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Intra-annual and interannual variability of ecosystem processes in shortgrass steppe

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Abstract. We used a daily time step ecosystem model (DAYCENT) to simulate ecosystem processes at a daily, biweekly, monthly, and annual time step. The model effectively represented variability of ecosystem processes at each of these timescales. Evolution of CO_2 and N_2O, NPP, and net N mineralization were more responsive to variation in precipitation than temperature, while a combined temperature-moisture decomposition factor (DEFAC) was a better predictor than either component alone. Having established the efficacy of CENTURY at representing ecosystem processes at multiple timescales, we used the model to explore interannual variability over the period 1949–1996 using actual daily climate data. Precipitation was more variable than temperature over this period, and our most variable responses were in CO_2 flux and NEP. Net ecosystem production averaged 6 g C m^{-2} yr and varied by 100% over the simulation period. We found no reliable predictors of NEP when compared directly, but when we considered NEP to be lagged by 1 year, predictive power improved. It is clear from our study that NEP is highly variable and difficult to predict. The emerging availability of system-level C balance data from a network of flux towers will not only be an invaluable source of information for assessments of global carbon balance but also a rigorous test for ecosystem models.

1. Introduction

For many systems it is clear that year-to-year variations in climate lead to fluctuations in other ecosystem processes [*Ciais et al.*, 1995; *Francey et al.*, 1995; *Keeling et al.*, 1995]. In a northeastern U.S. forest system, *Goulden et al.* [1996] demonstrated that this inconstancy of climate may lead to large variations in net system C exchange (up to 1 Gt C in 1 year). *White et al.* [1997] point out the importance of developing models that may provide accurate pictures of seasonality of ecosystem processes, as a disparity in phenology may have a disproportionately large effect on ecosystem processes across biomes.

Grassland field studies have documented significant deviation in time of onset [*Sims et al.*, 1978], maximum net growth rate [*Sims and Singh*, 1978a], and crown production [*Sims and Singh*, 1978b] from year to year. *Lauenroth and Sala* [1992] related variability in production primarily to precipitation. *Sala et al.* [1988] also found precipitation as a controlling factor at a larger scale. By exploring current responses to anomalous climate, we may improve our ability to conceptualize effects of future climate change on ecosystem function.

Simulation models have been widely used for the investigation of possible responses to climatic variability (or global climate change) because of their ability to extrapolate beyond the current record. Activities in the VEMAP project have shown not only the variability of ecosystem processes but also the variability among predictions made by some well-recognized models of ecosystem function [*VEMAP members*, 1995; *Schimel et al.*, 1997]. These models are useful tools when informed by a good deal of information from field and laboratory studies. Therefore it is first necessary to establish a model's ability to simulate accurately current conditions in order to gain some confidence in any non-data-based projections. This has been particularly difficult to accomplish for short timescale processes (trace gas flux, short-term soil water dynamics) because some of the better tested models were not designed to handle such a fine timescale.

Therefore our specific objectives are to (1) present a validation of the model's ability to predict daily fluctuations, (2) compare intra-annual (biweekly to seasonal) dynamics of observed and simulated ecosystem processes, and (3) evaluate interannual fluctuations in major ecosystem processes (N_2O and CO_2 fluxes, net ecosystem production (NEP), net primary production (NPP), net nitrogen (N) mineralization, precipitation, temperature, and an abiotic decomposition factor (DEFAC) which combines the effects of moisture and temperature).

2. Methods

2.1. Model Description

We used a daily time step ecosystem model based on CENTURY [*Parton et al.*, 1987, 1988] version 4 [*Parton*, 1996], a monthly time step model of carbon and nutrient (N, P, S) transfer among the atmosphere, plants, and soil. This daily version was developed to simulate more temporally resolved ecological processes with implications for linkage to atmospheric and trace gas models. The primary difference between CENTURY and daily CENTURY (DAYCENT) lies in the water model, and computation of other processes on a finer timescale. *Parton et al.* [1998] provide a full description of the development of this daily version of CENTURY. The version of DAYCENT used here was linked to a trace gas model

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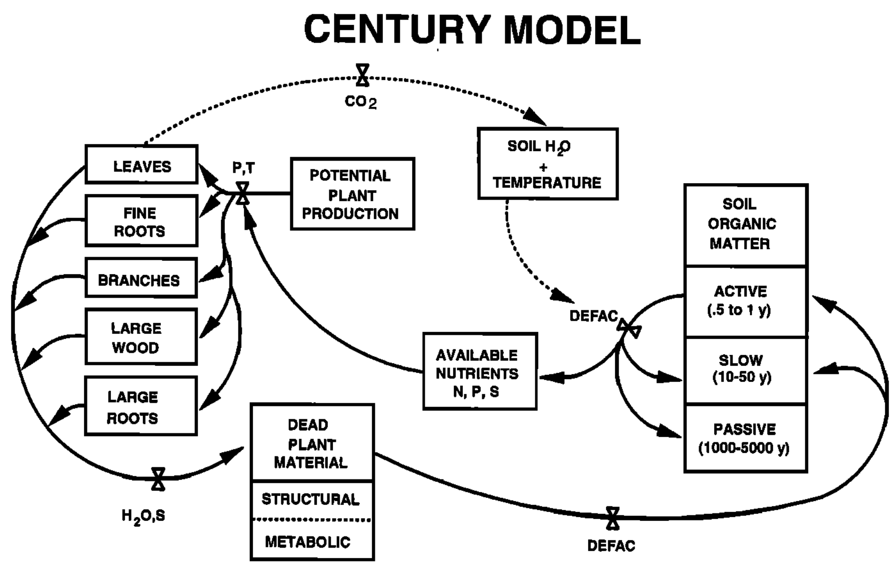

Figure 1. Simple conceptual diagram of the CENTURY model.

[*Parton et al.*, 1996] developed and tested using data from the shortgrass steppe of northern Colorado [*Mosier et al.*, 1996].

A daily water flow submodel and a daily soil temperature submodel were incorporated to compute soil water content and temperature by depth; these submodels replaced the monthly water budget and soil surface temperature submodels from CENTURY (Figure 1). Decomposition occurred daily instead of weekly, and organic and inorganic leaching occurred daily instead of monthly. Potential production estimates and growth of trees, crops, and grasses were updated weekly instead of monthly. New equations for the impact of water and temperature on decomposition were implemented (Figures 2a and 2b). When daily solar radiation, relative humidity, and wind speed climate drivers were available, DAYCENT used a Penman potential evapotranspiration calculation [*Penman*, 1948], otherwise it used the air-temperature-based Linacre calculation from the CENTURY model. Event scheduling had to be adjusted to accommodate multiple time steps in a given month. When an event or management practice was scheduled for a given month, it either occurred weekly (irrigation), on the first week of the month (organic matter addition, fertilization, and cultivation), or on the last week of the month (grazing, fire, tree removal, harvest).

2.2. Validation Exercises

We conducted our validation with data from the shortgrass steppe of northern Colorado. The shortgrass steppe ecosystem of northeastern Colorado is characterized by scant and highly variable precipitation and less variable temperature. The long-term intensive field study conducted at the Central Plains Experimental Range (CPER) has yielded an impressive collection of field measurements utilized in this study.

A paper by *Mosier et al.* [1996] and A. R. Mosier (personal communication, 1997) were our main sources of daily validation data. These data include N_2O flux, CO_2 flux, average soil NO_3 content, soil water content, and soil temperature measured at the CPER. We also obtained vital input information for DAYCENT such as soil texture and bulk density from this publication. Soil organic matter and nutrient content in the model were initialized using a long-term simulation (2000 years) with a well-tested vegetation parameterization from the VEMAP modeling activity [*VEMAP*, 1995]. The resulting SOM and N output compared favorably to field values and were used to initialize the simulations discussed herein.

Our validation of the ability of DAYCENT to simulate processes occurring on a monthly to seasonal basis included actual evapotranspiration (AET), aboveground live carbon accumulation (compared to normalized difference vegetation index (NDVI)), soil temperature (monthly average), CO_2 and N_2O fluxes (monthly total), monthly average soil NO_3 content, and N mineralization. Observations of AET [*Lapitan and Parton*, 1996] were obtained from the Shortgrass Steppe Long-Term Ecological Research Site home page (http://sgs.cnr.colostate.edu/), where observations from the weighing lysimeter are recorded. Field observations of N mineralization were obtained from D. W. Valentine (unpublished data, 1997).

We were unable to make direct comparisons between observations and simulations in some cases. Simulations of daily CO_2 flux in DAYCENT include only soil fluxes, while field observations include both soil and plant flux. Simulated daily CO_2 flux in DAYCENT includes soil heterotrophic respiration, while field observations of CO_2 flux is measured weekly between 1000 and 1100 in the morning and includes live root and shoot respiration (dark chambers are used to estimate CO_2 fluxes) and soil heterotrophic respiration. The observed CO_2 fluxes are extrapolated to represent monthly respiration fluxes and tend to overestimate daily CO_2 fluxes since they represent daytime values when respiration rates are higher (respiration increases exponentially with higher temperatures). The overestimation problem is most significant during the winter when daytime is less than 9 hours of the day. The net result is that modeled CO_2 fluxes correlate well with observed estimates of CO_2 fluxes (Figure 3) and represent the seasonal and year-to-year patterns in CO_2 respiration; however, the model results are 10–15% of the observed CO_2 flux data.

Our simulations of N_2O flux are consistently lower in winter and spring than observed (by about 0.15 g N ha^{-1} month). These follow the same pattern observed by *Parton et al.* [1996] and has been attributed to denitrification losses not adequately accounted for by the model. Model development activities, to lessen this disparity, are currently in progress. Observations of

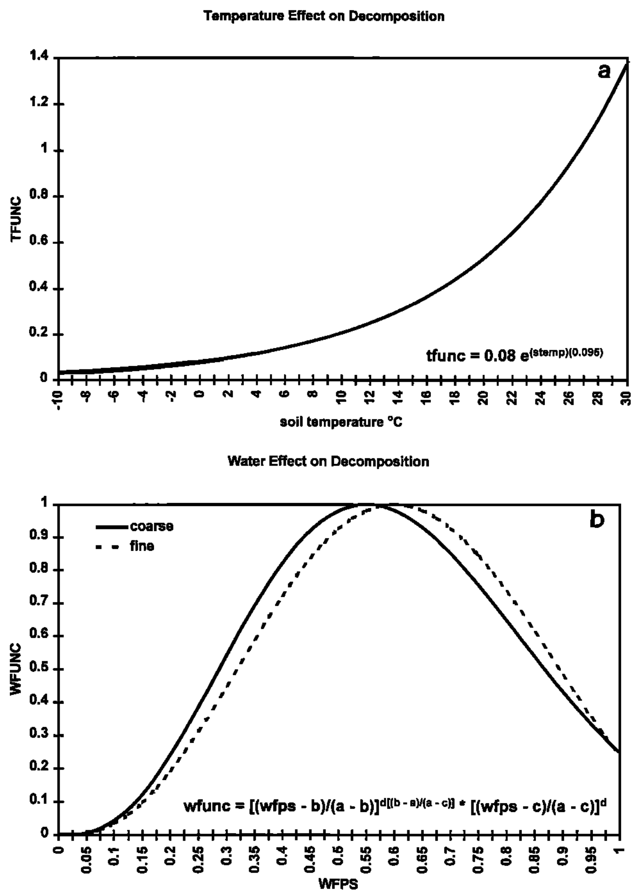

Figure 2. DAYCENT temperature (a) and moisture (b) effects on decomposition. The multiplicative result of TFUNC and WFUNC is DEFAC, an abiotic decomposition factor that reduces potential decomposition rates for each pool in the DAYCENT model. In Figure 2a, stemp = soil temperature, which is calculated using the method of *Parton* [1984], which reduces diurnal variability in air temperature based on the presence of plant biomass and surface litter. In Figure 2b, Wfps is water-filled pore space (fraction), (Swc/width)/Porespace; Swc is soil water content of a soil layer (cm); width is thickness of a soil layer (cm); Porespace is the total porespace of a soil layer (fraction) = 1.0 − (bulkd/partd); Bulkd is bulk density of a soil layer (g cm^{-3}); and Partd is particle density of soil layer (constant = 2.65). For fine textured soils, $a = 0.60$, $b = 1.27$, $c = 0.0012$, $d = 2.84$. For coarse-textured soils, $a = 0.55$, $b = 1.70$, $c = -0.007$, $d = 3.22$.

net N mineralization tend to be considerably greater than those simulated by DAYCENT because plant uptake is considered in the model and not included in the field measurements. Observations of net N mineralization tend to be higher than the simulated values but follow the same seasonal pattern of higher N mineralization rates during the summer. The observed data should have higher N mineralization rates since the method used to estimate N mineralization rates (field soil cores with resin bags at the bottom of the core) excludes live roots, which uptake mineral N and transpire water from the soil (soil water would be higher in the N mineralization cores). Because of this inability to make direct comparisons, we were most interested in verifying the ability of DAYCENT to predict the correct trends or patterns.

Normalized difference vegetation index values were derived for the western part of the Pawnee National Grasslands, an area with vegetation composition similar to the Central Plains Experimental Range. Seasonal metrics were determined using a procedure developed by *Reed et al.* [1994]. Biweekly maximum NDVI composite data sets created by the EROS Data Center (EDC) were used to obtain time of onset of greenness, time of offset of greenness, maximum NDVI, duration of greenness, NDVI at onset and offset, rates of green-up and senescence, modality (whether there is more than one peak), and time-integrated NDVI (TINDVI). As the biweekly maximum NDVI has been shown to correlate with seasonality of vegetation in the Great Plains of the United States [*Di et al.*, 1994; *Reed et al.* 1994; *Tieszen et al.*, 1994], we compared CENTURY-simulated aboveground live carbon results (simulated using actual daily climate series) to NDVI. DAYCENT generates weekly aboveground live carbon data for 59 periods per year. To make a comparison to NDVI (composited on a biweekly basis for a total of 26 biweekly periods per year), it was necessary to first convert the 59-week CENTURY year to a 52-week year, then to generate biweekly values. To do this, the maximum biomass value for 2- to 3-week periods (depending on length of month) was calculated to create 26 biweekly results.

In addition to these variables measured in the field or remotely sensed, we present the monthly abiotic decomposition factor (DEFAC) (a CENTURY output variable illustrated in Figure 2 which reduces potential decomposition rates set for each pool in DAYCENT and is shown to correlate tightly to the evolution of trace gases), as an indication of the combined effects of temperature (TFUNC, Figure 2a) and moisture (WFUNC, Figure 2b) on decomposition.

We compared CENTURY-simulated peak live aboveground biomass (calculated as aboveground carbon accumulation (AGCACC) through August) to field observations from *Lauenroth and Sala* [1992] and to a regression model based on annual precipitation from the same paper. Though aboveground live biomass data were available from 1939 to 1990, we were unable to obtain reliable daily climate records for 1939–1948 only. We also discovered that the climate data presented by *Lauenroth and Sala* [1992] did not match exactly with the data we obtained from the SGS LTER web page (http://sgs.cnr.colostate.edu/). Therefore we recalculated the *Lauenroth and Sala* [1992] regression-based peak live aboveground biomass for the same period we were able to simulate (1949–1990) using both the precipitation data presented in the original paper and the daily data we used for our simulations. All statistics presented herein are significant at the $p = 0.05$ level unless otherwise noted.

2.3. Analyses of Interannual Variability

We modeled ecosystem processes over a long time period (1949–1996) using actual climate data. In order to characterize the variability of ecosystem characteristics (N_2O and CO_2 evolution, net ecosystem production, net primary production, net N mineralization, and total soil organic matter carbon) in response to climatic variability, we calculated a long-term mean, standard deviation, and coefficient of variation for each. These statistics will help elucidate the extent to which each variable may be affected by interannual differences in precipitation and temperature.

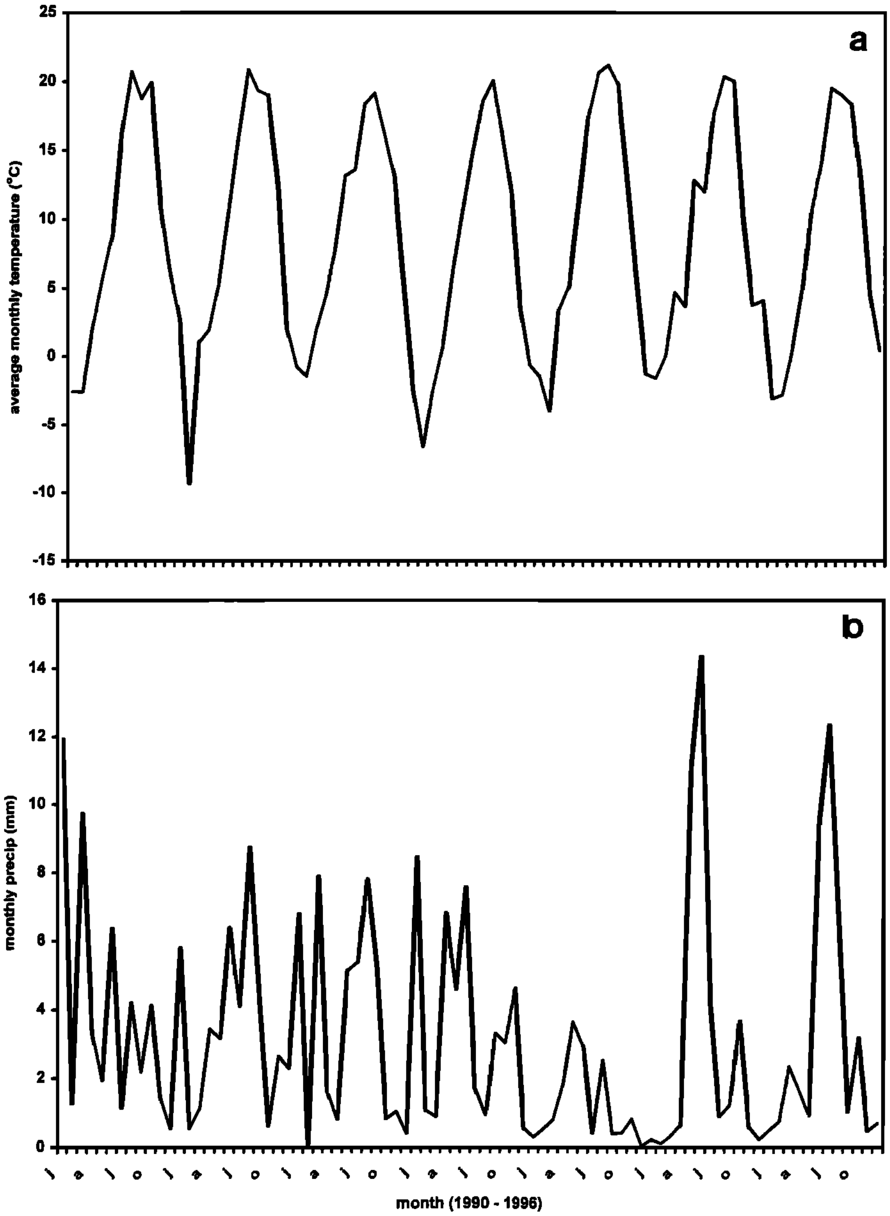

Figure 3. Shortgrass Steppe Long-Term Ecological Research site mean monthly temperature and precipitation 1990–1996.

3. Results

On a daily basis, DAYCENT results summed to the depth of measurement for soil water content ($r^2 = 0.54$), and results averaged over the DAYCENT layers, encompassing the depth of measurement for soil temperature, closely matched observed data ($r^2 = 0.54$ and 0.85, respectively, for soil water and soil temperature). Simulated soil heterotrophic respiration ($r^2 = 0.47$) tracked reasonably well with observed dark total ecosystem respiration rates. Not surprisingly, given the highly variable nature of N_2O measurements [*Mosier et al.*, 1996], N_2O was not well simulated for the entire period ($r^2 = 0.02$), but mean observed values were reasonably close to mean simulated values (Table 1). Daily N_2O emissions were much more satisfactorily simulated in the first two years (1990 ($r^2 = 0.50$), 1991 ($r^2 = 0.32$)) than in later years (1992, 1993, 1994, and 1995 with r^2 values of 0.05, 0.01, 0.05, and 0.05, respectively).

Our comparison of observed monthly processes and simulated monthly processes allowed us to compare not only the absolute values but also the seasonality. Seasonal temperature patterns were reasonably constant from 1990 to 1996, while precipitation varied somewhat more (Figures 3a, 3b). In particular, 1994 was abnormally dry, and 1995 and 1996 were wetter than normal (Figure 3b). It follows, then, that the DAYCENT abiotic decomposition factor (DEFAC) was low in 1994 and high in 1995 and 1996. Similarly, AET was lowest in 1994 and higher in 1995 and 1996 than in earlier years (Figure 4a). For AET there was relatively good agreement between observations and simulations ($r^2 = 0.89$) from 1990 to 1992 when field observations were available.

Soil temperature was successfully simulated on a monthly basis ($r^2 = 0.61$, Figure 4b), as was CO_2 evolution ($r^2 = 0.53$, Figure 4d). Monthly average soil nitrate content was fairly successfully simulated ($r^2 = 0.33$), while average am-

Table 1. Comparison of Observed and Simulated Daily Observations in the Shortgrass Steppe of Northern Colorado

	Observed			Simulated		
Variable	*n*	Mean	SE	*n*	Mean	SE
Soil water content	240	7.62	3.55	267	9.12	4.65
Soil temperature	247	12.12	0.63	247	13.50	0.71
CO_2 flux	159	22.04	6.04	160	22.03	2.54
N_2O flux	264	0.41	0.62	267	0.28	0.53
Soil NO_3 content	167	1.39	0.08	267	0.53	0.03
Soil NH_4 content	167	0.75	0.04	266	0.52	0.02

monium content was not ($r^2 = 0.04$). Monthly nitrous oxide fluxes were simulated better than daily values, but there was still a fairly weak correspondence ($r^2 = 0.10$, Figure 4e). This relationship did not improve when comparisons were made over the growing season (May–September) only. Single-year comparisons of observed and simulated mean monthly N_2O flux were generally better than for an entire period (r^2 of 0.30 or better for 1990, 1991, 1992, and 1995) with the exception of 1993 and 1994 when there was no discernible agreement. Simulations of N mineralization were generally good ($r^2 = 0.33$). Aboveground live C, as simulated by DAYCENT, corresponded fairly closely with NDVI ($r^2 = 0.63$), though the model again seemed to miss the 1994 values (Figure 4c).

In general, DAYCENT simulations followed the same seasonal patterns as the observations. The comparison between the simulated onset of plant growth and the NDVI showed that the model was beginning growth somewhat later than indicated by AVHRR data (with the exception of 1992, Figure 4c) and seems to have been reaching a later peak. Seasonal patterns of AET, soil temperature, CO_2 evolution, and N mineralization were similar between observations and simulations. Where clear patterns were discernible, the seasonality of N_2O flux was reasonably well simulated, though DAYCENT consistently underestimated winter values by ~0.15 gN/ha per month, most likely due to inadequate accounting for denitrification fluxes [*Mosier et al.*, 1996].

Our DAYCENT simulations of annual peak aboveground live biomass were reasonably successful for 1949–1990 ($r^2 = 0.41$, observed mean = 65.9 g biomass m^{-2}, simulated mean = 69.8 g biomass m^{-2}). A regression model (recalculated from *Lauenroth and Sala* [1992] for our shorter simulation period) based on annual precipitation was equally successful ($r^2 = 0.40$, regression mean = 69.6 g biomass m^{-2}). When we recalculated the *Lauenroth and Sala* [1992] regression equation with the same climate observations we used for DAYCENT simulations (see section 2), the correspondence improved slightly ($r^2 = 0.43$, regression mean = 69.0 g biomass m^{-2}). Paired *t*-tests indicate that there is no significant difference between DAYCENT output and the *Lauenroth and Sala* [1992] regression equation results. It is important to note that the efficacy of any model in predicting the observed peak live biomass may not be able to be reliably assessed on the basis of these observations because the data represent the average of grass-clipped plots from sites at the Shortgrass Steppe Long-Term Ecological Research site which have different grazing levels (ungrazed up to heavy grazed sites) and which were collected at different times during the year, which may explain the relatively poor correspondence between our simulation results and field observations. This data set, although imperfect, is a reasonably good indicator of long-term biomass dynamics, particularly in a system as relatively homogenous as the shortgrass steppe.

We were particularly interested in the long-term interannual variability of ecosystem processes as predicted by the DAYCENT model. Unique to the daily model is our ability to simulate nitrous oxide and carbon dioxide fluxes as well as standard monthly CENTURY output variables [*Metherell et al.*, 1993]. Over the period of simulation (1949–1996), annual precipitation (cv = 29%) was more variable than mean annual temperature (cv = 13%). Ecosystem processes most strongly affected by this variability were CO_2 flux (Figure 5a, cv = 57%) and net ecosystem production (Figure 5g, cv = 104%). The annual abiotic decomposition factor (Figure 5e, cv = 27%), N_2O flux (Figure 5b, cv = 27%), total net N mineralization (Figure 5d, cv = 26%), and aboveground and belowground production (Figure 5c, cv = 21%) were also fairly variable. Total soil organic matter carbon did not change substantially in response to climate variability (cv = 3%), nor did microbial biomass C, though there was a consistent, long-term increase (Figure 5f). Descriptive statistics are summarized in Table 2.

It is clear from our analysis of interannual variability that a number of ecosystem processes were highly correlated. Visual examination indicates that CO_2 (Figure 5a), N_2O (Figure 5b), NPP (Figure 5c), net N mineralization (Figure 5d), and the abiotic decomposition factor (Figure 5e) followed a similar pattern. Net ecosystem production (Figure 5g) did not appear to follow the same pattern. To quantify the correspondence between pairs of ecosystem processes, we ran multiple linear regressions and reported r^2 values (Table 3).

4. Discussion

In this paper we have described a daily time-step model of ecosystem processes (DAYCENT) which allows the user to not only simulate standard monthly CENTURY outputs [*Metherell et al.*, 1993] but also add the ability to simulate trace gas fluxes, short-term soil water dynamics, and weekly aboveground and belowground live biomass. Nitrous oxide flux data from 1990 to 1992 were used in the development of NGAS, the stand-alone regression model of trace gas flux which was a precursor to the trace gas model included in DAYCENT [*Parton et al.*, 1996], but all other data included in this comparison are independent of model development.

Our validation of DAYCENT for the shortgrass-steppe of northern Colorado suggests that the model does a good job simulating soil water dynamics and CO_2 flux and less well simulating N_2O fluxes on a daily basis. Comparisons of aboveground live carbon to NDVI curves were successful, suggesting that it may be possible to conduct large-scale, multisite validations of DAYCENT using widely available AVHRR

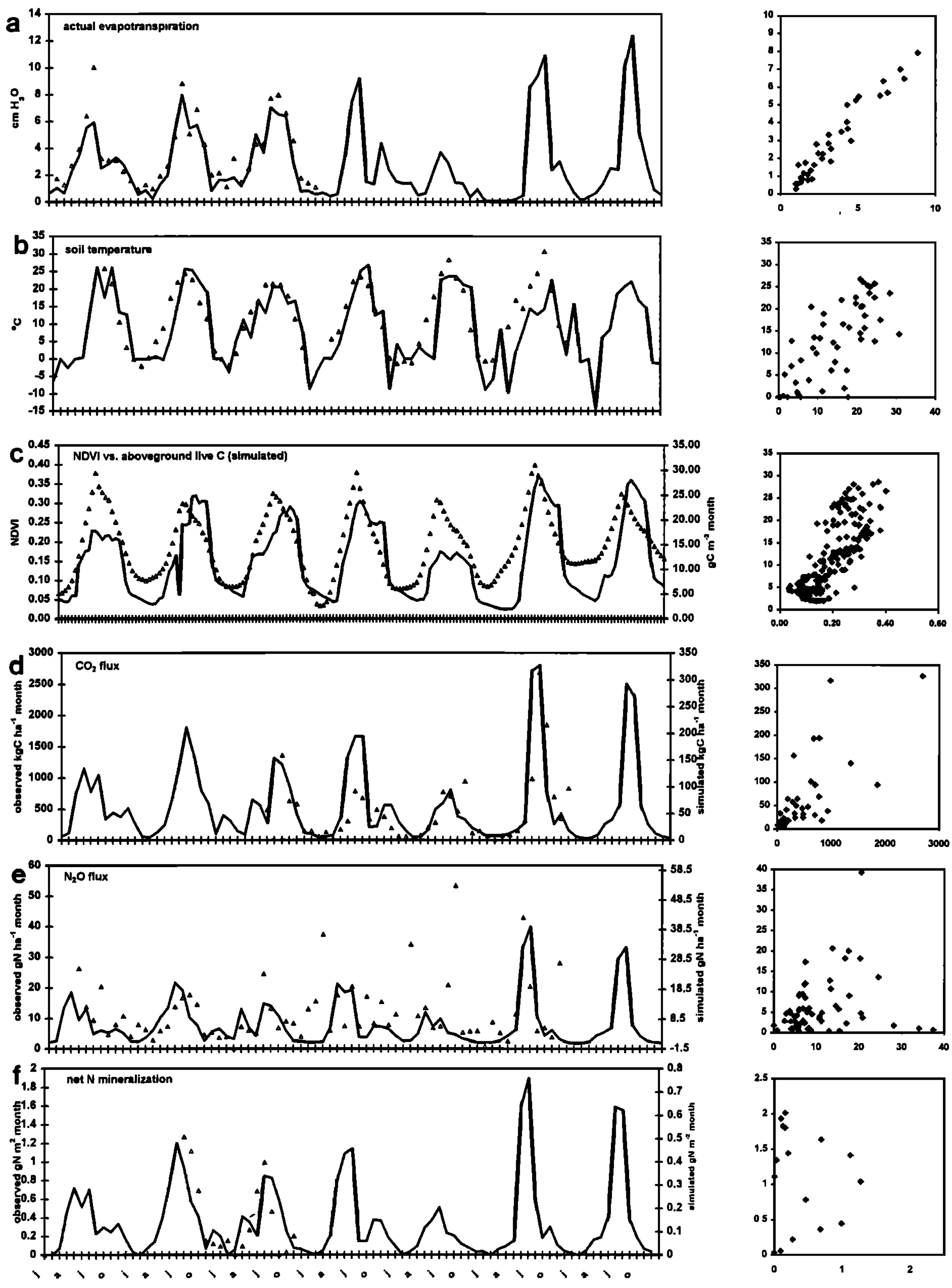

Figure 4. Monthly and seasonal simulations and observations of ecosystem characteristics for the shortgrass steppe of northern Colorado. Solid line represents results of a daily CENTURY (DAYCENT) simulation, symbols represent observations. On the scattergrams the X axis is observed data, and the Y axis is simulation results.

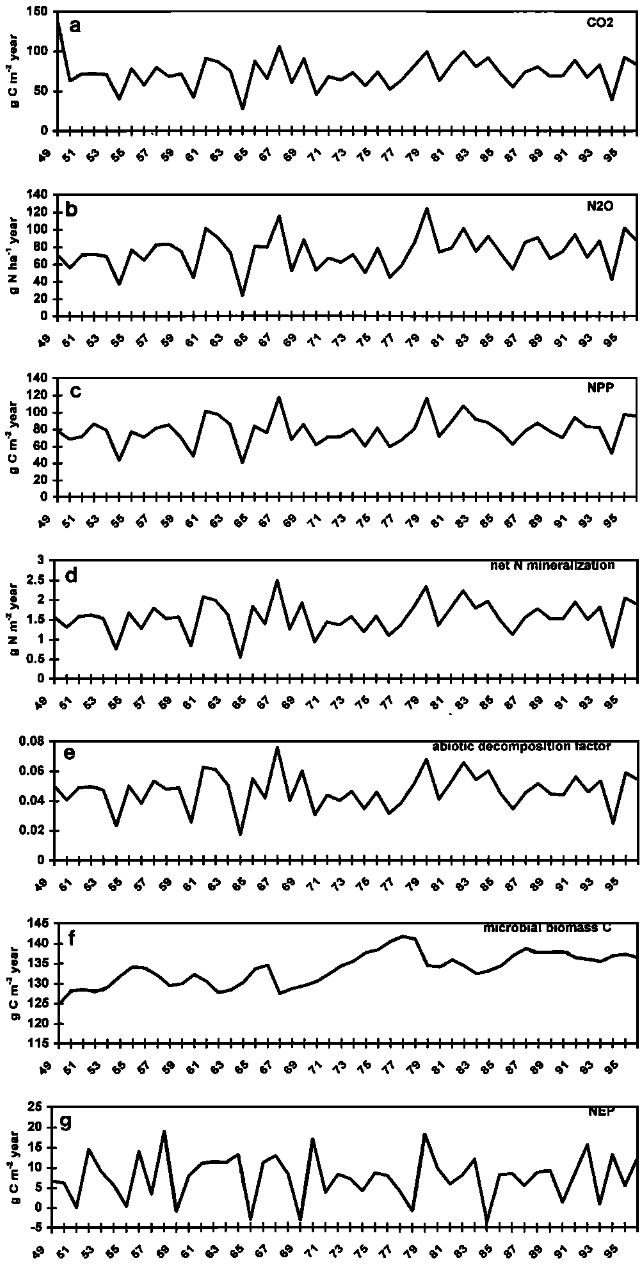

Figure 5. Interannual variability of major ecosystem processes in the shortgrass steppe of northern Colorado as simulated by DAYCENT.

data. Our monthly comparisons of DAYCENT to observations suggest that this more temporally resolved model remains effective at the temporal scale of the original CENTURY model. Our analysis of the DAYCENT ability to simulate peak live aboveground biomass (PLAB) (shown to correlate with aboveground net primary productivity [*Lauenroth and Sala*, 1992]) suggests that DAYCENT provides no better estimate of PLAB than a simple regression model based on annual precipitation. Though DAYCENT does not provide a dramatically improved estimate of production, its strength lies in its ability to explore the effects of different management strategies or climate scenarios on total ecosystem status.

Having established that DAYCENT does a reasonable job of simulating ecosystem processes over time, we used the model to assess the effects of interannual climate variability on N_2O and CO_2 fluxes, NEP, NPP, net N mineralization, precipitation, temperature, and an abiotic decomposition factor (DEFAC). Annual CO_2 flux and NEP were particularly susceptible to climate variability. Precipitation, which is low and variable in the shortgrass steppe, predicts a substantial proportion of the variability in most ecosystem processes. The abiotic decomposition factor (a combined function of precipitation and temperature) tracked more closely with each ecosystem process than precipitation or temperature alone. Precipitation was more tightly related to CO_2 and N_2O flux, NPP, and net N mineralization than temperature. In just one case was temperature a better predictor than precipitation and that was for the DAYCENT active aboveground and belowground soil organic matter pools (which are indices of microbial biomass C).

Table 2. Interannual Variability of Major Ecosystem Processes From 1949 to 1996 Using a Daily Model of Ecosystem Function (DAYCENT)

Variable	*n*	Mean	SE	CV
Mean temperature, °C	48	8.90	0.17	13.45
Precipitation, cm H_2O	48	33.66	1.42	29.25
CO_2 flux, kg C ha^{-1}	48	177.81	14.51	56.55
N_2O flux, g N ha^{-1}	48	73.85	2.85	26.71
ANPP, g C m^{-2}	48	30.70	0.93	20.95
BNPP, g C m^{-2}	48	47.74	1.44	20.95
Total SOM, g C m^{-2}	48	2885.11	13.00	3.12
N mineralization, g N m^{-2}	48	1.56	0.06	26.00
Abiotic decomposition factor	48	0.05	0.00	27.19
NEP, g C m^{-2}	48	6.09	0.91	103.93

Over the period of simulation, NEP averaged 6 gC m^{-2} yr, indicative of a system not at steady state, but gaining C, because we did not manage the system with grazing. Interestingly, no DAYCENT output parameter was a reliable predictor of NEP when compared without lag (r^2 values ranging from 0.00 to 0.04 for CO_2 and N_2O evolution, NPP, net N mineralization, and DEFAC). However, when NEP was lagged by 1 year, the predictive power improved considerably (r^2 values between 0.2 and 0.3). This suggests that net ecosystem production, as it is simulated by DAYCENT, is at least partially a function of the previous year's productivity and decomposition potential but is extremely difficult to predict. Net ecosystem production is the net result of two large and less variable numbers, but a small proportional change in either production or respiration leads to a large proportional change in NEP. Our analysis suggests that both components of NEP are strongly controlled by DEFAC, so the small year-to-year changes that drive high variability in NEP are difficult to tease out. The emerging availability of C flux data from a network of towers (eddy correlation and otherwise) will therefore provide an extremely rigorous test of ecosystem models. The high variability of our NEP result is not counter to results of one of these studies. In a study of Harvard Forest, United States, an eastern mixed hardwood forest, *Goulden et al.* [1996] detected 100% variability in NEP from year to year (ranging from 1.4 to 2.8 t ha^{-1} yr), whereas gross ecosystem exchange varied by no more than 16% and respiration by no more than 29% over the period of record. In addition to temperature and precipitation variability, they propose several intervening factors that may contribute to interannual fluctuations such as depth of snow in winter, soil temperature, and summertime drought.

The information gained from this exercise is particularly

Table 3. Multiple Pair-Wise Regressions (r^2) of Simulated Ecosystem Characteristics on an Annual Basis

	N_2O	NPP	TNETMN	ADEFAC	NEP	SOM1C	PRECIP
CO_2	0.65	0.67	0.74	0.76	0.04	0.04	0.55
N_2O		0.89	0.91	0.89	0.00	0.00	0.70
NPP			0.93	0.92	0.02	0.01	0.71
TNETMN				0.98	0.02	0.00	0.75
ADEFAC					0.02	0.03	0.75
NEP						0.03	0.00
SOM1C							0.00

Note the generally high agreement among processes with the exception of NEP (net ecosystem production) and SOM1C (active soil organic matter C). (TNETMN, total net N mineralization in gN m^{-2}. ADEFAC, annual abiotic decomposition factor similar to evapotranspiration; the combined effect of temperature and moisture on decomposition.)

useful because by identifying the greatest ecosystem responses to climate variability, we may not only draw some conclusions about the tenuous nature of some aspects of a system but also identify useful early indicators of climate change effects on ecosystems.

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