 1 century or more to alleviate N limitation to plant productivity. An increased flow of carbon to soil under elevated [CO₂], as litter, exudate, or a direct flow to mycorrhizae, that stimulates microbial activity could increase N mineralization and N fixation, and thus N availability for plants [Zak *et al.*, 1993]. Trends in foliar N concentration of herbarium specimens have declined over the last 250 years [Peñuelas and Estiarte, 1997], and leaf δ¹⁵N in the same specimens has declined as well, suggesting that increased N fixation and soil N mineralization, and decreased soil N losses, may have occurred during this period. Measurement of the atmospheric N fixation response to elevated [CO₂], and assessment of carbon costs (energy) and benefits (net C gain) associated with N fixation at particular sites, would be useful information. Although the treatments with added N inputs (CN and CTN) are fairly crude approximations to the complex N fixation process, our simulations highlight the importance of N availability on C sink saturation across these different sites.

[63] Thus our CN simulations are similar to Cramer *et al.*'s [2001] C simulation, in that both show large NPP responses and sustained positive NEP response with little evidence of sink saturation. In our simulations with rising [CO₂] without increased N input (treatments C and CT), there is evidence of sink saturation. This carbon sink

Table A1. Key Model Algorithms and Parameters, and CO₂, T, and N Effects^a

Process	G'DAY	DAYCENT
Light interception	Beer's law, separation into sunlit and shaded foliage for forest but not for grassland	radiation effect on NPP and transpiration
Leaf photosynthesis of forest	rectangular hyperbolic function of light and leaf [N], responsive to temperature and [CO ₂] [<i>Medlyn et al.</i> , 2000]; photosynthesis is calculated using the <i>Farquhar and von Caemmerer</i> [1982] model of C ₃ leaf photosynthesis, where key parameters (V_{cmax} , J_{max} , K_{mp} , Γ^*) are affected by temperature, and intercellular CO ₂ concentration c_i is a fixed fraction of atmospheric concentration c_a ; V_{cmax} , J_{max} are linearly related to leaf N content	N/A
GPP of forest	derived by integrating down the canopy with N declining exponentially giving GPP analytically as a function of LAI, mean foliage N:C ratio, incident photosynthetically active radiation (PAR), and mean temperature [<i>Medlyn et al.</i> , 2000]	N/A
GPP of grass	proportional to absorbed PAR with light use efficiency a function of leaf N:C ratio [<i>McMurtrie</i> , 1991]	N/A
Respiration	fixed fraction of GPP	function of NPP and temperature
Net primary production (NPP)	GPP minus respiration	function of radiation, nutrients, water, and temperature
c_i/c_a ratio	constant	N/A
C allocation	fixed fraction of NPP allocated to foliage, wood, fine roots	dynamic allocation based on plant phenology and water and nutrient stress
Senescence	constant litterfall rates for foliage, wood, fine roots	function of plant phenology and water and nutrient stress
Plant N:C ratios	leaf N:C ratio varies dynamically; fine root and wood N:C ratios proportional to live foliage N:C ratio	dynamic ratios based on N availability
Litter N:C ratio	retranslocation of a fixed fraction (e.g., 0–50%) of leaf N and fine root N at senescence	based on litter source N:C ratio
N retranslocation	fixed fractions (e.g., 0–50%) of foliage, nonstructural wood (sapwood), fine root N contents (no root N retranslocation for grass)	fixed fraction of leaf N content
Soil C dynamics	derived from CENTURY model [<i>Parton et al.</i> , 1987, 1993], decomposition rates of litter and SOM are a function of soil temperature, moisture, N:C ratio, and lignin content; soil texture effect on active and slow SOM	decomposition rates of litter and SOM are a function of soil temperature, moisture, N:C ratio, and lignin content; soil texture effect on active and slow SOM
Soil N dynamics	daily change of soil inorganic N (N_{inorg}) modeled as gross N mineralization plus N deposition minus microbial immobilization, plant N uptake, N loss via leaching/gaseous emission	rate of change of soil inorganic N (N_{inorg}) modeled as gross N mineralization plus N deposition/fixation, plant N uptake, N loss via leaching/gaseous emission
Soil N:C ratio	N:C ratios of substrate entering active, slow, passive SOM are linear functions of N_{inorg} ; dynamic	C:N ratios of substrate entering active, slow, passive SOM, are linear functions of N_{inorg} ; dynamic

Table A1. (continued)

	Process	G'DAY	DAYCENT
N input	constant inputs from atmospheric deposition and symbiotic fixation		atmospheric inputs and non-symbiotic fixation functions of precipitation and AET, symbiotic fixation function of vegetation type and NPP
N loss	leaching and soil gaseous emission rates proportional to soil inorganic N pool		gas losses from nitrification, denitrification, nitrate leaching from rooting zone
Plant N uptake	proportional to soil inorganic N content [McMurtrie <i>et al.</i> , 2001]; uptake is limited by maximum plant N:C ratios		function of soil inorganic N content, LAI, radiation, and vegetation type
Grazing	consumption rate expressed as a fraction of foliage production		consumption rate expressed as a fraction of foliage production
C loss in grazing	fixed fraction of C eaten, with remainder entering soil as faeces		fixed fraction of C eaten, with remainder entering soil as faeces
N input to soil by grazers	fixed fraction of N eaten, as either faeces with constant N:C ratio or urine		fixed fraction of N eaten, as either faeces with constant N:C ratio or urine
Water balance	Components: canopy interception, runoff and drainage, soil evaporation (top layer), evapotranspiration; tipping bucket model (soil evaporation and water factor on decomposition depend on moisture in top layer)		Components: canopy interception, runoff and drainage, soil evaporation (top layer), evapotranspiration from root zone; tipping bucket model; Richard's equation for water flow
Evapotranspiration	C ₃ and C ₄ : minimum of light- and water-limited rates; water-limited rate is determined from PAW and fine root mass; light-limited rate is NPP divided by WUE		function of PET, LAI, and soil water
Water-use efficiency	positively related to [CO ₂], inversely proportional to VPD (equation (1))		
CO ₂ , T, N effects GPP or NPP	CO ₂ effect: based on Farquhar and von Caemmerer model, only for light-limited productivity at Flakaliden; T effect: on photosynthesis; N effect: leaf N:C ratio affects photosynthesis		CO ₂ effect: under treatment C (Table 1) linear change in maximum NPP, $\Delta_{NPPmax} = +25\%$ Flakaliden, $+20\%$ Kansas, $+10\%$ Colorado T effect: bell-shaped curve with minimum, maximum, and optimum T specific for different vegetation N effect: N factor in NPP function
ET	CO ₂ effect: under treatment C (Table 1) change in WUE, $\Delta_{WUE} = +63\%$; T effect: increases soil evaporation and VPD; N effect: indirect increases to leaf N:C ratio increase transpiration via WUE effect		CO ₂ effect: under treatment C (Table 1) change in evapotranspiration; $\Delta_{ET} = -10\%$ Flakaliden; $\Delta_{ET} = -40\%$ grasslands; T effect: increases PET, N effect: indirect increases to LAI can impact transpiration and soil moisture
Decomposition	function of soil moisture, T, litter N:C ratio, litter lignin and soil texture; CO ₂ effect: increased WUE leads to increased soil moisture in the topsoil layer; reduced leaf N:C ratio affects litter quality; T effect: temperature activity factor is zero soil $T \leq 0^\circ\text{C}$ or a function of soil $T > 0^\circ\text{C}$, $0.0326 + 0.00351 \cdot (T_{soil})^{1.652} - \left(\frac{T_{soil}}{41.748}\right)^{7.19}$; N effect: N:C ratio of material entering SOM pools is a function of soil inorganic N pool; indirect increases to LAI can impact transpiration and soil moisture constraint on decomposition; lignin:N ratio of litter constrains decomposition rates		function of soil moisture, T, litter N:C, and litter lignin and soil texture; CO ₂ effect: increased WUE can lead to increased soil moisture; reduced leaf N:C ratio affects litter quality; T effect: variable Q10 used-Q10 value highest at low T, decreases with T increase, little effect for $T > 30^\circ\text{C}$ N effect: N:C ratio of material entering SOM pools is a function of soil inorganic N pool; indirect increases to LAI can impact transpiration and soil moisture constraint on decomposition; lignin:N ratio of litter constrains decomposition rates

^aAbbreviations used: AET, actual evapotranspiration; [CO₂], CO₂ concentration; T, temperature; N, nitrogen; ET, evapotranspiration; GPP, gross primary production; LAI, leaf area index; N/A, not applicable; NPP, net primary production; PAW, plant available water; PET, potential evapotranspiration; VPD, vapor pressure deficit; and Δ , change with a doubling of [CO₂] from 350 to 700 ppm, where subscripted abbreviations denote the variable to which the change applies.

saturation is consistent with Scholes' prediction of C sink saturation under rising [CO₂] and temperature [Scholes, 1999; Scholes *et al.*, 1999]. However, the mechanism invoked by Scholes (that NPP approaches CO₂ saturation whereas respiration increases exponentially with temperature) differs from the mechanism operating in our simulations, where saturation is a consequence of soil N feedbacks, and where the effect of rising temperature differs between forest and grasslands and between water- and N-limited ecosystems.

4.5.4. Key Sensitivities to Carbon Storage

[64] For increased C storage in an N-limited system, there must be (1) increased N input or (2) reduced N output, (3) reduced N:C ratios or (4) a shift of N from soil (with high N:C ratio) to plant (with low N:C ratio) [Rastetter *et al.*, 1992]. These four properties are useful for understanding key sensitivities of modeled C storage. The forest simulations under treatment T are consistent with the fourth property. The reduction in soil N:C ratio simulated under treatment C is consistent with the third property [McMurtrie *et al.*, 2001]. There is also evidence of the first property in the CN and CTN simulations. Feedbacks impacting on NPP or R_h are thus important for predicting long-term NEP response to global change, and may vary across contrasting ecosystems.

5. Conclusions

[65] Both G'DAY and DAYCENT predict that the C sink in two grasslands and a boreal forest will be sustained over the next century. The results of this study do not therefore support recent claims that increasing decomposition under rising temperature, in a [CO₂]-enhanced world, will lead to a negative C sink [Woodwell, 1990; Pearce, 1999; Scholes, 1999; Kirschbaum, 2000]. The future carbon sink in an ecosystem depends on site environmental factors (water, temperature, and nutrient status) and vegetation type (here grassland versus forest). The proportions of grass and forest in ecosystems will be important, especially for predicting NEP response to a warming climate. The sensitivities of ecosystem NPP and decomposition responses to gradually increasing [CO₂] and temperature are important for predicting the size of the terrestrial C sink. Key scientific uncertainties that will affect the size of the terrestrial C sink over the next century include future level of N inputs and changes in rates of N immobilization in soil organic matter.

Appendix A

[66] To assist with the comparison of G'DAY and DAYCENT models, major processes incorporated in the models are described in Table A1. Key effects of rising [CO₂], rising temperature, and increasing N input on productivity, water use, and decomposition are summarized toward the end of Table A1. Further details may be found in section 2 and references cited there.

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References

- Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez (1998), Nitrogen saturation in temperate forest ecosystems: Hypotheses revisited, *BioScience*, *48*, 921–934.
- Anderson, J. M. (1991), The effects of climate change on decomposition processes in grassland and coniferous forests, *Ecol. Appl.*, *1*, 326–347.
- Berg, B., and O. Theander (1984), Dynamics of some nitrogen fractions in decomposing Scots pine needle litter, *Pedobiologia*, *27*, 261–267.
- Bergh, J., R. E. McMurtrie, and S. Linder (1998), Climatic factors controlling the productivity of Norway spruce: A model-based analysis, *For. Ecol. Manage.*, *110*, 127–139.
- Bergh, J., S. Linder, T. Lundmark, and B. Elfving (1999), The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden, *For. Ecol. Manage.*, *119*, 51–62.
- Bonan, G. B., and K. van Cleve (1991), Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forests, *Can. J. For. Res.*, *22*, 629–639.
- Bremer, D. J., J. M. Ham, and C. E. Owensby (1996), Effect of elevated atmospheric carbon dioxide and open top chambers on transpiration in tallgrass prairie, *J. Environ. Qual.*, *25*, 691–701.
- Cao, M., and F. I. Woodward (1998), Net primary ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change, *Global Change Biol.*, *4*, 185–198.
- Comins, H. N., and R. E. McMurtrie (1993), Long-term response of nutrient-limited forests to CO₂-enrichment: Equilibrium behaviour of plant-soil models, *Ecol. Appl.*, *3*, 666–681.
- Cramer, W., and P. Canadell (2000), Future trajectories of global terrestrial carbon fluxes, *GCTE News*, *15*, 3 pp.
- Cramer, W., *et al.* (2001), Global response of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models, *Global Change Biol.*, *7*, 357–373.
- Dail, D. B., E. A. Davidson, and J. Chorover (2001), Rapid abiotic transformation of nitrate in an acid forest soil, *Biogeochemistry*, *54*, 131–146.
- Del Grosso, S. J., W. J. Parton, A. R. Mosier, D. S. Ojima, A. E. Kulmala, and S. Phongpan (2000), General model for N₂O and N₂ gas emissions from soils due to denitrification, *Global Biogeochem. Cycles*, *14*, 1045–1060.
- Del Grosso, S. J., W. J. Parton, A. R. Mosier, M. D. Hartman, J. Brenner, D. S. Ojima, and D. S. Schimel (2001), Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model, in *Modeling Carbon and Nitrogen Dynamics for Soil Management*, pp. 303–332, CRC Press, Boca Raton, Fla.
- Del Grosso, S. J., D. S. Ojima, W. J. Parton, A. R. Mosier, G. A. Peterson, and D. S. Schimel (2002), Simulated effects of dryland cropping intensification on soil organic matter and greenhouse gas exchanges using the DAYCENT ecosystem model, *Environ. Pollut.*, *116*, S75–S83.
- Dewar, R. C. (1997), A simple model of light and water use evaluated for *Pinus radiata*, *Tree Physiol.*, *17*, 259–265.
- Dewar, R. C., B. E. Medlyn, and R. E. McMurtrie (1999), Acclimation of the respiration photosynthesis ratio to temperature: insights from a model, *Global Change Biol.*, *5*, 615–622.
- Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski (1994), Carbon pools and flux of global forest ecosystems, *Science*, *263*, 185–190.
- Eitzinger, J., W. J. Parton, and M. Hartman (2000), Improvement and validation of a daily soil temperature submodel for freezing/thawing periods, *Soil Sci.*, *165*, 525–534.
- Eliasson, P. E., R. E. McMurtrie, D. A. Pepper, M. Strömberg, S. Linder, and G. I. Ågren (2004), The response of heterotrophic CO₂-flux to soil warming, *Global Change Biol.*, *10*, doi:10.1111/j.1365-2486.2004.00878.x.
- Farquhar, G. D., and S. von Caemmerer (1982), Modelling of photosynthetic response to environmental conditions, in *Physiological Plant Ecology II, Water Relation and Carbon Assimilation, Encycl. Plant Physiol., New Ser.*, vol. 12B, edited by O. L. Lange *et al.*, pp. 549–587, Springer-Verlag, New York.
- Finzi, A. C., E. H. DeLucia, J. G. Hamilton, D. D. Richter, and W. H. Schlesinger (2002), The nitrogen budget of a pine forest under free-air CO₂ enrichment, *Oecologia*, *132*, 567–578.
- Friend, A. D., A. K. Stevens, R. G. Knox, and M. G. R. Cannell (1997), A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0), *Ecol. Model.*, *95*, 249–287.

- Gifford, R. M. (1992), Interaction of carbon dioxide with growth limiting environmental factors in vegetation productivity: Implications for the global carbon cycle, *Adv. Bioclimatol.*, 1, 24–58.
- Gifford, R. M. (1994), The global carbon cycle: A viewpoint on the missing sink, *Aust. J. Plant Physiol.*, 21, 1–15.
- Gifford, R. M. (2003), Plant respiration in productivity models: Conceptualisation, representation and issues for global terrestrial carbon-cycle research, *Funct. Plant Biol.*, 30, 171–186.
- Glassy, J. M., and S. W. Running (1994), Validating diurnal climatological logic of the MT-CLIM model across a climatic gradient in Oregon, *Ecol. Appl.*, 4, 248–257.
- Hall, D. O., and J. M. O. Scurlock (1991), Climate change and productivity of natural grasslands, *Ann. Bot.*, 67, 49–55.
- Halliday, J. C., K. R. Tate, R. E. McMurtrie, and N. A. Scott (2003), Mechanisms for changes in soil carbon storage with pasture to *Pinus radiata* land-use change, *Global Change Biol.*, 9, 1294–1308.
- Ham, J. M., C. E. Owensby, P. I. Coyne, and D. J. Bremer (1995), Fluxes of CO₂ and water vapour from a prairie ecosystem exposed to ambient and elevated atmospheric CO₂, *Agric. For. Meteorol.*, 77, 73–93.
- Hamerlynck, E. P., C. A. McAllister, A. K. Knapp, J. M. Ham, and C. E. Owensby (1997), Photosynthetic gas exchange and water relation responses of three tallgrass prairie species to elevated carbon dioxide and moderate drought, *Int. J. Plant Sci.*, 158, 608–616.
- Houghton, J. T., L. G. Meira Filho, J. Bruce, H. Lee, B. A. Callander, E. Haites, N. Harris, and K. Maskell (Eds.) (1995), *Climate Change 1994: Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92 Emission Scenarios*, edited by J. T. Houghton et al., Cambridge Univ. Press, New York.
- Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (Eds.) (2001), *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge Univ. Press, New York.
- Houghton, R. A., E. A. Davidson, and G. M. Woodwell (1998), Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance, *Global Biogeochem. Cycles*, 12, 25–34.
- Hungate, B. A., J. S. Dukes, M. R. Shaw, Y. Luo, and C. B. Field (2003), Nitrogen and climate change, *Science*, 302, 1512–1513.
- Jarvis, P., and S. Linder (2000), Botany: Constraints to growth of boreal forests, *Nature*, 405, 904–905.
- Jastrow, J. D., R. M. Miller, and C. E. Owensby (2000), Long-term effects of elevated atmospheric CO₂ on below-ground biomass and transformations to soil organic matter in grassland, *Plant Soil*, 224, 85–97.
- Kelly, R. H., W. J. Parton, M. D. Hartman, L. K. Stretch, D. S. Ojima, and D. S. Schimel (2000), Intra-annual and interannual variability of ecosystem processes in shortgrass steppe, *J. Geophys. Res.*, 105, 20,093–20,100.
- Kirschbaum, M. U. F. (2000), Will changes in soil organic carbon act as a positive or negative feedback on global warming?, *Biogeochemistry*, 48, 21–51.
- Knapp, A. K., E. P. Hamerlynck, and C. E. Owensby (1993), Photosynthetic and water relations responses to elevated CO₂ in the C₄ grass *Andropogon gerardii*, *Int. J. Plant Sci.*, 154, 459–466.
- Knapp, A. K., M. Cocco, E. P. Hamerlynck, and C. E. Owensby (1994), Effect of elevated CO₂ on stomatal density and distribution in a C₄ grass and a C₃ forb under field conditions, *Ann. Bot.*, 74, 595–599.
- Knapp, A. K., E. P. Hamerlynck, J. M. Ham, and C. E. Owensby (1996), Responses in stomatal conductance to elevated CO₂ in 12 grassland species that differ in growth form, *Vegetatio*, 125, 31–41.
- Lieth, H. (1972), Modelling the primary productivity of the world, UNESCO, Paris, *Nature Resour.*, 8, 5–10.
- Luo, Y., et al. (2004), Progressive nitrogen limitation of ecosystem responses to rising atmospheric CO₂, *BioScience*, 54, 731–739.
- McMurtrie, R. E. (1991), Relationship of forest productivity to nutrient and carbon supply—A modelling analysis, *Tree Physiol.*, 9, 87–99.
- McMurtrie, R. E., and H. N. Comins (1996), The temporal response of forest ecosystems to doubled atmospheric CO₂ concentration, *Global Change Biol.*, 2, 49–57.
- McMurtrie, R. E., and Y. P. Wang (1993), Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures, *Plant Cell Environ.*, 16, 1–13.
- McMurtrie, R. E., D. A. Rook, and F. M. Kelliher (1990), Modelling the yield of *Pinus radiata* on a site limited by water and nitrogen, *For. Ecol. Manage.*, 31, 381–413.
- McMurtrie, R. E., H. N. Comins, M. U. F. Kirschbaum, and Y.-P. Wang (1992), Modifying forest growth models to take account of effects of elevated CO₂ concentrations, *Aust. J. Bot.*, 40, 657–677.
- McMurtrie, R. E., B. E. Medlyn, and R. C. Dewar (2001), Increased understanding of nutrient immobilization in soil organic matter is critical for predicting the carbon sink strength of forest ecosystems over the next 100 years, *Tree Physiol.*, 21, 831–839.
- Medlyn, B. E., R. E. McMurtrie, R. C. Dewar, and M. P. Jeffreys (2000), Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO₂ concentration, *Can. J. For. Res.*, 30, 873–888.
- Medlyn, B. E., A. Rey, C. V. M. Barton, and M. Forstreuter (2001), Above-ground growth responses of forest trees to elevated atmospheric CO₂ concentrations, in *The Impact of Carbon Dioxide and Other Greenhouse Gases on Forest Ecosystems: Report No. 3 of the IUFRO Task Force on Environmental Change*, pp. 127–146, CABI Pub., Wallingford, UK.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore, C. J. Vorosmarty, and A. L. Schloss (1993), Global climate change and terrestrial net primary production, *Nature*, 363, 234–240.
- Metherell, A. K., L. S. Harding, C. V. Cole, and W. J. Parton (1993), CENTURY Soil Organic Matter Model Environment: Technical documentation, agroecosystem version 4.0, *Great Plains Syst. Res. Unit Tech. Rep. 4*, USDA-ARS, Fort Collins, Colo.
- Monteith, J. L. (1986), How do crops manipulate water supply and demand?, *Philos. Trans. R. Soc. London, Ser. A*, 316, 245–259.
- Monteith, J. L., A. K. S. Huda, and D. Midya (1989), RESCAP: A resource capture model for sorghum and pearl millet, in *Modelling the Growth and Development of Sorghum and Pearl Millet*, edited by S. M. Virmani, H. L. S. Tandon, and G. Alagarswamy, pp. 30–34, *Res. Bull. 12*, Int. Crops Res. Inst. for the Semi-Arid Tropics (ICRISAT), Patancheru, India.
- Morgan, J. A., D. R. Lecaïn, A. R. Mosier, and D. G. Milchunas (2001), Elevated CO₂ enhances water relations and productivity and affects gas exchange in C₃ and C₄ grasses of Colorado shortgrass steppe, *Global Change Biol.*, 7, 451–466.
- Morgan, J. A., et al. (2004), Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂, *Oecologia*, 140, 11–25.
- Morison, J. I. L. (1993), Response of plants to CO₂ under water limited conditions, *Vegetatio*, 104/105, 193–209.
- Mosier, A. R., W. J. Parton, D. W. Valentine, D. S. Ojima, D. S. Schimel, and J. A. Delgado (1996), CH₄ and N₂O fluxes in the Colorado shortgrass steppe: I. Impact of landscape and nitrogen addition, *Global Biogeochem. Cycles*, 10, 387–399.
- Mosier, A. R., W. J. Parton, D. W. Valentine, D. S. Ojima, D. S. Schimel, and O. Hienemeyer (1997), CH₄ and NO_x fluxes in the Colorado shortgrass steppe: 2. Long-term impact of land use change, *Global Biogeochem. Cycles*, 11, 29–42.
- Mosier, A. R., J. A. Morgan, J. Y. King, D. Lecaïn, and D. G. Milchunas (2002), Soil-atmosphere exchange of CH₄, CO₂, NO_x and N₂O in Colorado shortgrass steppe under elevated CO₂, *Plant Soil*, 240, 201–211.
- Nadelhoffer, K. J., B. A. Emmett, P. Gundersen, O. J. Kjønaas, C. J. Koopmans, P. Schleppi, A. Tietema, and R. F. Wright (1999), Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests, *Nature*, 398, 145–148.
- Oren, R., et al. (2001), Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere, *Nature*, 411, 469–472.
- Owensby, C. E., P. I. Coyne, J. M. Ham, L. M. Auen, and A. K. Knapp (1993), Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂, *Ecol. Appl.*, 3, 644–653.
- Owensby, C. E., L. M. Auen, and P. I. Coyne (1994), Biomass production in a nitrogen-fertilized tallgrass prairie ecosystem exposed to ambient and elevated levels of CO₂, *Plant Soil*, 165, 105–113.
- Owensby, C. E., J. M. Ham, A. K. Knapp, and L. M. Auen (1999), Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂, *Global Change Biol.*, 5, 497–506.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima (1987), Analysis of factors controlling soil organic matter levels in Great Plains grasslands, *Soil Sci. Soc. Am. J.*, 51, 1173–1179.
- Parton, W. J., et al. (1993), Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide, *Global Biogeochem. Cycles*, 7, 785–809.
- Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel (1994), A general model for soil organic matter dynamics: Sensitivity to litter chemistry, texture and management, in *Quantitative Modeling of Soil Forming Processes*, *Spec. Publ. 39*, pp. 147–167, Soil Sci. Soc. of Am., Madison, Wis.
- Parton, W. J., A. R. Mosier, D. S. Ojima, D. W. Valentine, D. S. Schimel, K. Weier, and K. E. Kulmala (1996), Generalized model for N₂ and N₂O production from nitrification and denitrification, *Global Biogeochem. Cycles*, 10, 401–412.
- Parton, W. J., M. Hartman, D. S. Ojima, and D. S. Schimel (1998), DAYCENT: Its land surface submodel: Description and testing, *Global Planet. Change*, 19, 35–48.

- Parton, W. J., E. A. Holland, S. J. Del Grosso, M. D. Hartman, R. E. Martin, A. R. Mosier, D. S. Ojima, and D. S. Schimel (2001), Generalized model for NO_x and N₂O emissions from soils, *J. Geophys. Res.*, *106*(D15), 17,403–17,420.
- Pearce, F. (1999), That sinking feeling, *New Sci.*, *164*, 20–21.
- Pendall, E., et al. (2003), Elevated atmospheric CO₂ effects and soil water feedbacks on soil respiration components in a Colorado grassland, *Global Biogeochem. Cycles*, *17*(2), 1046, doi:10.1029/2001GB001821.
- Pendall, E., A. R. Mosier, and J. A. Morgan (2004), Rhizodeposition stimulated by elevated CO₂ in semiarid grassland, *New Phytol.*, *162*, 447–458.
- Peñuelas, J., and M. Estiarte (1997), Trends in plant carbon concentration and plant demand for N throughout this century, *Oecologia*, *109*, 69–73.
- Rastetter, E. B., R. B. McKane, G. R. Shaver, and J. M. Melillo (1992), Changes in C-storage by terrestrial ecosystems—How C-N interactions restrict responses to CO₂ and temperature, *Water Air Soil Pollut.*, *64*, 327–344.
- Running, S. W., R. R. Nemani, and R. D. Hungerford (1987), Extrapolation of synoptic meteorological data in mountainous terrain, and its use for simulating forest evapotranspiration, *Can. J. For. Res.*, *17*, 472–483.
- Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, and J. Gurevitch (2001), A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming, *Oecologia*, *126*, 543–562.
- Schimel, D. S. (1995), Terrestrial ecosystems and the carbon cycle, *Global Change Biol.*, *1*, 77–91.
- Schimel, D., I. G. Enting, M. Heimann, T. M. L. Wigley, D. Raynaud, D. Alves, and U. Siegenthaler (1995), CO₂ and the carbon cycle, in *Climate Change 1994: Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92 Emission Scenarios*, edited by J. T. Houghton et al., pp. 35–71, Cambridge Univ. Press, New York.
- Schimel, D. S., et al. (2001), Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems, *Nature*, *414*, 169–172.
- Schlesinger, W. H., and J. Lichter (2001), Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂, *Nature*, *411*, 466–469.
- Scholes, R. J. (1999), Will the terrestrial carbon sink saturate soon?, *IGBP Global Change Newsl.*, *37*, 2–3.
- Scholes, R. J., E. D. Schulze, L. F. Pitelka, and D. O. Hall (1999), Biochemistry of terrestrial ecosystems, in *The Terrestrial Biosphere and Global Change: Implication for Natural and Managed Ecosystems*, edited by B. H. Walker et al., pp. 271–303, Cambridge Univ. Press, New York.
- Shaver, G. R., et al. (2000), Global warming and terrestrial ecosystems: A conceptual framework for analysis, *BioScience*, *50*, 871–882.
- Shaw, M. R., E. S. Zavaleta, N. R. Chiariello, E. E. Cleland, H. A. Mooney, and C. B. Field (2002), Grassland responses to global environmental changes suppressed by elevated CO₂, *Science*, *298*, 1987–1990.
- Sims, P. L., J. S. Singh, and W. K. Lauenroth (1978), The structure and function of ten western North American grasslands: I. Abiotic and vegetational characteristics, *J. Ecol.*, *66*, 251–285.
- Strömberg, M., and S. Linder (2002), Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand, *Global Change Biol.*, *8*, 1195–1204.
- Tanner, C. B., and T. R. Sinclair (1983), Efficient water use in crop production: Research or re-search?, in *Limitations to Efficient Water Use in Crop Production*, edited by H. M. Taylor, W. R. Jordan, and T. R. Sinclair, pp. 1–27, Am. Soc. Agron., Madison, Wis.
- Vitousek, P. M., et al. (2002), Towards an ecological understanding of biological nitrogen fixation, *Biogeochemistry*, *57/58*, 1–45.
- Walker, B. H., W. L. Steffen, and J. Langridge (1999), Interactive and integrated effects of global change on terrestrial ecosystems, in *The Terrestrial Biosphere and Global Change: Implication for Natural and Managed Ecosystems*, edited by B. H. Walker et al., pp. 329–375, Cambridge Univ. Press, New York.
- Waring, R. H., J. J. Landsberg, and M. Williams (1998), Net primary production of forests: A constant fraction of gross primary production?, *Tree Physiol.*, *18*, 129–134.
- Williams, M. A., C. W. Rice, and C. E. Owensby (2000), Carbon dynamics and microbial activity in tallgrass prairie exposed to elevated CO₂ for 8 years, *Plant Soil*, *227*, 127–137.
- Williams, M. A., C. W. Rice, A. Omay, and C. Owensby (2004), Carbon and nitrogen pools in a tallgrass prairie soil under elevated carbon dioxide, *Soil Sci. Soc. Am. J.*, *68*, 148–153.
- Woodward, F. I., M. R. Lomas, and R. A. Betts (1998), Vegetation-climate feedbacks in a greenhouse world, *Philos. Trans. R. Soc. London, Ser. B*, *353*, 29–39.
- Woodward, F. I., M. R. Lomas, and S. E. Lee (2001), Predicting the future production and distribution of global terrestrial vegetation, in *Terrestrial Global Productivity*, edited by B. Saugier, J. Roy, and H. A. Mooney, pp. 519–539, Academic, San Diego, Calif.
- Woodwell, G. M. (1990), The effect of global warming, in *Global Warming: The Greenpeace Report*, edited by J. Leggett, pp. 116–132, Oxford Univ. Press, New York.
- Wullschleger, S. D., R. B. Jackson, W. S. Currie, A. D. Friend, Y. Luo, F. Mouillot, Y. Pan, and G. Shao (2001), Below-ground processes in gap models for simulating forest response to global change, *Clim. Change*, *51*, 449–473.
- Zak, D. R., K. S. Pregitzer, P. S. Curtis, J. A. Teeri, R. Fogel, and D. Randlett (1993), Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles, *Plant Soil*, *151*, 105–117.

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