

OBSERVATIONS AND MODELING OF BIOMASS  
AND SOIL ORGANIC MATTER DYNAMICS FOR THE  
GRASSLAND BIOME WORLDWIDE

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*Abstract.* Century is a model of terrestrial biogeochemistry based on relationships between climate, human management (fire, grazing), soil properties, plant productivity, and decomposition. The grassland version of the Century model was tested using observed data from 11 temperate and tropical grasslands around the world. The results show that soil C and N levels can be simulated to within  $\pm 25\%$  of the observed values (100 and 75% of the time, respectively) for

a diverse set of soils. Peak live biomass and plant production can be simulated within  $\pm 25\%$  of the observed values (57 and 60% of the time, respectively) for burned, fertilized, and irrigated grassland sites where precipitation ranged from 22 to over 150 cm. Live biomass can be generally predicted to within  $\pm 50\%$  of the observed values (57% of the time). The model underestimated the live biomass in extremely high plant production years at two of the Russian sites. A comparison of Century model results with statistical models showed that the Century model had slightly higher  $r^2$  values than the statistical models. Data and calibrated model results from this study are useful for analysis and description of grassland carbon dynamics, and as a reference point for testing more physiologically based models prediction's of net primary production and biomass. Results indicate that prediction of plant and soil organic matter (C and N) dynamics requires knowledge of climate, soil texture, and N inputs.

INTRODUCTION AND OBJECTIVES

Under the aegis of the Scientific Committee on Problems of the Environment (SCOPE) Project on "Effect of climate change on production and decomposition in coniferous forests and grasslands," the Century model for plant-soil ecosystems has been further developed by a Grasslands Modelling Group in order to apply it to a wide range of temperate and tropical grasslands worldwide. This study was undertaken to meet the overall aims of the SCOPE Project, to review and identify models with wide application and predictive ability, in order to link plant and soil responses to the large-scale modeling of global change effects. Climate changes are expected to be manifest as a rise in mean annual temperature, together with perturbation of rainfall patterns, alongside a continuing rapid increase in atmospheric CO<sub>2</sub>. Other modifications to the environment

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may follow in the form of changes in nutrient availability and the rate of cycling of carbon and nitrogen between the biosphere, atmosphere, and geosphere.

The carbon in terrestrial vegetation and soils worldwide outweighs the amount found in the atmosphere and the ocean surface layers. The role of grasslands in global biogeochemical cycles should not be overlooked, especially when the contribution of worldwide grassland burning is considered [Hao et al., 1990; Hall and Scurlock, 1991]. Tropical grasslands occupy 15 million km<sup>2</sup>, and in terms of both land area and productivity are nearly equal to tropical forests. Together with 9 million km<sup>2</sup> of temperate grasslands, they cover nearly one fifth of the Earth's land surface and are likely to remain constant in area for the near future [Lieth, 1972; Hall and Scurlock, 1991]. Carbon stored in grassland soils, temperate and tropical, has been estimated at 30% of the world total of soil carbon [Anderson, 1991].

The role of ecosystem models to evaluate the importance of various ecosystems to global environmental change and subsequent impacts is fundamental to global change research. The Century model is being applied to global change impacts and has been critically evaluated by the SCOPE Project Grasslands Modelling Group. Century was developed into its present form (Version 3.0) [Parton et al., 1992] by the incorporation of routines derived from more mechanistic models or suggested by detailed site data. The model has now been parameterized and successfully validated for many different grassland sites in temperate and tropical regions [Parton et al., 1987, 1989a,b]. The grassland sites used in this study range from temperate grasslands in the United States and Russia and natural and converted grasslands in wet and dry regions of the tropics.

The ability of the model to respond to burning, irrigation, and N fertilization were tested using observed data from these sites. We specifically tested the ability of the model to simulate: (1) seasonal patterns of live biomass, (2) peak live biomass, (3) annual plant production, and (4) soil C and N levels. All of the sites used for model testing have at least 3 years of seasonal live biomass data, observed soil C and N levels and required climate data. The statistical comparisons used to test the model include linear regression of observed and simulated results, comparison of Century model predictions with frequently used regression models (i.e., production versus annual precipitation), and an evaluation of the number of times that the difference between the Century model and the observed data was less than  $\pm 25\%$  of the observed data.

## MODEL DESCRIPTION

Century is a general computer model of plant-soil ecosystems which simulates the dynamics of grasslands, forests, crops, and savannas. It incorporates simplified representations of key processes relating to carbon assimilation and turnover, based on existing models. Century has been previously described in detail [Parton et al., 1987, 1988; Sanford et al., 1991] and is designed to work with the View output module of the program "Time-zero: the integrated modelling environment" [Kirchner 1989].

Century simulates the dynamics of carbon (C), nitrogen (N), phosphorus (P), and sulphur (S) for different plant-soil systems, although only the carbon and nitrogen outputs will be reported here. Different plant production submodels for grasslands, forests and crops are linked to a common soil organic matter (SOM) submodel, with grasses and trees both included under Century's savanna option. The SOM submodel simulates the flow of selected elements through the different inorganic and organic pools in the soil, running on a monthly time step.

Version 3.0 of Century was used for these model runs [Parton et al., 1992]. This version includes a substantial number of changes not described in the original publications. These changes include (1) adding an effect of clay on formation of passive SOM; (2) improving the surface litter decomposition model; (3) including the effect of anaerobiosis on decomposition; (4) simulating leaching of soluble organic material; (5) improving the inorganic leaching equations; and (6) developing a robust grassland production submodel. This paper will describe these significant changes to the model and present a general description of the overall model.

## DECOMPOSITION AND SOIL ORGANIC MATTER SUBMODEL

The soil organic matter (SOM) submodel simulates the dynamics of C, N, P, and S in the organic and inorganic parts of the soil system. The flow diagram for soil C (Figure 1) shows that soil C is divided up into three major components which include active, slow, and passive soil C. Active SOM includes live soil microbes plus microbial products (the total active pool is approximately 2 to 3 times the live soil microbial biomass), the slow pool includes resistant plant material (for instance, ligninlike components) and soil-stabilized plant and microbial material, while the passive material is very resistant to decomposition and includes physically and chemically stabilized SOM. The flows of C are controlled by the inherent maximum decomposition rate of the different pools and the water and temperature-controlled decomposition factor (Figure 2). Average monthly soil temperature at the soil surface controls the temperature function, and the ratio of stored water (0-30 cm depth) plus current monthly precipitation to potential evapotranspiration is the input for the moisture function. Microbial respiration occurs for each of the decomposition flows. The partitioning of decomposition between stabilized SOM and CO<sub>2</sub> is a function of soil texture for the stabilization of active C into slow C (increasing CO<sub>2</sub> for sandy soils and less soil C storage). Justification for these assumptions are presented in the earlier Century paper [Parton et al., 1987].

Plant residues (shoots and roots) are partitioned into structural (resistant to decomposition) and metabolic (readily decomposable) plant material as a function of the initial residue lignin (L)-to-nitrogen (N) ratio (L:N) using the following equation:

$$F_m = 0.99 - (L/N) \cdot 0.018 \quad (1)$$

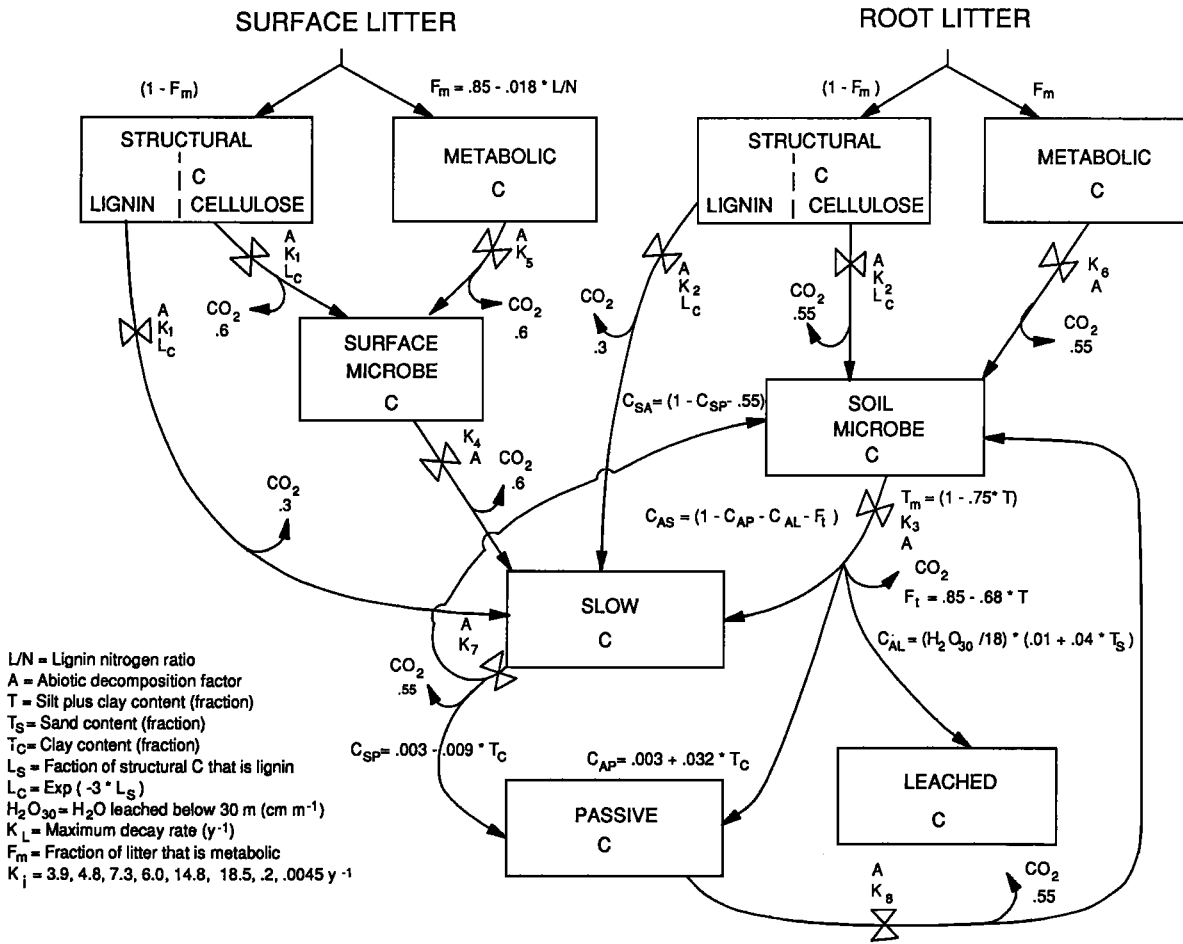


Fig. 1. Flow diagram for the Century soil organic C model.

where  $F_m$  is the metabolic fraction. The lignin fraction is assumed to be part of the structural material, and (i.e., L:N ratio) controls the decomposition rate of structural material. The lignin fraction of the plant material does not create microbial biomass and is assumed to go directly to the slow C pool as structural material decomposes. Surface litter decomposition is treated separately, and surface live microbes are assumed to be in close association with the surface litter. The surface microbial pool turnover rate is independent of soil texture, while soil texture influences turnover of active SOM (higher rates for sandy soils). The model assumes a 60% loss of C due to microbial respiration for surface microbes. The surface litter decomposition submodel has been recently tested using litter decay data from an environmental gradient in Hawaii [Vitousek et al., 1993].

Decomposition of each state variable is calculated using the following equations:

$$\frac{dC_I}{dt} = K_I L_C A C_I \quad I = 1, 2 \quad (2)$$

$$\frac{dC_I}{dt} = K_I A T_m C_I \quad I = 3 \quad (3)$$

$$\frac{dC_I}{dt} = K_I A C_I \quad I = 4, 5, 6, 7, 8 \quad (4)$$

$$T_m = (1 - 0.75 T) \quad (5)$$

$$L_C = e^{(-3 L_s)} \quad (6)$$

where  $C_I$  = the carbon in state variable;  $I=1,2,3,4,5,6,7,8$  for surface and soil structural material, active SOM, surface microbes, surface and soil metabolic material, slow and passive SOM fractions;  $K_I$  is the maximum decomposition rate (year<sup>-1</sup>) parameters for the  $i$ th state variables ( $K_1 = 3.9, 4.9, 7.3, 6.0, 14.8, 18.5, .2, .0045$  year<sup>-1</sup>);  $A$  is the combined

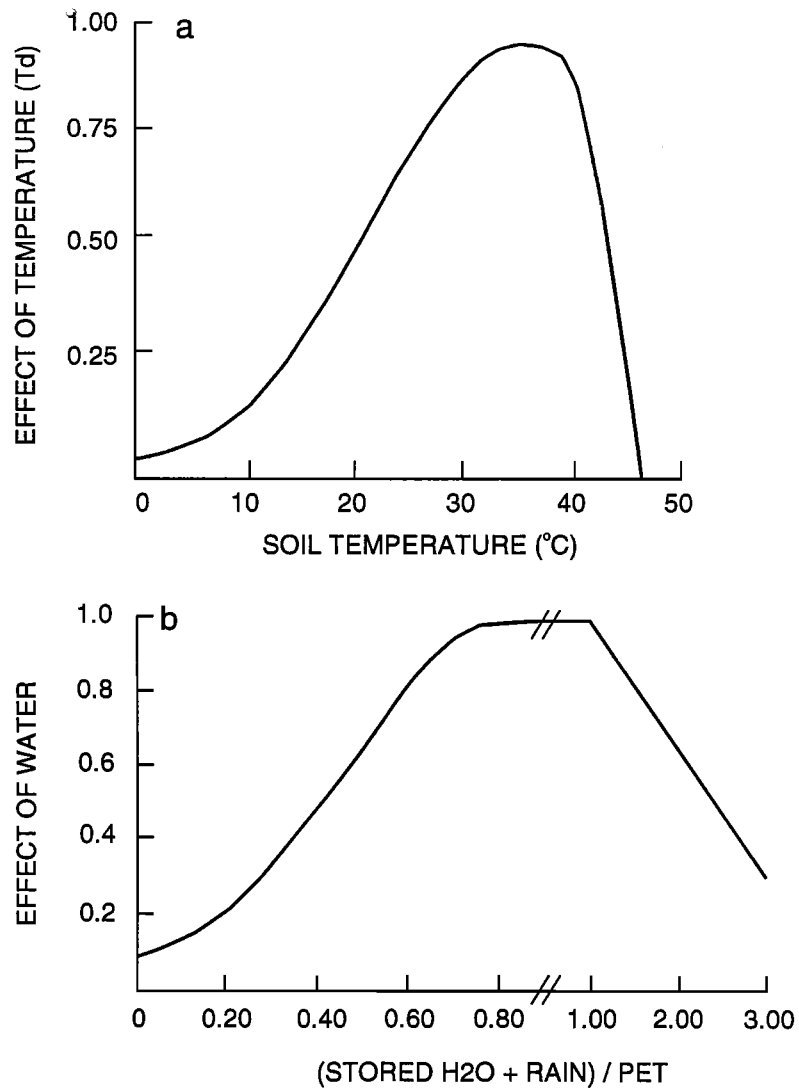


Fig. 2. The abiotic effect of (a) soil temperature and (b) soil moisture on decomposition.

abiotic impact of soil moisture and soil temperature on decomposition (product of the soil moisture and temperature terms - see Figure 2),  $T_m$  is the effect of soil texture on active SOM turnover,  $T$  is the silt plus clay content (fraction); and  $L_c$  is the impact of lignin content of structural material ( $L_s$ ) on structural decomposition.

The model assumes that all C decomposition flows are associated with microbial activity and that microbial respiration occurs for each of these flows. The fraction of C lost due to microbial respiration with each C flow is shown in Figure 1 next to the  $CO_2$  arrows. Carbon leaving the active SOM box is divided into four different flows which include microbial respiration, leaching of soluble organic C, and stabilization of C in the slow and passive pools (equations (7)-(10)), while the C flows out of slow SOM is allocated to passive SOM and active SOM (equations (11) and (12)).

$$F_r = 0.85 - .68 T \quad (7)$$

$$C_{AL} = (H_2O_{30}/18) (0.01 + 0.04 T_p) \quad (8)$$

$$C_{AP} = 0.003 + 0.032 T_c \quad (9)$$

$$C_{AS} = (1 - C_{AL} - C_{AP} - F_r) \quad (10)$$

where  $F_r$  is the fraction of C lost due to microbial respiration,  $L_c$  is the fraction lost due to organic leaching,  $C_A$  is the fraction allocated to passive SOM,  $C_s$  is the fraction sent to the slow pool,  $H_2O_{30}$  is the monthly water leached

below the 30 cm soil depth ( $\text{cm month}^{-1}$ ),  $S$  is the sand content (fraction),  $T_c$  is the clay content (fraction).  $C_p$  is the fraction of slow C allocated to passive pool, and  $C_s$  is the fraction of slow C allocated to the active pool (55% of the C is lost due to microbial respiration).

$$C_{sp} = 0.003 - 0.009 T_c \quad (11)$$

$$C_{sa} = (1 - C_{AP} - 0.55) \quad (12)$$

The formation of passive SOM is a function of clay content (higher for clay soils) and is primarily controlled by the stabilization of active SOM in microaggregates. Some passive SOM is also created by the decomposition of slow SOM, and includes a similar effect of clay. The effect of clay on these flows is based on soil  $^{14}\text{C}$  data [Becker-Heidman 1985] which show that the percent of modern  $^{14}\text{C}$  decreases with clay content, suggesting that clay soils have a higher fraction of passive SOM. This is also consistent with the way that Jenkinson [1990] included the impact of clay on SOM dynamics.

Leaching of soluble organic matter out of the top 30-cm of the soil is calculated as a function of the decay rate for active SOM ( $D_a$ ), the sand content of the soil, and the water flow below the 30-cm soil depth. The parameter values for formation of passive SOM were determined by fitting the model to observed soil C data at the U.S. Great Plains sites (Konza and Central Plains Experimental Range (CPER)) and while the organic leaching parameters were derived by fitting the model to observed water chemistry data from a watershed in Puerto Rico (W. H. McDowel and C. E. Asbury, Export of carbon, nitrogen and major ions from three tropical montane watersheds, submitted to *Journal of Limnology and Oceanography*, 1993) (hereinafter referred to as McDowel and Asbury, submitted manuscript, 1993). A more complete description and justification for the C flows is presented by Parton et al. [1993].

#### BIOPHYSICAL SUBMODELS

The Century model includes a simplified water budget model which calculates monthly evaporation and transpiration water loss, water content of the soil layers, snow water content and saturated flow of water between soil layers (Appendix B). If the average air temperature is less than  $0^\circ\text{C}$  monthly precipitation occurs as snow. Sublimation and evaporation of water from the snow pack occurs at a rate equal to the potential evapotranspiration rate. Snow melt occurs if the average air temperature is greater than  $0^\circ\text{C}$  and is a linear function of the average air temperature. The potential evapotranspiration rate (PET) is calculated as a function of the average monthly maximum and minimum air temperature using the equations developed by Linacre [1977]. Bare soil water loss is a function of standing dead and litter biomass (lower for high biomass levels), rainfall,

and PET. Interception water loss is a function of aboveground biomass (increases with biomass level), rainfall, and PET. Transpiration water loss is function of the live leaf biomass (exponential function of leaf biomass), rainfall, and PET. Interception of water and bare soil water losses are calculated as fractions of the monthly precipitation and are subtracted from the total monthly precipitation, with the remainder of the water added to the soil.

Water is distributed to the different layers by adding the water to the top layer (0-15 cm) and then draining excess water (water above field capacity) to the next layer. Transpiration water loss occurs after the water was added to the soil. Water loss occurs first as interception, followed by bare soil evaporation and transpiration (the sum does not exceed the PET rate). The field capacity and wilting point for the different soil layers is calculated as a function of the bulk density, soil texture, and organic matter content using an equation developed by Gupta and Larson [1979]. The number of soil layers is an input variable in the model, and we used 15-cm increments for each layer up to the 60-cm soil depth and 30-cm increments below the 60-cm depth. Water leached below the last soil layer is not available for evapotranspiration and is a measure of interflow, runoff, or leaching losses from the soil profile. Water going below the profile can be lost as stream flow or leached into the subsoil where it can accumulate or move into the stream flow. Appendix B gives all the equations used in the water flow model and detailed validation and descriptions are presented by W. J. Parton et al. (manuscript in preparation, 1993).

Average monthly soil temperature near the soil surface is calculated using equations developed by Parton [1984]. These equations calculate near surface maximum soil temperature as a function of the maximum air temperature (2 m height) and the canopy biomass (lower for high biomass) while the minimum soil temperature is a function of the minimum air temperature (2 m height) and canopy biomass (higher for higher biomass). The actual soil temperature used for decomposition and plant growth rate functions is the average of the minimum and maximum soil temperatures.

Leaching of labile mineral N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) occurs when saturated water flows between soil layers. The fraction of mineral N that flows from the upper layer to the lower layer ( $F_n$ ; 0-1) is calculated as a function of the sand content of the soil ( $T_s$ ; 0-1), and the amount of saturated water flow between layers using the following equation:

$$F_n = (H_2O_{(i)}/18) (0.2+0.7 T_s) \quad (13)$$

where  $H_2O_{(i)}$  is the saturated water flow ( $\text{cm H}_2\text{O}$  per month) from layer  $i$  to layer  $i+1$ . Parameter values in 13 were determined by fitting the model to observed water chemistry data from Puerto Rico (McDowel and Asbury, submitted manuscript, 1993).

#### NITROGEN SUBMODEL

The N submodel has the same general structure as the soil C model (Figure 3). The organic-N flows follow the C

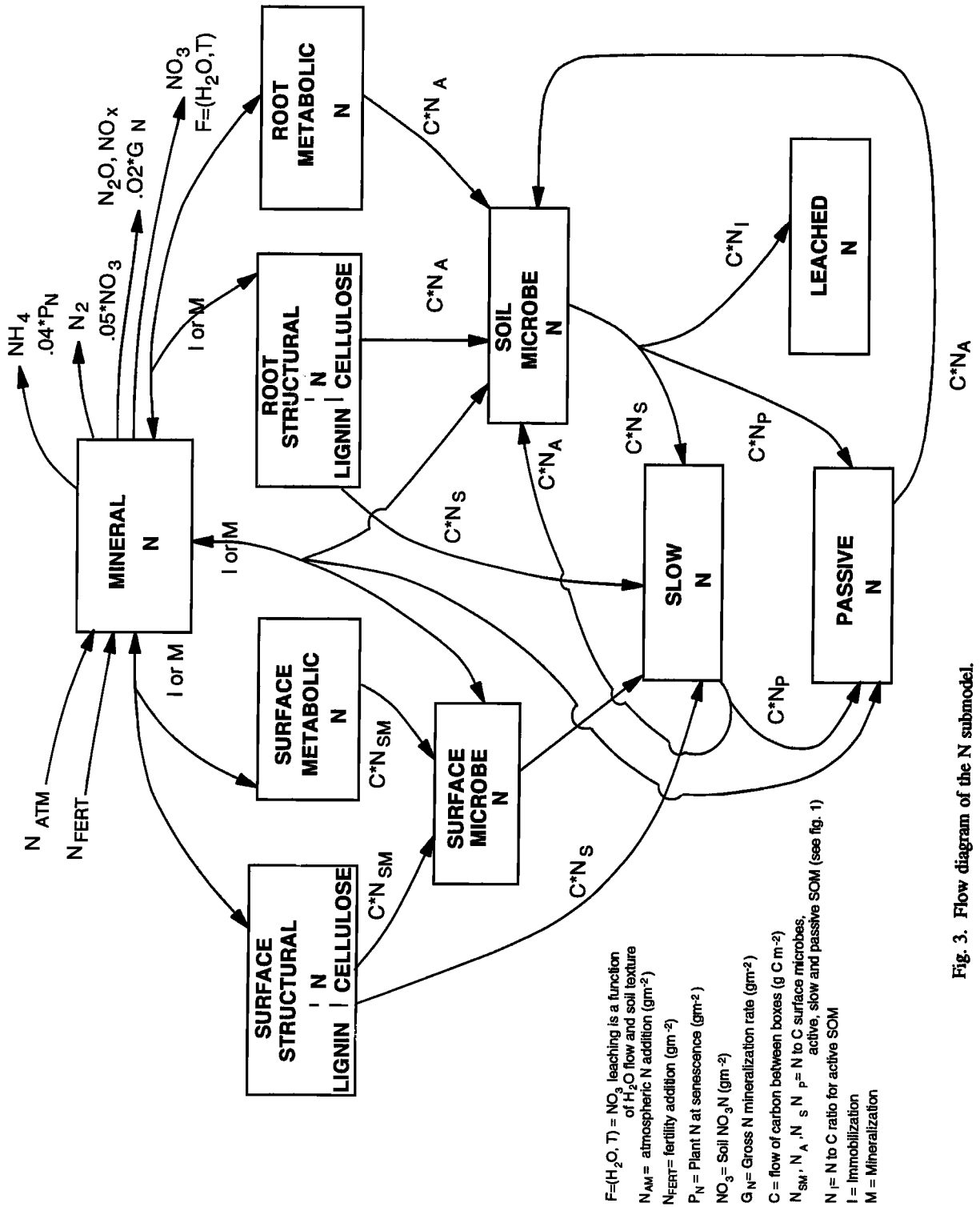


Fig. 3. Flow diagram of the N submodel.

flows and are equal to the product of the carbon flow and the N:C ratio of the state variable that receives the C. The C:N ratios of the soil state variables receiving the flow of C are a function of the mineral N pool ( $\text{NO}_3^-$  plus  $\text{NH}_4^+$ ) and vary within the ranges 3-15, 12-20, and 7-10, respectively, for active, slow and passive SOM (Figure 4). The C:N ratio of newly formed surface microbial biomass is a linear function of the N content of the material being decomposed, and increases from 10 to 20 as the N content decreases from 2.0% to 0.01% (see Figure 3). The C:N ratio of slow SOM material formed from surface microbes is equal to the C:N ratio of the microbes plus 5.0. N associated with carbon lost in respiration is assumed to be mineralized. Given the C:N ratio of the state variables and the microbial respiration loss, decomposition of metabolic residue, active, slow, and

passive pools generally results in net mineralization of N, while decomposition of structural material immobilizes N. The model also uses simple equations to represent N inputs due to atmospheric deposition and N fixation and calculates N losses due to  $\text{N}_2$ , NO,  $\text{N}_2\text{O}$ , and  $\text{NH}_3$  gas fluxes (see Figure 3) and  $\text{NO}_3^-$  leaching. A more complete description and justification for the N submodel is presented by Parton et al. [1987, 1988].

#### PLANT PRODUCTION SUBMODEL

Century simulates plant production for grasslands, agricultural crops, forests, and mixed tree-grass (savanna) systems. The grassland submodel (Figure 5) simulates grass growth and includes the impact of grazing and fire on plant

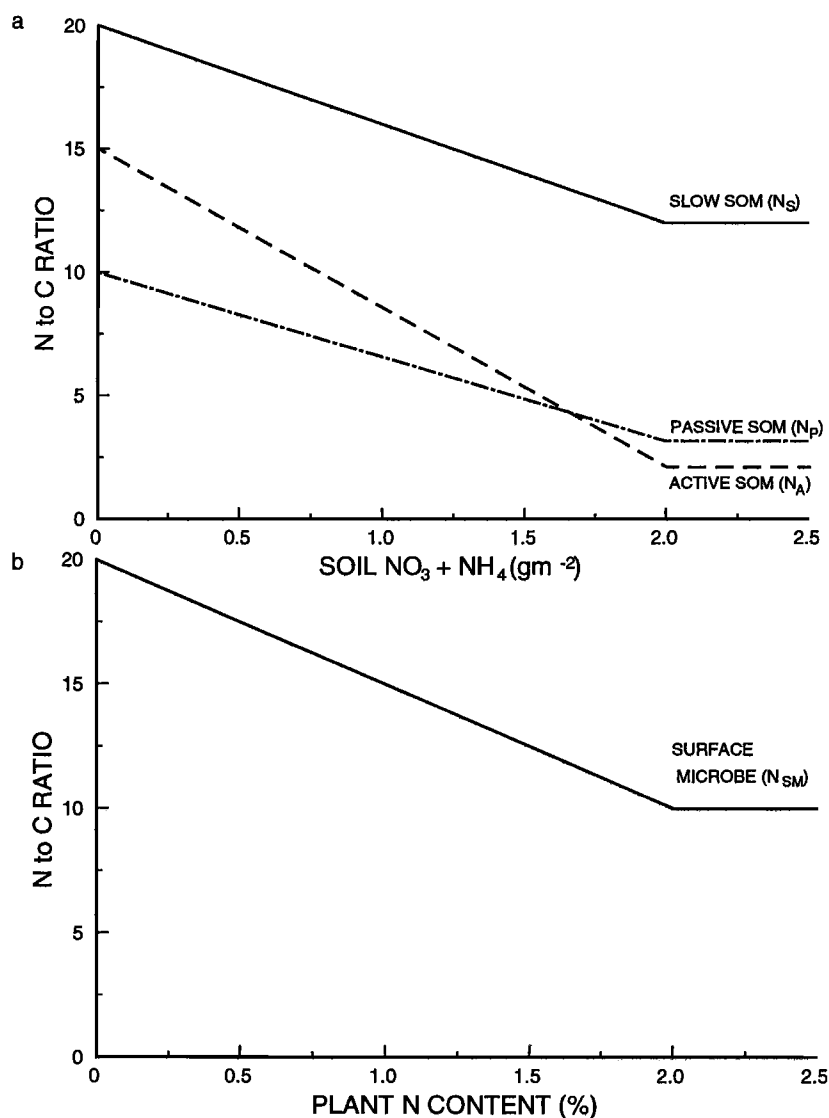
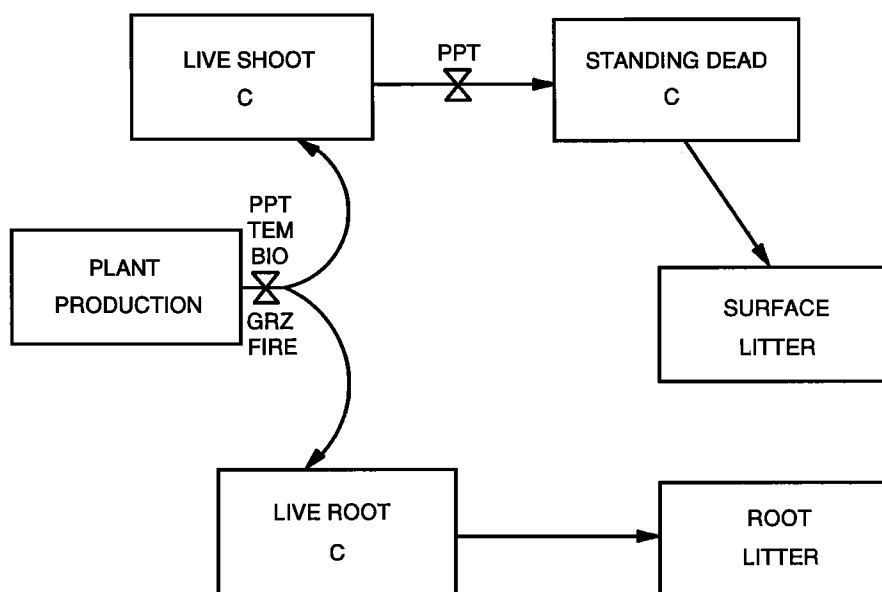


Fig. 4. Variation in C:N ratios of (a) the active, slow and passive SOM pools as a function of the mineral N pool, and (b) the newly formed microbial biomass as a function of the N content of decomposing plant matter.

## GRASS MODEL



PPT = Monthly Precipitation  
 TEM = Monthly Soil Temperature  
 BIO = Plant Biomass  
 GRZ = Grazing Rate  
 FIRE = Fire Frequency

Fig. 5. Flow diagram for the grassland production submodel.

production. Potential plant production is calculated as function of soil temperature, available water, and a self-shading factor using the following equation:

$$P_p = P_{mx} T_p M_p S_p \quad (14)$$

where  $P_p$  is the aboveground potential plant production rate ( $\text{g m}^{-2} \text{ month}^{-1}$ ),  $P_{mx}$  is the maximum potential aboveground plant production rate ( $250 \text{ g m}^{-2} \text{ month}^{-1}$ ),  $T_p$  (Figure 6b) is the effect of soil temperature on growth,  $M_p$  is the effect of moisture on production (Figure 6a), and  $S_p$  is the effect of plant shading on plant growth (Figure 6c). The effect of moisture on production  $M_p$  is a function of the ratio of current monthly precipitation plus the previous month's stored soil water (0-60 cm) to the potential evapotranspiration rate. The soil water holding capacity also influences  $M_p$  by modifying the amount of stored soil water, so that lower water holding soils (e.g., sandy soils) have a higher growth rate under dry conditions (see Figure 6a). This function was added to the model in order to represent the observation that sandy soils are more productive in dry environments [Sala et al., 1988]. The temperature response curves for plant growth are based on data from Christie and Detling [1982] for  $C_3$  and  $C_4$  plants. The shading factor

reduces plant production in the presence of large amounts of standing dead matter (Figure 6c).

The potential plant production rate ( $P_p$ ) is reduced if there is insufficient nutrient supply of N, P, or S, with the most limiting nutrient constraining production. A maximum and minimum carbon to element (E) ratio is specified for roots and live shoots, and the nutrient concentration not allowed to be greater than the minimum C:E ratio for each nutrient. The live shoot C:E ratio is a linear function of the live plant biomass. The fraction of the labile nutrient pools that are available for plant growth ( $F_g$ ) are a function of the live root biomass (ROOT;  $\text{g m}^{-2}$ ) according to the following equation:

$$F_g = 1.0 - 0.8 \exp(-0.015 \text{ ROOT}) \quad (15)$$

This equation is based on data presented by Wedin and Tilman [1990]. Live root and shoot death are calculated as a function of the available soil water in the 0-60 cm layer ( $H_2O_{(a)}$ ) using the following equations:

$$R_d = 0.12 [\exp(-5.0 H_2O_{(a)})] \quad (16)$$



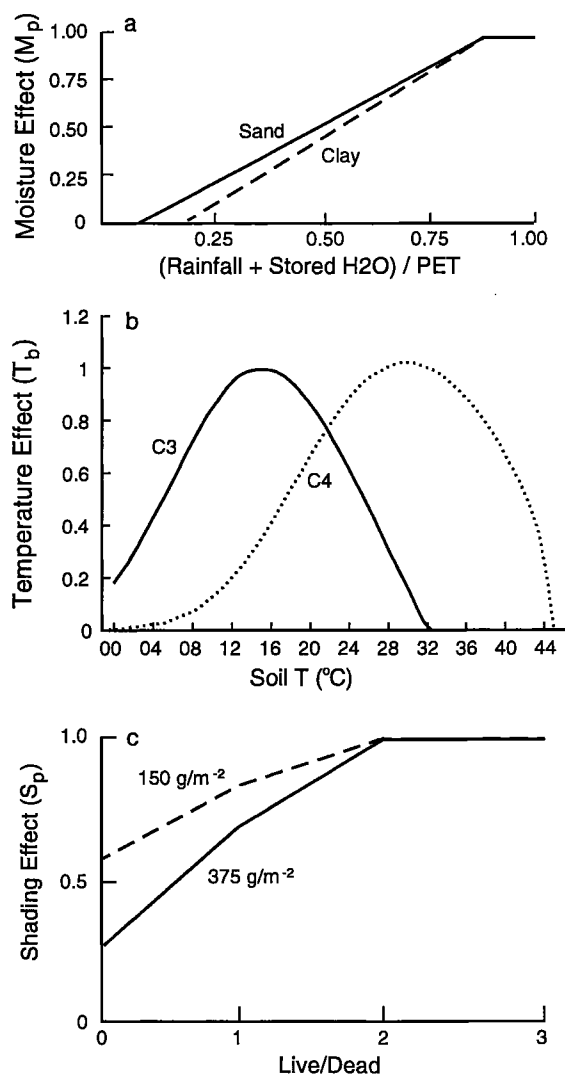


Fig. 6. The effect of (a) moisture, (b) soil temperature, and (c) shading on potential grass growth.

$$S_d = 0.20 [\exp(-5.0 H_2O_{(p)})] \quad (17)$$

where  $R_d$  and  $S_d$  are the fraction of roots and shoots, respectively, which die per month. Shoot death also occurs when live plant biomass exceeds 400 g m<sup>-2</sup> at a rate of 10% per month. This death rate is designed to simulate death due to shading of lower leaves in the canopy.

The model calculates root/shoot ratios as a function of the annual rainfall using equations presented in the original description of Century [Parton et al., 1987]. The effect of fire and grazing on plant production are based on data from Holland et al. [1992] and Ojima et al. [1990], respectively. The impacts of fire are to increase the root/shoot ratio, and to increase the C:N ratio of live shoots (plus 10 for temperate sites; 0 for tropical sites) and roots (plus 30 for all sites), removing vegetation and returning inorganic nutrients.

Grazing removes vegetation, returns nutrients to the soil (by urination and defecation), alters the root/shoot ratio and increases the N content of live shoots and roots [Holland et al., 1992].

Note that Century assumes that incoming solar radiation does not contribute significantly to interannual variability and so can be neglected as a control on the time-scales of interest here. This assumption is born out by the generally high correlations between observed and simulated NPP. Increasingly, climatic data and ecological data [Knapp and Smith, 1990] suggest this may be a poor assumption for the future, given trends in cloudiness suggested as part of global change scenarios. Future versions of the model will need to include this interaction, as well as CO<sub>2</sub> interactions.

#### DESCRIPTION OF SITES

The grassland study sites used for the modeling work (see Figure 7) reported here cover most of the world's major grassland types, ranging from the continental plains of the United States and Russia (22 to 81 cm per year precipitation) to both natural and converted grasslands in wet and dry regions of the tropics (59 to 154 cm per year precipitation). Soil types cover a wide range of textures: 20-85% sand, 10-40% silt, and 2-70% clay. Six of the important biogeographic regions identified by the International Geosphere-Biosphere Programme (IGBP) for global change research are included: temperate northern hemisphere, central arid Asia, Caribbean, northern Africa (including West Africa), southern and eastern Africa, and the tropical Asian Monsoon Region [Eddy et al., 1991]. Site descriptions are summarized in Table 1. The diversity of soils, climatic conditions and plant growth patterns of these sites provide a robust test of Century for global grasslands. While the sites permit a general global intercomparison, each site has made a unique contribution to the analysis presented here.

The large grassland region of the U.S. Central Plains represents a natural west-to-east moisture gradient. The Central Plains Experimental Range (CPER) at the arid end of the gradient is a shortgrass steppe experiencing wide diurnal, seasonal, and annual variation in temperature and precipitation. Vegetation there is dominated by C<sub>4</sub> shortgrasses. The Konza Prairie Research Natural Area at the more mesic end of the moisture gradient, is characterized by warm-season (C<sub>4</sub>) tallgrass prairie species. Data available at CPER include a 5-year time series (1971-1975) of aboveground live biomass and plant production, for control, irrigated, fertilized, and both irrigated and fertilized plots. Konza data include estimates of aboveground plant production (1976-1990) and seasonality of aboveground live biomass (1984-1990) for annually burned and unburned plots. None of the data from Konza were used to develop the model. Soil data from the CPER was used in model development; CPER live biomass data was not used in model development.

The five sites in the Commonwealth of Independent States (CIS; formerly Russia) characterize the "continentality" climate gradient from the European temperate meadows of Kursk and Otradnoye in western Russia, through the typical

## SCOPE GLOBAL GRASSLAND STUDY

- SITE NAME
- 1 NAIROBI NAT. PARK  
KENYA
  - 2 KLONG HK HAT YAI  
THAILAND
  - 3 MONTECILLOS CHAPINGO  
MEXICO
  - 4 LAMTO  
IVORY COAST
  - 5 CPER PAWNEE  
COLORADO U.S.A
  - 6 KONZA PRAIRIE  
KANSAS U.S.A
  - 7 KHOMUTOV  
UKRAINE
  - 8 KURSK  
RUSSIA
  - 9 OTRADNOYE 1  
RUSSIA
  - 10 SHORTANDY  
RUSSIA
  - 11 TUVA  
KAZAKHSTAN



Fig. 7. Location of the sites used to test the Century model.

steppes of Khomutov in Ukraine, to the ultracontinental steppes of Tuva, at the geographical center of the Asian continent. The long time series of aboveground biomass data (1954-1983) for the Kursk site covers a wide range of year-to-year variation in weather conditions. At Otradnoye, 5 years of monthly data (1967-1972) are available on aboveground biomass for a loamy and a sandy soil. The Khomutov site has 4 years of aboveground biomass data (1967-1970). More detailed data on vegetation dynamics is available for the Shortandy site, with monthly determinations of live and dead matter, both aboveground and belowground, over the period 1975-1979. The cold, dry Tuva site (aboveground biomass, 1977-1984) is a particularly interesting test for the Century model, since its climatic and physiological characteristics differ markedly from the grasslands of the U.S. Central Plains which were used originally to formulate Century [Parton et al., 1987].

In view of the importance of tropical grass-containing ecosystems or grasslands and savannas as perhaps the largest terrestrial biome [Hall and Scurlock, 1991], it was an important objective of the present SCOPE Project to adapt Century for modeling of tropical grasslands. Three of the four tropical grassland sites (Kenya, Thailand, and Mexico) were studied under a United Nations Environment Programme Project, and have used a common methodology to collect data on live and dead matter, aboveground and belowground, over the period 1984-1990 [Long et al., 1992]. The fourth tropical site was located at Lamto, Ivory Coast.

The Kenyan grassland is a dry grassland, established over

a long period on an ancient soil. By contrast, the Thailand site was probably converted from forest within the last 50-100 years, characteristic of many grasslands in southeast Asia. The Mexican grassland is derived from the bed of a saline lake, drained in 1911. The continuous record of aboveground and belowground data from this site is one of the most detailed for any grassland worldwide. The humid grass savanna site at Lamto, Ivory Coast, has been intensively studied by J. C. Menaut and coworkers for the past 30 years, and a discontinuous record kept of monthly aboveground live and dead matter, and total root matter [Menaut and Cesar, 1979]. Like most tropical grasslands, all four sites were subjected to burning during the period of study. Century's ability to simulate the effects of burning has thus been tested under treatments ranging from annual fires to burning every 6 years.

#### ESTIMATION OF MODEL PARAMETERS

The robustness of the Century model at a variety of grassland sites, from tropical savannas to temperate steppes and wet meadow grasslands is tested using a single model with minimal changes to parameters. Most parameters used by Century are intended to remain constant in the majority of applications and are referred to as the fixed parameters. Other parameters which are particular to an individual site or group of sites are contained within a site-specific file. With the comparisons between different grassland sites worldwide, it was desirable for the majority of the model parameters to

TABLE 1. Grassland Site Descriptions

	Nairobi National Park, Kenya	Klong HK Hat Yai, Thailand	Montecillos Chapingo, Mexico	Lamto, Ivory Coast	CPER Pawnee, Colorado	Konza Prairie, Kansas	Khomutov, Ukraine	Kursk, Russia	Otradnoye, Russia	Shortandy, Kazakhstan	Tuva, Russia
Latitude/longitude (approximately)	1 S 36 E	6 N 101 E	19 N 99 W	6 N 5 W	40 N 105 W	39 N 97 W	47 N 38 E	52 N 37 E	61 N 30 E	52 N 71 E	52 N 94 E
Elevation	1500 m	100 m	2220 m	100 m	1625 m	400 m	75 m	250 m	50 m	367 m	800 m
Annual precipitation	680 mm	1540 mm	590 mm	1170 mm	300 mm	818 mm	441 mm	560 mm	543 mm	351 mm	214 mm
Mean monthly minimum temperature (month)	10.8 (July)	21.5 C (Jan.)	1.4 C (Jan.)	21.5 C (Jan.)	-9.8 C (Feb.)	-10.2 C (Feb.)	-4.1 C (Dec.)	-12.6 C (Jan.)	-9.2 C (Feb.)	-24.6 C (Jan.)	-39.2 C (Jan.)
Mean monthly maximum temperature (month)	28.5 C (March)	31.2 C (March)	26.9 C (May)	36.0 C (Feb.)	30.7 C (July)	36.5 C (Aug.)	30.0 C (July)	24.7 C (July)	26.3 C (July)	27.2 C (July)	26.7 C (July)
Soil type	black clay vertisol	humic gley	solonnet	sandy	sandy loam	clay loam	Chernozem/vermiboroll	Chernozem/haplaboroll	soddy-podzolic I. loamy	Calciboroll/calciustosol	Haplustosol/calciustosol
Grassland type	dry grassland	humid savanna	saline	savanna	shortgrass prairie	tallgrass prairie	typical steppe	meadow steppe	meadow I. loamy	dry steppe	semi-desert ultra-continental steppe
Dominant species (C <sub>3</sub> C <sub>4</sub> )	Themeda triandra (C <sub>4</sub> )	Eulalia trispicata (C <sub>4</sub> )	Distichlis spicata (C <sub>4</sub> )	Loudetia simplex (C <sub>4</sub> )	Bouteloua gracilis (C <sub>4</sub> )	Andropogon scoparius/gerardii (C <sub>4</sub> )	Stipa lessingiana (C <sub>3</sub> )	Bromus riparius (C <sub>3</sub> )	I. Alchemilla monticola(C <sub>3</sub> )	Stipa zaleskyi (C <sub>3</sub> )	Agropyron crystatum (C <sub>3</sub> )
Maximum aboveground live biomass (typical month)	337 g m <sup>-2</sup> (July)	442 g m <sup>-2</sup> (Nov.)	430 g m <sup>-2</sup> (Aug.)	450 g m <sup>-2</sup> (Nov.)	40 g m <sup>-2</sup> (June)	380 g m <sup>-2</sup> (July)	340 g m <sup>-2</sup> (June)	362 g m <sup>-2</sup> (July)	I. 244 g m <sup>-2</sup> II. 277 g m <sup>-2</sup> (June)	142 g m <sup>-2</sup> (July)	103 g m <sup>-2</sup> (July)
Historical long-term management regime (est.)	grazing with fire every 5 years	n/a (converted grassland)	n/a (alluvial grassland)	annual burning	annual grazing	grazing with fire every 3 years	annual mowing	annual mowing	annual mowing	annual grazing	annual grazing

TABLE 2. Site-Specific Differences Between Functions Controlling Plant Growth

	Kenya	Thailand	Mexico	Lamto	CPER	Konza	Khomutov	Kursk	Oradnoye	Shortandy	Tuva
Root/shoot ratio as a function of total precip.	-	-	0	-	0	0	0	0	0	0	0
Root turnover as function of soil water	0	0	0	0	-	0	0	0	0	0	0
Atmospheric and soil N inputs	0	-	0	0	0	0	+	+	+	+	+
Number of soil layers available for plant growth	-	-	0	0	0	0	0	0	-	0	-
Shoot turnover as function of soil water	+	+	0	0	0	0	0	0	0	0	0
Fall rate of standing dead matter to litter	-	-	-	-	0	-	0	0	0	0	0
C:N ratio of shoot matter as a function of biomass	0	0	0	+	0	+	0	0	0	0	0

0, standard function; +/-, increase or decrease in value of function (see text for details).

comprise a universal "world grassland" set, with a relatively small number of site-specific parameters changing according to data available from each study site.

Some of these site-specific parameters consist of the "minimum input" data required to run the Century model, which include latitude and longitude, soil texture (sand, silt and clay), soil pH, soil depth for modeling water budget, plant type ( $C_3$ ,  $C_4$ ), and growing season, and weather data (monthly precipitation, monthly maximum, and monthly minimum temperatures). The remaining site-specific parameters relate mainly to plant physiological functions controlling growth, death, turnover, and N inputs. These differences were kept to a minimum (Table 2 and Figure A1 lists values for all site specific parameters). A site file was first created by entering basic site identification and "minimum input" data into the "universal" grassland file. Phenological differences (length of growing season) and plant growth responses to temperature were also entered at this stage. The Century model was then run for a period of 5000 years, using repeated weather sequences based on long-term weather data from the sites. Appropriate patterns of grassland management (grazing and burning) were incorporated in these long-term runs, based on the known history of the sites (see Table 1).

The equilibrium levels of soil organic matter (SOM) of the long-term runs were used as initial conditions for the validation study. The validation runs were simulated using actual weather data recorded at the site, and a comparison of simulated and observed values of monthly biomass and dead matter, aboveground and belowground was made. For these short-term model runs, the management regime was based on recent grazing/burning practice at each site (see Appendix A for details).

Differences in physiological parameters between the 11 grassland sites are summarized in Table 2. At the Kenyan, Lamto, and Thailand sites, the relatively low belowground live biomass compared with aboveground live biomass required a change in the equations determining root/shoot ratio. Root death rate, determined by available soil water, was satisfactorily modeled by a common function at all the sites except for CPER, where a lower rate was required to achieve the observed balance between live and dead root biomass. Atmospheric deposition and N fixation inputs are normally determined as a simple linear function of precipitation based on data from the U.S. Great Plains, but increased inputs were required to predict the observed production at the (relatively dry) Confederation of Independent States (CIS) sites. This is consistent with the higher rates of N deposition in continental Europe compared with the U.S. Central Plains [Bónis et al., 1980]. Reduced N inputs were necessary at the Thailand site in order to limit production under conditions of high rainfall. At Konza, Lamto, and Kenya, the function determining C:N ratio was modified to allow wider ratios based on detailed information available on the N content of plant matter. This modification was important because all these sites have frequent burning which would otherwise result in too much loss of nitrogen.

The death rate of aboveground biomass is determined in Century by the number of soil layers contributing water to

plant growth (and how quickly they dry), as well as by a direct soil water function. In order to produce sufficiently rapid turnover of aboveground matter, the number of soil layers was reduced at the Kenya, Thailand, Otradnoye, and Tuva sites (this had the effect of possibly reflecting differences in soil structure). The death rate function was further increased at the Kenya and Thailand sites. The transfer of standing dead to litter was highest for continental sites with snowfall (0.20 per month) and much lower for the tropical sites (0.10 per month). Most of these site specific differences reflect species specific and soil differences at the site. Documentation of the specific values of these sites are presented in Appendix A and a copy of site specific parameters are available from the authors.

## MODEL TESTING

In this section we show a comparison of observed data and simulated model output variables. The model output variables that we will test include the following: (1) dynamics of live shoot biomass, (2) aboveground plant production, (3) peak standing live shoot biomass, and (4) soil C and N levels. These variables were selected because they characterize grassland systems and interact with GCM models. Soil C level and plant production are important for the global C cycle, live plant biomass has a big impact on the energy and water budgets, and peak live biomass is frequently used as an estimate of aboveground plant biomass. Live plant biomass influences the energy budget by altering the canopy albedo and soil temperature latent heat fluxes.

We employed three techniques for testing the Century model: (1) linear regression of observed data versus simulated model results, (2) comparison of the Century model predictions with empirical regression models predicted from climate variables [Lauenroth, 1978], and (3) calculating the number of times the difference between Century model prediction and observed data differed by less than a threshold proportion (25%) of the observed data. The results show that in general the observed versus simulated  $r^2$  for the Century model and the empirical regression models are fairly similar. The advantage of the Century model is that it can predict total system behavior (e.g., nutrient cycling, N gas fluxes, water fluxes, leaching inorganic and organic compounds) and responses to manipulations such as fertilization, irrigation, and land use changes, while regression models can only predict what will happen for the particular observed data set used to generate the regression model coefficients. As a minimum criterion, in general, we felt Century should predict observed data at least as well as empirical climate regression models, which have limited extrapolation potential without including nutrient interactions [Esser, 1986].

## ABOVEGROUND NET PRIMARY PRODUCTION

Aboveground plant production data were available from the CPER shortgrass prairie site and the Konza tallgrass site. The CPER site has plant production from 1971 to 1975 for a control, fertilized, irrigated, and irrigated and fertilized sites

[Lauenroth, 1978]. The Konza site has plant production data from 1976-1990 for annual burned and unburned sites [Abrams et al., 1986, Briggs et al., 1989] (also see unpublished Long-Term Ecological Research records). The comparison of observed and simulated production data (Figure 8) shows that the model simulates these different treatments with an  $r^2$  of 0.70. A linear regression where the independent factors were annual precipitation, fertilization, and burning has an  $r^2 = 0.67$ . While Century may not greatly improve on predicting observations under current conditions, compared to simple regression models, its concurrent ability to predict the seasonality of foliage production has substantial significance to vegetation-atmosphere interactions studies and models of ecosystem dynamics. Sixty percent of Century's predicted plant production values have errors less than  $\pm 25\%$  of the observed plant production. The standard errors of the observed plant production across field replicates generally ranged from 10 to 20% of the observed values.

#### PEAK LIVE BIOMASS

The simulated peak live biomass from all of the different sites and treatments were compared to the observed peak live biomass (Figure 9). The observed peak live biomass is the maximum live biomass observed in a particular calendar year (January to December). Century results have an  $r^2 = 0.45$ . The  $r^2$  for the best regression model was 0.40, with annual precipitation as the independent variable. Peak live biomass is frequently used to estimate annual plant production in ungrazed grasslands, with annual production being approximately 50% greater than the peak live biomass [Lauenroth and Sala, 1992].

An analysis of the residual error showed that all of the large underestimates of peak live biomass by Century came from the Khomutov and Kursk sites. For comparison, removing the extreme Khomutov and Kursk points from the analysis increased the  $r^2$  from 0.45 to 0.65. Fifty-seven percent of the Century predictions had errors that were less than  $\pm 25\%$  of the observed data. In general, the model simulated peak live biomass reasonably well for all of the sites, with the exception of peak live biomass for the observed high plant production years (9 years out of 32 years) at the Kursk and Khomutov sites. The reason for the Russian site errors is unclear. We suspect that changes in species composition occurred during the high production years. It is also important to note that these two sites recorded some of the highest peak live biomass observed at any site in spite of the fact that precipitation at the Russian sites is 1/2 to 1/3 of the values for the tropical sites.

#### LIVE PLANT BIOMASS DYNAMICS

The comparison of observed and simulated live biomass for some of the temperate (Figure 10) and tropical (Figure 11) sites shows that general seasonal patterns were well simulated by the model. Difference between very dry and wet years (1989 versus 1990 at Konza and 1981 versus 1980 at Tuva) were well simulated, however, more subtle differences between years with similar precipitation (Konza 1984-1987 and Kursk 1975-1979) were not well simulated. For the tropical sites (Figure 10) the response to fire (1986 and 1989 at Thailand, 1986 at Lamto) was fairly well simulated. The death of live biomass at Mexico was underestimated during the dry season.

### Observed vs Simulated Production Burned, Unburned, & CPER

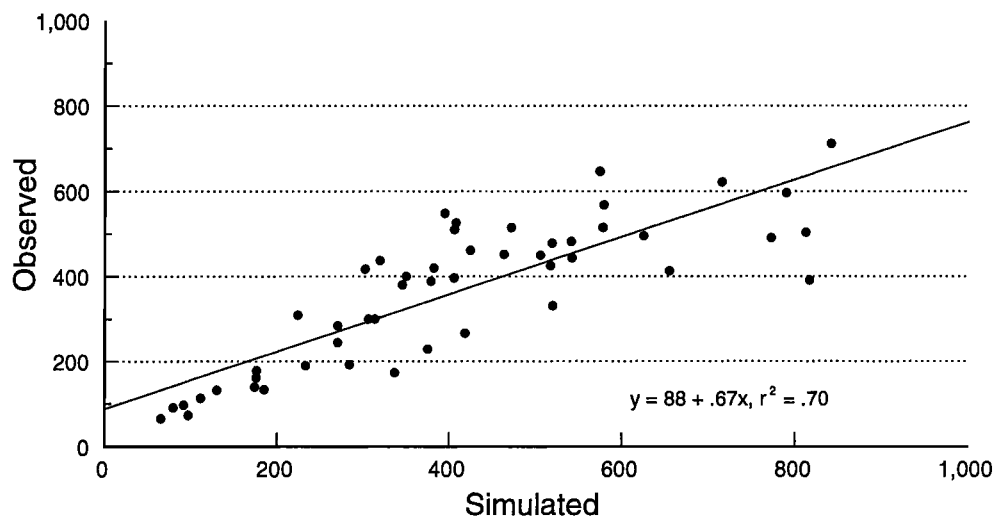


Fig. 8. Comparison of observed and simulated aboveground plant production for all the CPER treatment and burned and unburned sites at Konza.

## Peak Live Biomass - All Sites

Observed vs Simulated

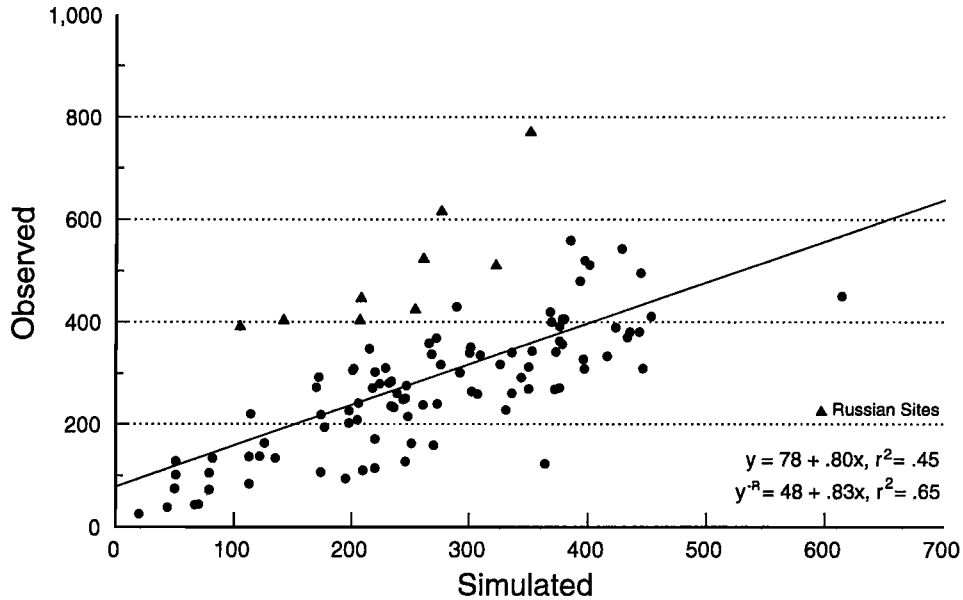


Fig. 9. Comparison of observed and simulated peak live biomass from all of the sites. The Kursk and Khomutov site data are shown with a.

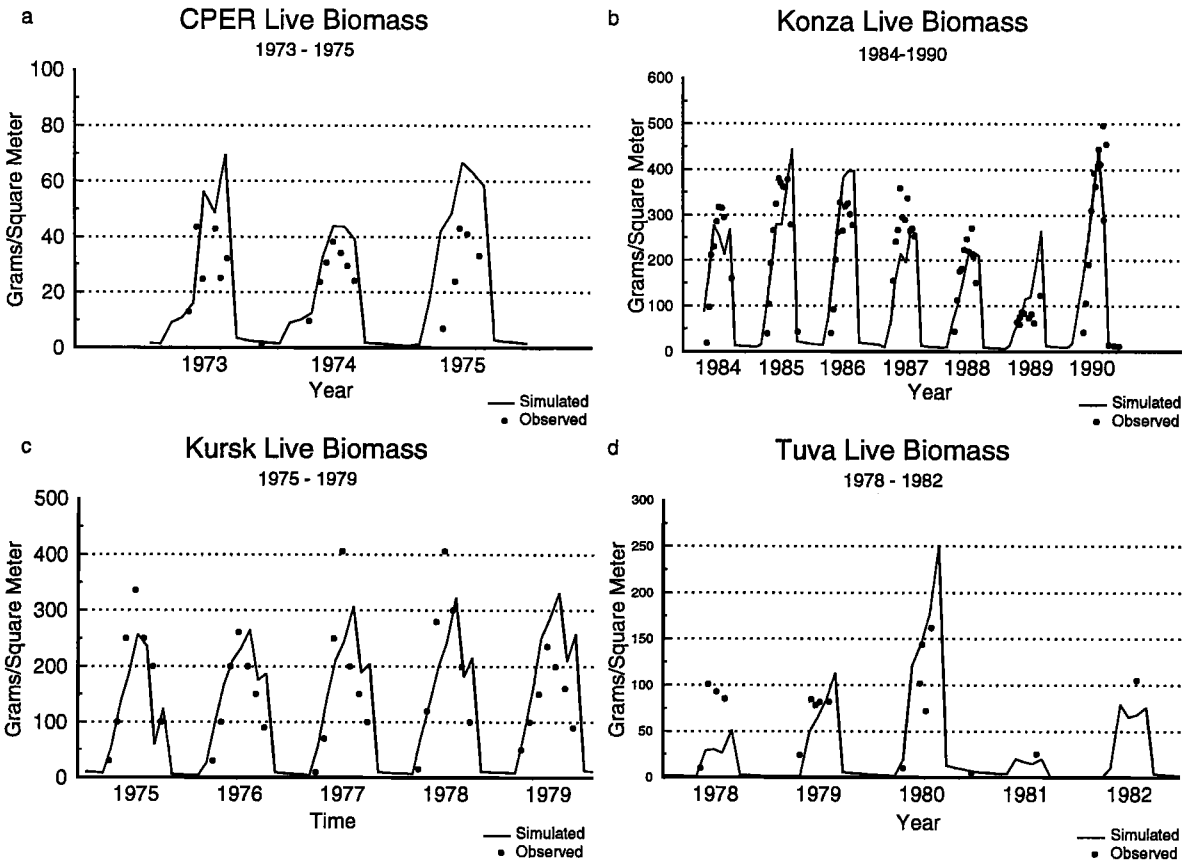


Fig. 10. Comparison of simulated and observed live biomass for (a) CPER, (b) Konza, (c) Kursk, and (d) Tuva sites.

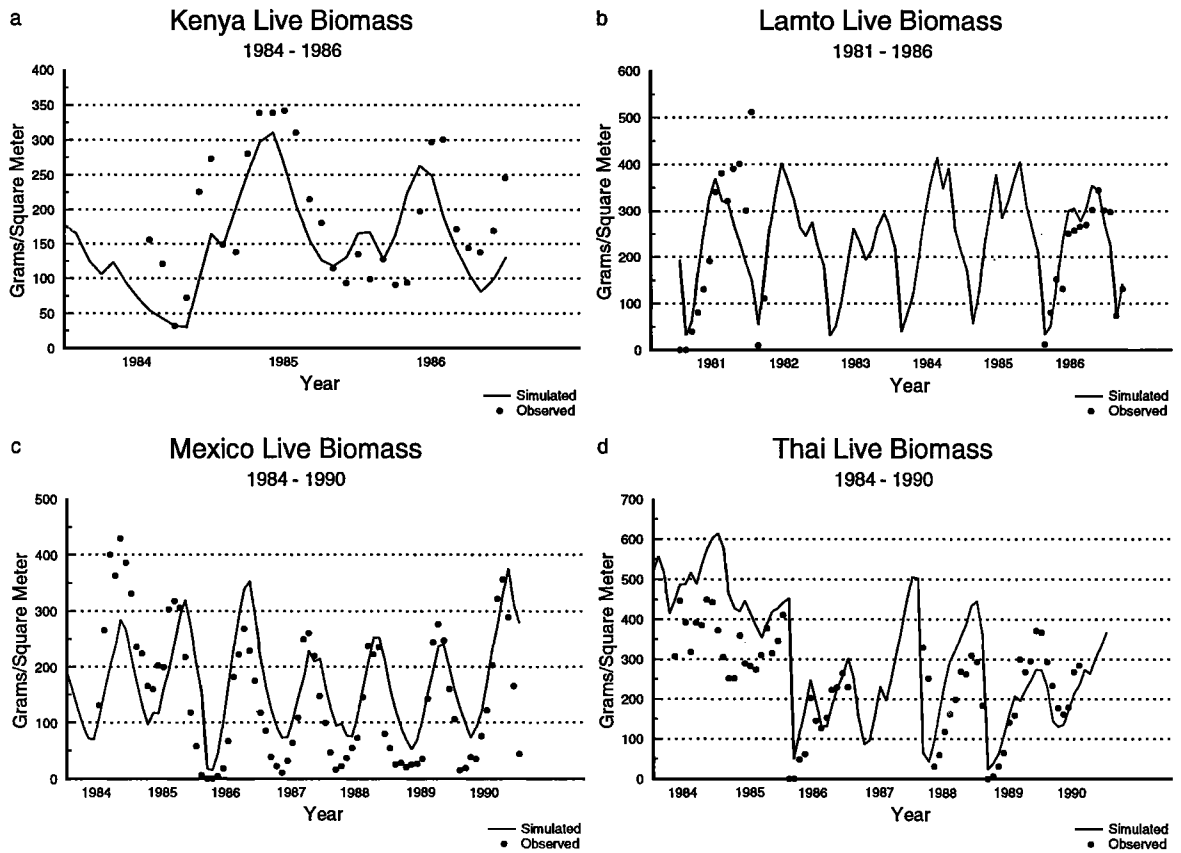


Fig. 11. Comparison of simulated and observed live biomass for (a) Kenya, (b) Lamto, (c) Mexico, and (d) Thailand sites.

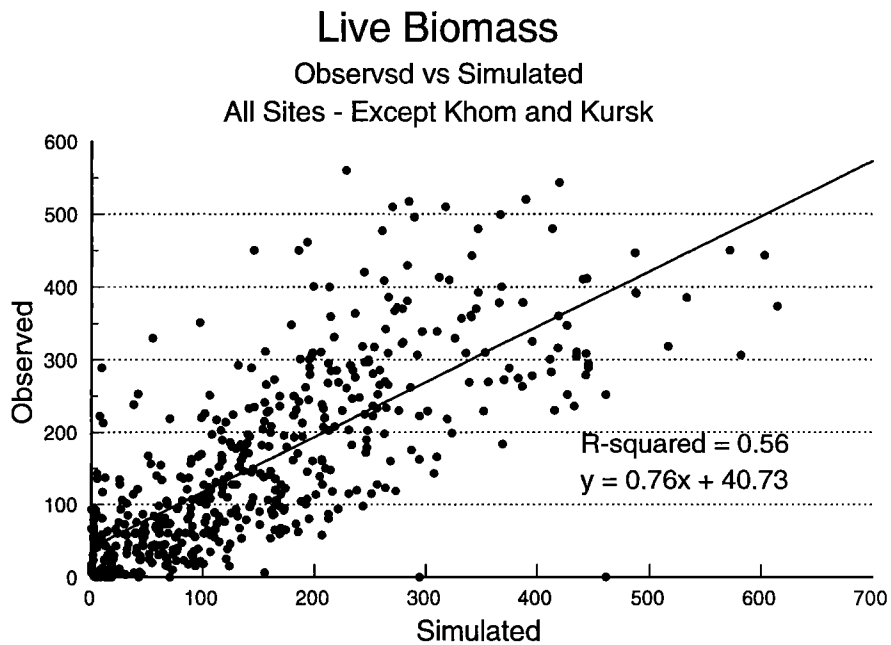


Fig. 12. Comparison of simulated and observed live biomass for all of the sites and treatments except Khomutov and Kursk.



A comparison of observed versus simulated live plant biomass for all of the sites and different treatments showed  $r^2 = 0.39$ . Again, the model tended to underestimate live biomass for high production years at the Kursk and Khomutov sites. Removing the data from the Kursk and Khomutov sites increased the  $r^2$  to 0.56 (Figure 12), suggesting that the errors for the Russian high plant production years greatly reduce the  $r^2$ . Thirty-one percent of the Century predictions had errors less than  $\pm 25\%$  of the observed data, while 57% of Century predictions had errors less than  $\pm 50\%$  of the observed data. These results

show that the model simulates peak live biomass and aboveground plant production better than live biomass.

SOIL C AND N

Soil C and N levels are fairly well simulated ( $r^2 = 0.93$  and 0.89, respectively for C and N) across a range of soil C levels ranging from less than 2000  $\text{g C m}^{-2}$  at Lamto to greater than the 10,000  $\text{g C m}^{-2}$  at the Kursk site (Figure 13). The assumptions used to control soil C stability and decomposition (clay impact on passive SOM and silt plus

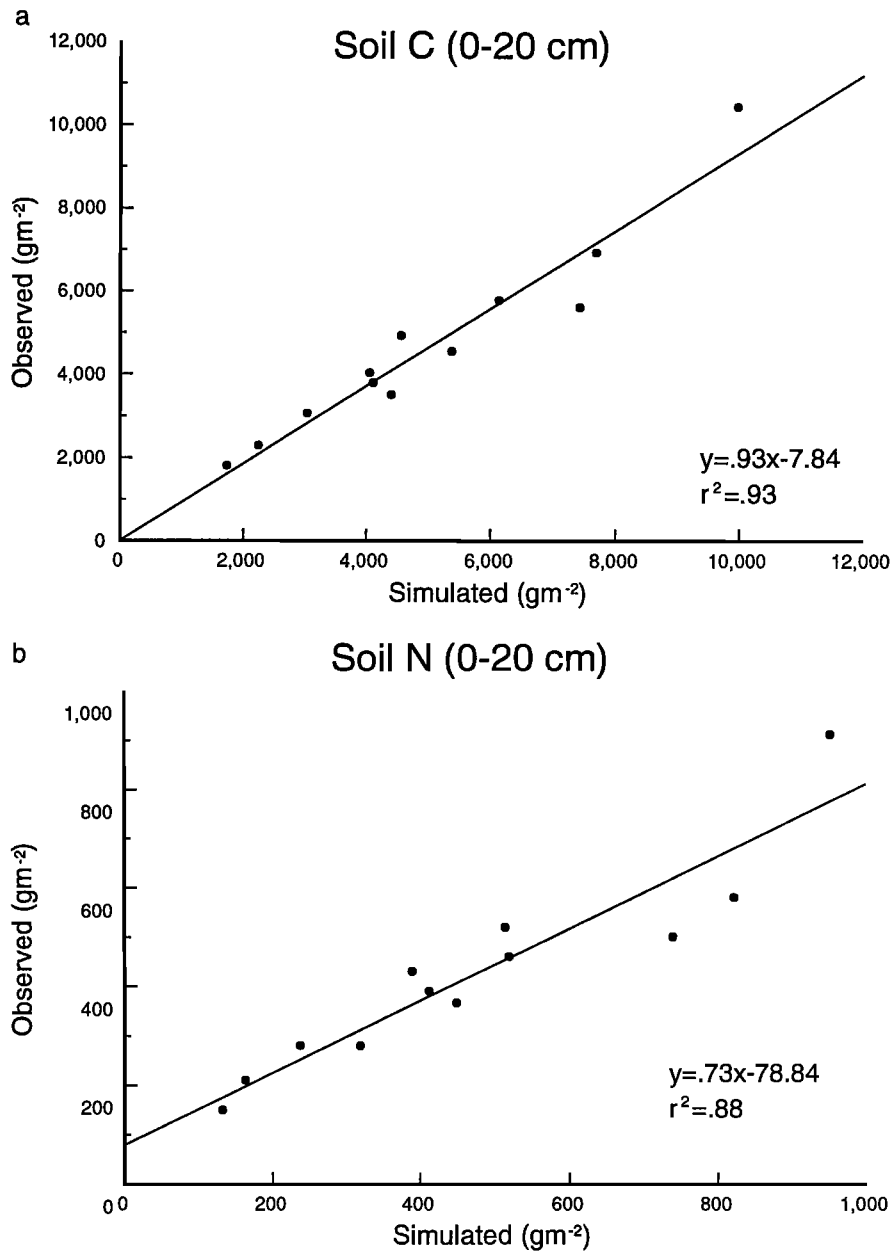


Fig. 13. Comparison of simulated and observed steady state soil (a) C and (b) N for 9 of the 11 sites. Mexico and Thailand sites were not used because they are not at equilibrium with their present land uses.

clay on slow SOM) seem to work across a diverse set of soil textures and soil mineralogies. One hundred percent for C and 75% for N of the model predictions had errors less than  $\pm 25\%$  of the observed values. Soil C data from the CPER and Konza site were used to fit some of the model parameters in the SOM model. Burke et al. [1989] have developed a regression model for predicting soil C and N levels in grasslands as a function of climate and soil texture. We used the Burke et al. [1989] model to predict soil C and N levels at the different sites (excluding Thailand and Mexico), and  $r^2$  between observed and simulated soil C and N levels were 0.89 and 0.90, respectively.

Appendix A shows the equilibrium soil C level for the different soil pools (presented as initial values for model runs). The data show that the fraction of soil C in active SOM generally ranged from 2% to 4%, and 35-60% for passive SOM. Sites with high clay (>35%) content had high amounts of passive SOM and less slow SOM. For example, the sandy soils at CPER had 61% slow SOM and 36% passive, while the clay loam soils at Konza has 41% slow and 55% passive SOM.

## DISCUSSION

We think that difficulty in simulating live plant biomass is primarily a result of the fact that plant species changes are not considered in the model. Changes in species composition from  $C_3$  and  $C_4$  vegetation or structural changes resulting from shifts between grasslands and savannas affect nutrient dynamics, water utilization, biomass allocation, and other characteristics which modify plant production and seasonality of plant growth. Numerous grassland studies have shown that shifts in  $C_3$  and  $C_4$  grass dominance can be induced by drought [Albertson and Weaver, 1944], grazing and fire regime [Owensby et al., 1970; Towne and Owensby, 1984; Bragg and Hulbert 1976], or nitrogen additions [Owensby et al., 1970; Dodd and Lauenroth, 1978; Wedin and Tilman 1990; Seastedt et al., 1991]. Modifications of resource use efficiency among various vegetation communities are important to projecting how an ecosystem will respond to increased atmospheric  $CO_2$ , change in climate, or increases in atmospheric deposition of N [Wedin and Tilman, 1990]. Studies of N additions to grassland ecosystems indicate that grassland communities are sensitive to the soil nitrogen status [Dodd and Lauenroth, 1978; Wedin and Tilman, 1990; Seastedt et al., 1991]. These shifts in plant communities have potentially major impacts on soil organic matter dynamics via controls of nitrogen immobilization and storage, however, our ability to predict changes in plant species composition is limited.

Additional factors contributing to these subtle interannual differences may result from (1) interannual variations in incident PAR, not included in the model, (2) effects of timing of rainfall not captured with a monthly time step, or (3) lag effects of nutrient or photosynthate storage in plants. Investigation of the above effects is ongoing.

Models like Century which simulate NPP form an important complement to more physiologically oriented

models which simulate photosynthesis and respiration. Physiological models require detailed climatic information, such as hourly incoming solar radiation relative humidity and wind speeds, that are not widely available for retrospective analyses such as are presented here. Physiological models may also be sensitive to species-dependent traits, though this sensitivity may be tractable for large-scale calculations [Schimel et al., 1990; McGuire et al., 1992]. The extensive body of NPP data over time, reflecting both geographic variability and the effects of climate variability allows the development of powerful calibrated models like Century. Such data and models are a crucial benchmark test for predicted time integral quantities (e.g., NPP, biomass levels) from models based on calculation of instantaneous exchanges of  $CO_2$ .

## SUMMARY

The comparison of observed and simulated live peak biomass and plant production had  $r^2$  values of 0.45 and 0.70, respectively; Century error terms for these variables were generally less than  $\pm 25\%$  of the observed data. Seasonal live biomass was not as well represented by the model ( $r^2 = 0.39$ ) and had errors less than  $\pm 50\%$  of the observed data. The model simulated differences between wet and dry years well, but was unable to simulate more subtle differences between years with similar precipitation. The model substantially underestimated live biomass for unusually high production years at the Kursk and Khomutov sites.

A comparison of the Century model predictions for plant production and peak live biomass with empirical regression equations fit to observed data showed that the Century model was slightly more successful than the regression equations. Steady state soil C and N levels were well simulated by the model ( $r^2 = 0.93$  and  $0.89$ ) for a set of sites with differing climate and soil textures. The model was able to predict soil C and N levels to within  $\pm 25\%$  of observed data. Globally, key controls over C storage, NPP, and biomass include climate, N inputs and losses, and soil particle size distribution. This model, rigorously calibrated against a large body of observations, is useful both as a descriptive and analytical tool, and as a baseline test for time-integrated predictions (e.g., of NPP or biomass) for physiologically based models, explicitly simulating  $CO_2$  exchange [e.g., Coughenour, 1984; Hunt et al., 1991].

## APPENDIX A

Site-specific parameters found in the SITENAME.DAT file may be divided into a number of categories (see Figure A1): (1) Basic site identification (e.g., SITLAT, SITLNG); (2) "minimum input" data required to run the Century model ((a) environmental information such as PRECIP, TMN2M, TMX2M; and (b) physical features such as sand, silt, clay); (c) parameters relating mostly to plant and soil physiology.

Figure A1 shows the parameters from categories 2b and 3 for all the grassland sites reported here, with notes on the differences between sites.

APPENDIX B

All equations used in the water flow model and variable definitions. For detailed validation and descriptions, see Parton et al. (manuscript in preparation, 1993). See Figure B1.

- ADD water added to the soil (cm mo<sup>-1</sup>).
- A<sub>i</sub> depth of ith layer (cm).
- ATM atmospheric H<sub>2</sub>O sink or source (cm).
- AWL<sub>i</sub> relative root density in the i layer (0-1).
- BS fraction of PPT lost as bare soil H<sub>2</sub>O loss (0-1).
- D deep H<sub>2</sub>O storage (cm).
- E<sub>i</sub> fraction of H<sub>2</sub>O loss by transpiration (0-1).
- EVAP bare soil plus interception H<sub>2</sub>O loss (cm).
- EVBS bare soil evapotranspiration (cm mo<sup>-1</sup>).
- F<sub>AV</sub> total H<sub>2</sub>O available for transpiration H<sub>2</sub>O loss (cm).
- F<sub>i</sub> saturated H<sub>2</sub>O flow from i layer to the i+1 layer (cm mo<sup>-1</sup>).
- INT fraction of PPT lost as interception H<sub>2</sub>O loss (0-1).
- K<sub>d</sub> fraction of excess H<sub>2</sub>O flowing to D<sub>s</sub> (0-1).
- K<sub>F</sub> fraction of excess H<sub>2</sub>O flowing to S<sub>F</sub> (0-1).
- K<sub>X</sub> fraction of D flowing to S<sub>F</sub>
- L liquid snow pack (cm).
- L<sub>b</sub> aboveground live plant biomass (gm<sup>-2</sup>).
- L<sub>d</sub> surface litter biomass (gm<sup>-2</sup>).
- M the H<sub>2</sub>O melting from S (cm mo<sup>-1</sup>).
- N the number of soil layer units with roots
- PET potential evapotranspiration H<sub>2</sub>O loss (cm).
- PPT monthly precipitation (cm mo<sup>-1</sup>).
- RWC<sub>i</sub> the relative water content for the ith layer
- S frozen snow pack (cm).
- S<sub>d</sub> standing dead plus live plant biomass (gm<sup>-2</sup>).
- S<sub>D</sub> saturated drainage to deep storage (cm mo<sup>-1</sup>).
- S<sub>F</sub> stream flow (cm mo<sup>-1</sup>).
- S<sub>i</sub> soil water in the ith layer (cm).
- S<sub>i</sub><sup>F</sup> field capacity of i layer (cm).
- S<sub>i</sub><sup>W</sup> wilting point of i layer (cm).
- S<sub>s</sub> H<sub>2</sub>O flow from D to S<sub>F</sub> (cm mo<sup>-1</sup>).
- S<sub>l</sub> sublimation H<sub>2</sub>O loss (cm m<sup>-1</sup>).
- T transpiration H<sub>2</sub>O loss (cm m<sup>-1</sup>).
- T<sub>i</sub> transpiration H<sub>2</sub>O loss ith layer (cm m<sup>-1</sup>).
- T<sub>P</sub> potential transpiration H<sub>2</sub>O loss (cm mo<sup>-1</sup>).
- W<sub>i</sub> weight factor for transpiration H<sub>2</sub>O loss from the ith layer (0-1).

	KENTYADAT	THALDADAT	MEXICO.DAT	LANTO.DAT	CPERDAT	KONZADAT	KHOM.DAT	KURSK.DAT	OTRAD.DAT	SHORTADAT	TUVADAT
SOMIC(2,1)	30	30	30	30	20	30	30	30	30	30	30
SOMIC(2,1)	59	190	190	60	60	190	270	333	150	170	100
SOMZC(1)	1480	1230	3050	850	1250	2100	3700	5506	3100	2200	1500
SOMSCI(1)	880	570	2100	610	740	2800	2150	5415	2900	3530	2530
(initial carbon content of soil organic matter pools, obtained from long-term model runs; suitable initial values here greatly reduce the time taken for the model to reach equilibrium. In the case of relatively recently converted grasslands such as Mexico and Thailand, values are based on observed soil carbon)											
BULKD	1.2	1.2	1.2	1.5	1.5	1.2	1.2	1.2	1.2	0.96	1.25
(soil bulk density; measured value used if available; this controls erosion and is important in calculating actual soil C and N content from % values)											
EPNFA(1)	.21	.21	.21	.21	.21	.21	.21	.21	.21	.21	.21
EPNFA(2)	.0028	.0028	.0028	.0028	.0028	.0028	.0028	.0028	.0028	.0028	.0028
EPNFS(1)	-1.32	-0.92	-1.32	-1.32	-1.32	-1.32	-0.86	-0.86	-0.86	-0.86	-0.86
EPNFS(2)	.033	.01	.033	.033	.033	.033	.07	.07	.07	.07	.07

Fig. A1. Parameters from categories 2b and 3 for all the grassland sites reported here, with notes on the differences between sites.

	KENYA.DAT	THAL.DAT	MEXICO.DAT	LAMTO.DAT	CFER.DAT	KONZA.DAT	KHOM.DAT	KURSK.DAT	OTRAD.DAT	SHORTA.DAT	TUVA.DAT
(intercept and slope for equations describing atmospheric N deposition and soil (symbiotic and non-symbiotic) N fixation, respectively, as a function of annual precipitation in cm. Mean annual rainfall at Kenya, Thailand, Mexico, Lamto, CFER, Konza, Khomutov, Kurak, Otradnoye, Shortandy and Tuva, is 68, 154, 59, 117, 90, 82, 44, 56, 54, 35 and 21 cm, respectively; hence total N inputs (g m <sup>-2</sup> ) of 1.32, 1.26, 1.00, 3.08, 0.28, 1.83, 2.55, 3.45, 3.28, 1.90 and 0.88, respectively)											
NLAYER	3	5	5	5	5	5	5	5	5	6	6
NLAYPG	2	3	4	4	4	4	3	4	3	4	3
(NLAYER is the number of "layers" in the soil water/nutrient flow sub-model; this simulates actual soil depth over bed rock or hard pan. NLAYPG is the number of these layers which the plants use for active growth; this is equivalent to the depth of the majority of roots)											
PH	7.5	5.5	7.5	6.0	6.8	6.3	7.4	6.3	5.2	7.4	7.3
(soil pH; measured value used if available; mainly of importance to the phosphorus sub-model, if used)											
PTYPE	2	2	2	2	2	2	1	1	1	1	1
(plant type; determines temperature response of primary production. "2" denotes plants with higher temperature optimum, i.e. mainly C4 photosynthetic type. "1" denotes cooler temperature optimum, i.e. mainly C3 type. N.B. some C4 plants in temperate regions show type "2" temperature response)											
ACPPA	-40	-40	-40	-40	-40	-40	-40	-40	-40	-40	-40
ACPPB	11	11	7.7	7.7	7.7	7.7	7.7	7.7	7.7	7.7	7.7
BCPPA	60	100	100	100	100	100	100	100	100	100	100
BCPPB	4	4	7	7	7	7	7	7	7	7	7
(intercept and slope for above ground and below ground maximum NPP as a function of annual precipitation (cm); used only to determine roof/shoot ratio. Mean annual rainfall at Kenya, Thailand, Mexico, Lamto, CFER, Konza, Khomutov, Kurak, Otradnoye, Shortandy and Tuva, is 68, 154, 59, 117, 90, 82, 44, 56, 54, 35 and 21 cm, respectively; hence mean roof/shoot ratios of 0.47, 0.48, 1.24, 1.07, 1.62, 1.14, 1.37, 1.47, 1.27, 1.50 and 2.00, respectively)											
FALLRG	0.1	0.15	0.1	0.1	0.2	0.15	0.2	0.2	0.2	0.2	0.2
(monthly fraction of standing dead matter which falls as litter. Note that CENTURY assumes that decomposition occurs only to litter, so this parameter should also take into account direct decomposition of standing dead)											
FDPREM(1)	0.85	0.85	0.85	0.90	0.85	0.85	0.85	0.85	0.85	0.85	0.85
FDPREM(2)	0.85	0.85	0.85	0.95	0.60	0.60	0.60	0.60	0.60	0.60	0.60
FLFREM	0.85	0.90	0.85	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
(fraction of standing dead matter, litter and live matter which is consumed by fire. Note that these values act in combination with FALLRG, litter decomposition and FSDETH, respectively; complete disappearance may therefore be produced by values of 0.95 or lower. In particular, standing dead matter may assume negative values if FDFREM(1) is greater than (1-FALLRG)).											
FDGREM	0.06	N/A	N/A	N/A	0.06	0.06	0.80	0.80	0.80	0.06	0.06
FLGREM	0.12	N/A	N/A	N/A	0.12	0.12	0.80	0.80	0.80	0.12	0.12

Fig. A1. (continued).

	KENYA.DAT	THAL.DAT	MEXICO.DAT	LAMTO.DAT	CFER.DAT	KONZADAT	KHOM.DAT	KURSK.DAT	OTRAD.DAT	SHORTA.DAT	TUYA.DAT
GREMON(1)-(7)	4-7, 10-11	N/A	N/A	N/A	5-9	5-9	9	9	9	4-10	4-10
(fraction of standing dead matter and live matter which is consumed by a grazing event (these values also act in combination with FALLRG, FDPREM, FSEDETH, etc.) N.B. the high consumption in a single month at Khomlov, Kurak, and Otradnoye represents mowing of the grass for forage or thatch)											
FRET(1)	.30	.30	.30	.50	.25	.30	.30	.15	.30	.30	.50
FFCRET	0	0	0	0	.05	.05	.05	.05	.05	.05	.05
(fraction of burned nitrogen which returns to soil as ash, and fraction of carbon returned to the soil as charcoal. N.B. since the latter does not normally enter BOM pools, it is often ignored and set to zero)											
FLING(1,1)	0.2	0.12	0.2	0.106	0.2	0.2	0.2	0.2	0.2	0.2	0.2
FLING(2,1)	0.0012	0	0.0012	0	0.0012	0.0012	0.0012	0.0012	0.0012	0.0012	0.0012
FLING(1,2)	0.26	0.16	0.26	0.106	0.26	0.26	0.26	0.26	0.26	0.26	0.26
FLING(2,2)	-0.0015	0	-0.0015	0	-0.0015	-0.0015	-0.0015	-0.0015	-0.0015	-0.0015	-0.0015
(intercept and slope of equations predicting lignin content as a function of annual precipitation (cm), equations fitted to US Great Plains data, so actual lignin determinations are preferable for wet tropical sites)											
FSEDETH(1)	0.25	0.45	0.25	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
FSEDETH(2)	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
(FSEDETH(1) is maximum fraction of above ground live matter which dies monthly; this is a function of estimated monthly water deficit; FSEDETH(2) relates to death in the senescence month for a temperate grassland and is not used for tropical systems)											
GFCRET	.30	.30	.30	.30	.30	.30	.30	0	0	.30	.30
GRET(1)	.30	.30	.30	.30	.30	.30	.30	0	0	.30	.30
(fraction of carbon, and fraction of nitrogen, respectively, returned to soil by a grazing event. 0 indicates mowing (total removal of grass) at the Kurak and Otradnoye sites.											
GPFLAG	2	2	2	2	2	2	2	2	2	2	2
(method used to estimate monthly primary production: "2" means that NPP is calculated as a function of monthly water availability and temperature, limited by the most limiting nutrient and any significant shading by standing dead matter)											
GRASCH(1)	1	1	1	1	3	3	3	3	3	3	3
GRASCH(2)	12	12	12	12	9	9	9	10	8	8	8
GRASCH(3)	13	13	13	13	10	10	11	11	9	9	9
(grass schedule parameters, describing the start month, end month and senescence month of the growing season, respectively; for tropical systems without a clear annual senescence event, the senescence month is set to 13 and is therefore not used)											
GRDR	0.12	0.12	0.12	0.12	0.06	0.12	0.12	0.12	0.12	0.12	0.12

Fig. A1. (continued).

	KENYADAT	THALDAT	MEXICODAT	LAMTODAT	CPERDAT	KONZADAT	KHOMDAT	KURSEKDAT	OTRADDAT	SHORTADAT	TUVALDAT
(monthly turnover rate for grass roots; this determines the total level of root matter and the balance between live and dead below-ground)											
FRAMNG(1,1)	20	20	20	30	20	20	20	20	20	20	20
FRAMNG(1,2)	0.20	0.15	0.15	0.25	0.15	0.20	0.15	0.15	0.15	0.15	0.15
FRAMXG(1,1)	30	30	30	35	30	30	30	30	30	30	30
FRAMXG(1,2)	0.20	0.15	0.15	0.25	0.15	0.20	0.15	0.15	0.15	0.15	0.15
FRBMNG(1,1)	50	50	50	50	50	50	50	50	50	50	50
FRBMNG(1,2)	0	0	0	0	0	0	0	0	0	0	0
FRBMXG(1,1)	60	60	60	60	60	60	60	60	60	60	60
FRBMXG(1,2)	0	0	0	0	0	0	0	0	0	0	0
(intercept and slope for equations relating plant C:N ratio to biomass for above and below ground matter, respectively; new growth at low biomass has a low C:N ratio, increasing with biomass so that grasslands with high live biomass have a high C:N ratio)											
SAND	0.40	0.58	0.47	0.85	0.70	0.25	0.20	0.52	0.425	0.35	0.74
SILT	0.25	0.40	0.35	0.10	0.15	0.35	0.28	0.31	0.40	0.27	0.17
CLAY	0.35	0.02	0.18	0.05	0.15	0.40	0.52	0.37	0.175	0.57	0.09
(soil texture at the study site; in particular, sand content affects microbial turnover rate and stabilization of "slow" organic matter (SOM2); clay soils stabilize more passive organic matter (SOM3); sandy soils are more productive at low rainfall, whereas clay soils are more productive at high rainfall)											
Management regimes for short-term model runs (repeated pattern of up to 20 years, where f = fire year, b = both grazing and fire, n = no grazing or fire)											
year-to-year repeated pattern	nnmf	nnmf	mmmf	f	f	gnb	n	n	n	n	n
month in which fire occurs	3	2	2	2	.	4	.	.	.	.	.

Fig. A1. (continued).

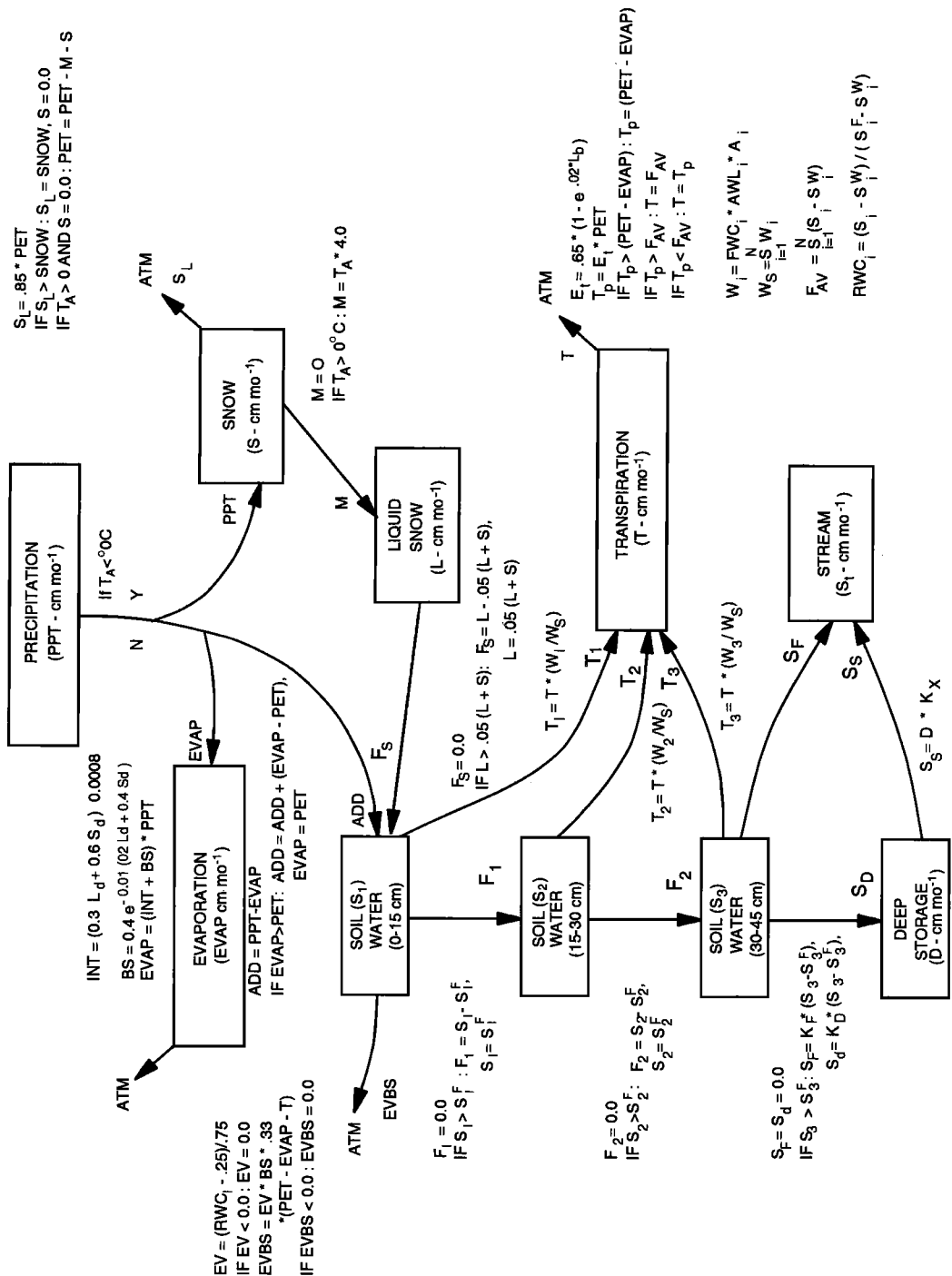


Fig. B1. Water submodel used in Century.

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