SCOPE 56 - Global Change: Effects on Coniferous Forests and Grasslands

11 Global Grassland Ecosystem Modelling: Development and Test of Ecosystem Models for Grassland Systems

W. J. PARTON,[1] M. B. COUGHENOUR,[1]
J. M. O. SCURLOCK,[2] D. S. OJIMA,[1] T. G. GILMANOV,[3]
R. J. SCHOLES,[4] D. S. SCHIMEL,[5] T. B. KIRCHNER,[1]
J.-C MENAUT,[6] T. R. SEASTEDT,[7] E. GARCIA MOYA,[8]
A. KAMNALRUT,[9] J. I. KINYAMARIO[10] and D. O. HALL[2]

[1] *Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, USA*

[2] *Division of Life Sciences, King's College London, U K*

[3] *Department of Vertebrate Zoology and Ecology, Moscow State University, Russia*

[4] *Division of Water, Environment and Forest Technology, CSIR, Pretoria, South Africa*

[5] *Climate System Modelling Program, NCAR, Boulder, USA*

[6] *Laboratoire d'Ecologie, Ecole Normale Supérieure, Paris, France*

[7] *Institute of Arctic and Alpine Research, University of Colorado, Boulder, USA*

[8] *Centro de Botanica, Colegio de Postgraduados, Chapingo, Mexico*

[9] *Faculty of Natural Resources, Prince of Songkla University, Hatyai, Thailand*

[10] *Department of Botany, University of Nairobi, Kenya*

11.1 INTRODUCTION

Natural grasslands, both in the tropics and in temperate regions, playa major but poorly defined role in the global carbon (C) cycle. Grasslands are one of the most widespread vegetation types worldwide, covering nearly one-fifth of the earth's land surface (24 x 10^6 km^2, Lieth 1972; Hall and Scurlock 1991), and containing approximately 30% of global soil C stocks (Anderson 1991). Ranging from the savannas of Africa to the North American prairies and the converted grasslands of Latin America and South-East Asia, these ecosystems are geographically extensive. The dynamics of these ecosystems are often jointly controlled by climate and biogeochemical factors. The interaction of these factors control fluxes of C through plant and soil organic matter (SOM) in grasslands. The magnitude of the fluxes and storages of C in these ecosystems have been little studied, especially in the tropics, and may have been underestimated in the past (Long *et al.* 1989).

Grassland ecosystems are globally important as meat and grain producing regions. Human utilization of these ecosystems has occurred for thousands of years. These ecosystems are noted by their high climate variability and high frequency of drought events. The climate variability coupled with high human use makes these ecosystems more susceptible to rapid degeneration of ecosystem properties and soil C levels. An improved understanding of the factors affecting the long-term productivity of the ecosystems will be beneficial to those individuals living in those ecosystems, as well as to developing a better understanding of the role these ecosystems play in global environmental change.

The amount of C in terrestrial vegetation and soils worldwide is greater than the amount found in the atmosphere and the ocean surface layers, which cycle C on annual to millennial time scales. The role of grasslands in global biogeochemical cycles cannot 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^2, and in terms of both land area and productivity are nearly equal to tropical forests. Carbon stored in grassland soils, temperate and tropical, are the major C component in these ecosystems and are a significant C reservoir globally (Anderson 1991).

Grasslands are susceptible to changes in climate and land use. These semiarid and arid ecosystems tend to develop under highly variable rainfall regimes which are conducive to rapid changes in ecosystem structure given modifications in fire and grazing patterns (Archer *et al.* 1994; Ojima *et al.* 1994), and in altered climate regimes (OIES 1991). In order to better understand what factors control grassland dynamics across a broad environmental gradient, we have employed two types of ecosystem models. These models are able to evaluate the influence of climate, edaphic, and land use factors that control grassland dynamics.

Under the aegis of the SCOPE Project, the CENTURY and GRASS models for plant-soil ecosystems were used. This chapter provides general information of the different grassland sites used for model development and testing, methodology of parameterization, description of models, and finally the analysis of model behavior across a suite of grassland sites.

11.2 DESCRIPTION OF SITES

The grassland study sites used for the modelling work (Figure 11.1) reported here cover most of the world's major grassland types, ranging from the continental steppes and plains of the USA and Russia (22-81 cm yr^{-1} precipitation) to both natural and converted grasslands in wet and dry regions of the tropics (59-154 cm yr^{-1} 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 11.1. The diversity of soils, climatic conditions and plant growth patterns of these sites provides 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.

Figure 11.1 Location of the sites used to test the CENTURY model

The large grassland region of the US 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 variations in temperature and precipitation. Vegetation at the CPER is dominated by C_4 shortgrasses. The Konza Prairie Research Natural Area, at the more mesic end of the moisture gradient, is characterized by warm-season (C_4) tallgrass prairie species. Data available at CPER include a five-year time series (1971-75) 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 (1976-90) and seasonality of aboveground live biomass (1984-90) for annually burned and unburned plots. None of the data from Konza was used to develop the model. Soil data from the CPER were used in model development; CPER live biomass data were not used in model development.

The five sites in the Commonwealth of Independent States (CIS; formerly USSR) represent the 'continental' climate-gradient from the European temperate meadows of Kursk and Otradnoye in western Russia, through the typical steppes of Khomutov in Ukraine, to the ultracontinental steppes of Tuva, at the geographical centre of the Asian continent. The long time series of aboveground biomass data (1954-83) for the Kursk site covers a wide range of year-to-year variation in weather conditions. At Otradnoye, five-year monthly time series (1967-72) are available on aboveground biomass for a loamy and a sandy soil. The Khomutov site has four years of aboveground biomass data (1967-70). More detailed data on vegetation dynamics are available for the Shortandy site, with monthly observations of live and dead matter, both above- and below ground, over the

period 1975-79. The cold, dry Tuva site (aboveground biomass, 1977-84) is a particularly interesting test for the CENTURY model, since its climatic and physiological characteristics differ markedly from the grasslands of the US Central Plains which were used originally to formulate CENTURY (Parton *et al.* 1987).

In view of the large areal extent of tropical grass-dominated ecosystems and savannas (Hall and Scurlock 1991), it was an important objective of this SCOPE Project to develop an ecosystem model to simulate these tropical grasslands.

Table 11.1 Grassland site descriptions

	Nairobi National Park Kenya	Klong HK, Hat Yai, Thailand	Montecillos, Chapingo, Mexico	Lamto, Ivory Coast	CPER, Pawnee, Colo USA	Konza Prairie Kansas USA	Khomutov Ukraine	Kursk Russia	Otradnoye1 Russia	Shortandy Russia	Tuva, Kazakhstan
Latitude/ longitude (approx.)	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 (m)	1500	100	2220	100	1625	400	75	250	50	367	800
Annual precipitation (mm)	680	1540	590	1170	300	818	441	560	543	351	214
Mean monthly minimum temperature (°C) (month)	10.8 (Jul.)	21.5 (Jan.)	1.4 (Jan.)	21.5 (Jan.)	-9.8 (Feb.)	-10.2 (Feb.)	-4.1 (Dec.)	-12.6 (Jan.)	-9.2 (Feb.)	-24.6 (Jan.)	-39.2 (Jan.)
Mean monthly maxim	28.5 (Mar.)	31.2 (Mar.)	26.9 (May)	36.0 (Feb.)	30.7 (Jul.)	36.5 (Aug.)	30.0 (Jul.)	24.7 (Jul.)	26.3 (Jul.)	27.2 (Jul.)	26.7 (Jul.)

um temperature (°) (month)

Soil type	Black clay vertisol	Humid gley	Solonet	Sandy	Sandy loam	Clay loam	Chernozem/vermiboroll	Chernozem/haplaboroll	Soddy-podzolic 1. Loamy II. Sandy	Calciboroll/calciustosol	Haplustosol/calciustosol
Grassland type	Dry grassland	Humid savanna	Saline	Savanna	Short grass prairie	Tallgrass prairie	Typical steppe	Meadow steppe	Meadow I. Loamy II. Sandy	Dry steppe	Semidesert ultra-continental steppe
Dominant species (C_3/C_4)	*Themeda triarndra?* (C_4)	*Eulalia trispicata* (C_4)	*Distichlis spicata* (C_4)	*Louditia* (C_4)	*Bouteloua gracilis* (C_4)	*Andropogon scoparius/ gerardii* (C_4)	*Stipa lessingiana* (C_3)	*Bromus ripariaus* (C_3)	*I.Alchemilla monticola*(C3) *II.Alopecurus pratellsi* (C3)	*Stipa zalesskyi* (C3)	*Agropyran crystatum* (C3)
Maximum aboveground live biomass ($g\ m^{-2}$) (typical month)	337 (Jul.)	442 (Nov.)	430 (Aug.)	450 (Nov.)	40 (Jun.)	380 (Jul.)	340 (Jun.)	362 (Jul.)	1.244 11.277 (Jun.)	142 (Jul.)	103 (Jul.)
Historical long-term management regime (estima	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

ted)

Three of the four tropical grassland sites (Kenya, Thailand and Mexico) were studied under a UN Environment Programme Project, and have used a common methodology to collect data on live and dead matter, above- and below ground, over the period 1984-90 (Long *et al.* 1992). The fourth tropical site was located at Lamto, Ivory Coast (Menaut and César 1979).

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 South-East Asia. The Mexican grassland is derived from the bed of a saline lake, drained in 1911. The continuous record of above- and below ground 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 Dr J.-C. Menaut and co-workers for the past 30 years, and a discontinuous record kept of monthly aboveground live and dead matter, and total root biomass (Menaut and César 1979). Like most tropical grasslands, all four sites were subjected to burning and/or mowing removal during the period of study. The CENTURY model's ability to simulate the effects of burning has thus been tested under treatments ranging from annual fires to burning every six years. We selected two well- characterized grassland sites: the CPER site, a temperate grassland; and the Kenya site, a tropical grass-dominated savanna, for the comparison between CENTURY and GRASS.

11.3 MODELLING PROTOCOL

Two types of ecosystem models have been employed in this SCOPE study, a simple ecosystem model, CENTURY (Parton *et al.* 1987, 1988, 1992) and a revised version of the more detailed ecophysiologically based model, GRASS. The original description of the GRASS model, is provided by Coughenour (1984). The CENTURY model is a 'lumped' parameter model that aggregates plant production processes with SOM dynamics. It uses a monthly time step and simulates aboveground and below ground processes, soil water budgets at various depths, SOM C (Figure 11.2) and N dynamics in the top 20 cm of the soil, and incorporates various land use practices that include grazing, fire, and cropping systems. The GRASS model is a mechanistic physiologically based grassland model which simulates shoot number, C and N budgets, energy balance, and water budget (Coughenour 1984). The model is different from the CENTURY model in that it uses a daily time step, mechanistic photosynthetic and plant growth functions, and dynamic representations of plant C and N allocation. The GRASS model was originally designed to represent the impact of grazing on grassland systems in Africa.

Simulations of ecosystem dynamics (i.e. annual net plant productivity, seasonal patterns of live aboveground biomass, peak live aboveground biomass, soil organic matter C and N dynamics, N mineralization, evapotranspiration) at all 11 sites were conducted using CENTURY. The ability of the model to respond to burning, irrigation and N fertilization was tested using observed data from these sites.

Figure 11.2 Flow diagram for the CENTURY soil organic C model

The CENTURY and GRASS models were both run for a shortgrass steppe site in Colorado, USA (CPER) and a site near Nairobi, Kenya and the results of the different models were compared. The comparison is intended to evaluate the dynamic responses of a more mechanistic model and the use of a finer time step (day vs month) on simulated grassland dynamics. Assessment of the relative merits of the two classes of models in determining various ecosystem processes was evaluated.

The sites used to evaluate CENTURY and GRASS all have at least 3 years (several sites have more than 10 years of data) of seasonal live biomass data, observed soil C and N levels and climate data. The statistical comparisons used to test the model include linear regression of observed and simulated results, comparison of model predictions with frequently used regression models (i.e. production vs annual precipitation), and an evaluation of the number of times that the difference between the model outputs and the observed data was less than $\pm25\%$ of the observed data.

While there are more parameters affecting plant growth in GRASS than in CENTURY, the number of parameters in GRASS that vary among sites has been minimized to facilitate cross-site parameterization and application over large spatial scales.

11.4 CENTURY ECOSYSTEM MODEL DESCRIPTION

The CENTURY model is a general ecosystem type which simulates plant-soil dynamics of grasslands, forests, crops and savannas (Parton *et al.* 1987, 1988; Sanford *et al.* 1991). It was developed during this SCOPE project (Version 3.0; Parton *et al.,* 1992) by incorporating routines derived from more mechanistic models or suggested by detailed site data. The model has three major sub models. These include:

(a) biophysical submodel which calculates hydrological and temperature drivers; (b) a plant production submodel which calculates above- and below ground plant processes;

(c) a soil organic matter submodel that calculates changes in soil C and N and plant detritus.

Additional functions are used to simulate various management or disturbance regimes, such as fire and grazing intensity and frequency. 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). It incorporates simplified representations of key processes relating to C assimilation and turnover, based on existing models.

Modifications to the original version of CENTURY are described in Parton *et at.* (1992; 1994). These changes include adding the effect of clay on the formation of passive SOM; improving the surface litter decomposition model; including the effect of anaerobiosis on decomposition; simulating leaching of soluble organic material; improving the inorganic leaching equations; and developing a robust grassland production submodel.

11.4.1 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. 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 and interception water loss is a function of aboveground biomass, rainfall, and PET. Transpiration water loss is a function of the live leaf biomass (exponential function of leafbiomass), rainfall, and PET. The field capacity and wilting point for the different soil layers are calculated as a function of the bulk density, soil texture, and organic matter content using an equation developed by Gupta and Larson (1979).

Figure 11.3 The abiotic effect of soil temperature (a) and soil moisture (b) on decomposition

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 maximum air temperature (2 m height) and canopy biomass (lower for high biomass) while the minimum soil temperature is a function of 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 monthly soil temperatures ([Figure 11.3](#)).

11.4.2 Plant production submodel

The grassland submodel ([Figure 11.4](#)) simulates grass growth and includes the impact of grazing and fire on plant production. Potential plant production is calculated as a function of soil temperature, available water, and a self-shading factor using the following equation:

$$P_p = P_{max} \times f(T_p) \times f(M_p) \times f(S_p) \tag{1}$$

where P_p is the aboveground potential plant production rate (g m^{-2} month^{-1}), P_{max} is the maximum potential aboveground plant production rate (250 g m^{-2} month^{-1}), T_p (Figure 11.5b) is the effect of soil temperature on growth, M_p is the effect of moisture on production (Figure 11.5a), and S_p is the effect of plant shading on plant growth (Figure 11.5c). 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 11.5a). 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 11.5c).

The potential plant production rate *(P_p)* is reduced if there is insufficient N. A maximum and minimum C to N (C: N) ratio is specified for new production of live roots and shoots. The minimum C:N ratio sets the limit for maximum N concentration of new plant production. The live shoot C:N 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; g m^{-2}) according to the following equation:

$$F_g = 1.0 - 0.8 \exp(-0.015\ ROOT) \qquad\qquad (2)$$

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:

Figure 11.4 Flow diagram for the grassland production submodel

$$R_d = 0.12 \ [\exp \ (-5.0 \ H_2O_{(a)})] \qquad\qquad (3)$$

$$S_d = 0.20 \ [\exp \ (-5.0 \ H_2O_{(a)})] \qquad\qquad (4)$$

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^{-2} 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 effects of fire and grazing on plant production are based on data from Ojima *et al.* (1990, 1994) and Holland *et al.* (1992), respectively. The simulated impacts of fire are to increase the root/shoot ratio, and to increase the C:N ratio of live shoots (+ 10 for temperate sites; 0 for tropical sites) and roots (+ 30 for all sites), removing vegetation and returning inorganic nutrients (Ojima *et al.* 1990). Grazing removes vegetation, returns nutrients to the soil (by urination and defecation), alters the root/shoot ratio and increases the N content of live shoot and roots (Holland *et al.* 1992).

Figure 11.5 The effect of moisture (a), soil temperature (b) and shadding (c) on potential grass growth

11.4.3 Decomposition and soil organic matter submodel

The soil organic matter (SOM) submodel simulates the dynamics of C and N in the organic and inorganic parts of the soil system. The flow diagram for soil C (Figure 11.2) shows that soil C is divided into three components which include active, slow, and passive soil C. Active SOM includes live soil microbes plus microbial products (the total active pool is approximately two to three times the live soil microbial biomass), the slow pool includes resistant plant material (for instance, lignin-like 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 11.3](#)). 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_2 flux is a function of soil texture for the stabilization of active C into slow C (increasing CO_2 flux for sandy soils and less soil C storage). Justification for these assumptions is presented in 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. 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 N submodel has the same general structure as the soil C model ([Figure 11.6](#)). The organic- N flows follow the C flows and are equal to the product of the C 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 (NO_3^- plus NH_4^*) and vary within the ranges 3-15, 12-20, and 7-10, respectively, for active, slow and passive SOM ([Figure 11.4](#)). 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 11.6](#)). 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. The N associated with C 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 N_2, NO, N_2O, and NH_3 gas fluxes (see [Figure 11.6](#)) and NO_3 leaching. A more complete description and justification for the N submodel is presented by Parton *et al.* (1987, 1988, 1994).

Figure 11.6 Flow diagram for the CENTURY soil N submodel

11.5 GRASS MODEL DESCRIPTION

The GRASS model is more physiologically oriented relative to CENTURY (Figure 11.7), as it links physiological processes and morphometric traits (Coughenour 1984). Plant growth submodels represent tillering and C and N budgets. Additional modules simulate light penetration and soil water and heat budgets (Coughenour 1984). The model uses a time step of two hours for diurnal processes such as leaf and soil energy balance and photosynthesis, and two days for other plant growth processes. The model is driven by daily weather data, although daily data can also be generated stochastically from monthly weather data. Long-term model runs are possible on current microcomputers (e.g. 100 years in 30 minutes). The original version of the model was developed to examine plant responses to herbivory in Africa (Coughenour 1984). The model has been modified and updated over the last decade into a new version (GRASS) that is linked to daily soil and water flow submodels (Parton 1978) and to a daily time step implementation of the decomposition and nutrient cycling (CSOM) routines from CENTURY. The daily CSOM routines use the same CENTURY model structure and nearly identical parameters, but decomposition responds to actual daily soil moisture content.

Figure 11.7 Major submodules in the GRASS model and flows of information among sub modules. (LAI)-leaf area index; (Nl)-leaf nitrogen; (Al)-leaf age; (Cl)-labile carbon; (Ns)-soil N; (Bl)-litter biomass; (Ws)-soil water; (Ts)-soil temperature; (PAR)-photosynthetically active radiation; (g_s)-stomatal conductance; (Ev)-soil evaporation; (Ws)-soil water; (Tc)-canopy temperature; (Uc)-windspeed; (RHc)-humidity; (Tr)-transpiration; (Rg)-global radiation; (Tl)-leaf temperature

The submodel for C_3 photosynthesis used in GRASS is based on the model of Farquhar *et al.* (1980), which considers the relative limitations of rates of ribulose 1,5-biphosphate (RubP) carboxylase fixation of internal leaf CO_2 and RubP regeneration, and RubP oxygenation. Reaction rates respond to temperature according to Arrhenius functions, which generally exhibit temperature optima. The CO_2 fixation of RubP is limited by mesophyll CO_2 concentration in C_3 species and by bundle sheath CO_2 concentration in C_4 species. The maximum rate of RubP regeneration is asymptotically light limited. The C_4 cycle, present only in C_4 species, is limited by phosphoenylpyruvate (PEP) carboxylase fixation, which responds to mesophyll CO_2 concentration (Chen and Coughenour 1994). Assimilation rate is reduced by low soil water content and leaf N. Dark respiration responds to temperature with a Q_{10} function.

The empirical stomatal conductance submodel of Ball *et al.* (1987) is used to effect diffusion of CO_2 from the atmosphere into the mesophyll. Stomatal conductance (g_s) responds to leaf surface CO_2 concentration, relative humidity and net photosynthesis (A_n). The model calculates a simultaneous solution for mesophyll and bundle sheath CO_2, due to A_n and diffusion through stomates. The g_s value influences latent heat loss in the leaf energy balance.

Net fixed C can be stored as labile C within the plant. Respiration costs associated with tissue biosynthesis and maintenance are calculated after Ryan (1991). Maintenance respiration is a function of N content, as well as temperature according to a Q_{10} function. Carbon is allocated to structural root vs shoot tissues dependent upon water and N stress. Tissue mortality rates respond to water stress, and to tissue age in the case of leaves. Nitrogen is taken up by roots and allocated in relationship to leaf age. Nitrogen is retranslocated during tissue mortality to tissues that are still living.

Biomass production models interact with tillering and phenology submodels. Tillering depends on water, temperature, N and labile C. Phenology advances in response to growing degree day sums and daylength, but soil temperature and moisture may also trigger phenological change.

11.6 MODEL VERIFICATION OF CENTURY AND GRASS

11.6.1 CENTURY

The parameterization of CENTURY for the different grasslands was conducted to minimize the modifications of only a small number of site-specific model parameters (Appendix 11.10). Many of the 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. Simulated output of aboveground live biomass, aboveground net primary production and levels of SOM were used to validate the model relative to observations made at each of the sites. In evaluating the robust behavior of the model across the range of environmental factors, it was desirable for the majority of the model parameters to 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 changes in parameters consist of site-specific data required to run the CENTURY model, including latitude and longitude, soil texture (sand, silt and clay), soil pH, soil depth for modelling 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 11.2). Land management variables (frequency of burning and grazing) also differed among sites; CENTURY allows burning and grazing events to take place in specified months over a repeated pattern of up to 20 years.

Table 11.2 Site-specific differences between functions controlling plant growth

	Kenya	Thailand	Mexico	Lamto	CPER	Konza	Khomutov	Kursk	Otadnoye	Shortandy	Tuva
Root/shoot ratio as a	-	-	O	-	O	O	O	O	O	O	O

function of total precipitation											
Root turnover as function of soil water	O	O	O	O	-	O	O	O	O	O	O
Atmospheric and soil N inputs	O	-	O	O	O	O	+	+	+	+	+
Number of soil layers available for plant growth	-	-	O	O	O	O	O	O	-	O	-
Shoot turnover as function of soil water	+	+	O	O	O	O	O	O	O	O	O
Fall rate of standing dead matter to litter	-	-	-	-	O	-	O	O	O	O	O
C/N ratio of shoot matter as a function of biomass	O	O	O	+	O	+	O	O	O	O	O

O = standard function.
+/- = increase or decrease in value of function (see text for details).

For each site modelled, 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 500-5000 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 11.1).

Simulated levels of SOM were then evaluated for long-term stability, and compared with actual field measurements. This check for long-term stability was necessary to appropriately partition soil C to the slow and passive SOM pools of CENTURY, which have characteristic turnover times of 50 and 1000 years, respectively. The long-term values of SOM were then entered in the site file to provide stable initial conditions. The model simulations were made over periods of 20-30 years, using actual weather data recorded at the site, and a comparison of simulated and observed values of monthly biomass and dead matter, above- and belowground was made. For these short-term model runs, the management regime was based on recent grazing/burning practice at each site. For example, the CIS sites are all within Biosphere Reserves and not subject to either grazing or burning, although grazing and mowing for forage would have been common practice in the past and were included in the long-term initializations.

Differences in physiological parameters between the 11 grassland sites are summarized in Table 11.2. 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 modelled 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.

Estimating long-term N balance proved to be one of the most difficult aspects of the modelling exercise. Atmospheric deposition and N-fixation inputs are normally determined as a simple linear function of precipitation based on data from the US Great Plains, but increased inputs were required to predict the observed production at the (relatively dry) CIS sites, which is consistent with the higher rates of N deposition in continental Europe compared with the US 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 the 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 these sites have frequent burning which would otherwise result in too much loss of N.

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 modification reflected differences in soil depth and 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).

Models, like CENTURY, which simulate NPP are an important complement to more physiologically oriented models which simulate photosynthesis and respiration. Physiological models require detailed climatic information, such as incoming solar radiation and cloudiness, 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.* 1991; Sellers *et al.* 1992; 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.

11.6.1.1 Model testing-CENTURY

In this section we show a comparison of observed data and simulated model output variables. The model output variables that we will test include live shoot biomass dynamics, aboveground net primary production, peak standing live shoot biomass, and soil C and N levels. These variables were selected because they characterize general grassland ecosystem dynamics and can be evaluated at a variety of sites. 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. The importance of these latter considerations is related to evaluating potential changes in the terrestrial ecosystem resulting from different climate change scenarios.

We employed three techniques for testing the CENTURY model:

(a) linear regression of observed data vs simulated model results;

(b) comparison of the CENTURY model predictions with empirical regression models predicted from climate variables (Lauenroth 1978);

(c) calculating the number of times the difference between CENTURY model predictions and observed data differed by less than a threshold proportion (25%) of the observed data.

The results show that in general the observed vs simulated r^2 for the CENTURY model and the empirical regression models are fairly similar. The CENTURY model is able to predict the grassland ecosystem dynamics in more mechanistic fashion which allows for more reliable scenarios of grassland dynamics to climate changes. 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).

11.6.1.2 Aboveground NPP

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/fertilized site (Lauenroth 1978). The Konza site has plant production data from 1976 to 1990 for annual burned and unburned sites (Abrams *et al.* 1986; Briggs *et al.* 1989). The comparison of observed and simulated production data (Figure 11.8) 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 predictions under current conditions, compared to a simple regression model, its concurrent ability to predict the seasonality of foliage production has substantial significance to vegetation-atmosphere interactions studies and models of ecosystem dynamics, including examination of the effects of a changed climate regime. Of CENTURY's predicted aboveground plant production values, 60% had errors less than ±25% of the observed plant production. In comparison, standard errors of observed plant productivities across replicates generally ranged from 10 to 20% of the observed means.

Figure 11.8 Comparison of observed and simulated aboveground plant production for all the CPER treatment and burned and unburned sites at Konaz

Figure 11.9 Comparison of observed and simulated peak live biomass from all of the sites. The Kursk and Khomutov site data are shown with a "

11.6.1.3 Peak live biomass

The simulated peak live biomass from all of the sites and treatments were compared to the observed peak live biomass (Figure 11.9). (The observed peak live biomass is the maximum live biomass observed in a particular calendar year (January to December)). The results from CENTURY have an $r^2 = 0.45$. The r^2 for the best regression model (independent variables include annual precipitation, fertilization and fire) was 0.40. 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. Removing some of these points from the comparison increased the r^2 from 0.45 to 0.65. Of the CENTURY predictions, 57% had errors that were less than ±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 one-half to one-third of the values for the tropical sites.

11.6.1.4 Live plant biomass dynamics

The comparison of observed and simulated live biomass for some of the temperate (Figure 11.10) and tropical (Figure 11.11) sites shows that general seasonal patterns were well simulated by the model. Differences between very dry and wet years (1989 vs 1990 at Konza, and 1981 vs 1980 at Tuva) were well simulated; however, more subtle differences between years with similar precipitation (Konza 1984-87, and Kursk 1975-79) were not well simulated. These subtle interannual differences may result from factors including:

(a) interannual variations in incident PAR, not included in the model;

(b) effects of timing of rainfall not captured with a monthly time step, or

(c) lag effects of nutrient or photosynthate storage in plants, although this is not an inclusive list.

Investigation of the above effects is ongoing. For the tropical sites (Figure 11.11) 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.

Figure 11.12 shows a comparison of observed vs simulated live plant biomass for all of the sites and different treatments $(r^2 = 0.39)$. 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, suggesting that the errors for the Russian high plant production years greatly reduce the r^2. Of the CENTURY predictions, 31% had errors less than ±25% of the observed data, while 57% of CENTURY predictions had errors less than ±50% of the observed data. These results show that the model simulates peak live biomass and total annual aboveground primary production more precisely than it simulates the monthly dynamics of live shoot biomass.

Figure 11.10 Comparison of simulated and observed live biomass for (a) CPER, (b) Konza, (c) Kursk and (d) Tuva sites

Figure 11.11 Comparison of simulated and observed live biomass for (a) Konza, (b) Lamto, (c) Mexico, and (d) Thailand sites

Figure 11.12 Comparison of simulated and observed live biomass for all of the sites and treatments (except Khom and Kursk)

11.6.1.5 Soil C and N

Soil C and N levels are 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 g C m^{-2} at Lamto to greater than the 10000 g C m^{-2} at the Kursk site (Figure 11.13a, b). The assumptions used to control soil C stability and decomposition (clay impact on passive SOM and silt plus clay on slow SOM) seem to work across a diverse set of soil textures and soil mineralogies. All of the soil C simulated values and 75% of the soil N simulated values had errors less than ±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. We had insufficient data to develop empirical models for soil N and C storage in this study; however, other studies support the conclusion that climate and soil texture are required as predictors (Burke *et al.* 1989).

11.6.2 GRASS

The photosynthesis submodel was tested against measurements of photosynthetic responses to leaf internal (mesophyll) CO_2 concentration *(A/C$_i$ curves)*, incident photosynthetically active radiation (PAR), and leaf temperature (Mon son *et al.* 1982; Knapp *et al.* 1993; Polley *et al.* 1992). The measurements provided data for a tall C_4 grass *(Andropogon gerardii),* a short C_4 grass *(Bouteloua gracilis)* and mid-height C_3 grass *(Agropyron smithii),* all from North America. To support our predictions of ecosystem responses to climatic change, it is important to demonstrate that simulated plants respond realistically to temperature and CO_2. Since C_i depends upon stomatal conductance, *A/C$_i$* curves are also affected by the stomatal submodel (Ball *et al.* 1987; Chen and Coughenour 1994).

Figure 11.13 Comparison of simulated and observed steady-state soil C (a) and N (b) for 9 of the 11 sites. Mexico and Thailand sites were not used because they are not at equilibrium with their present land uses

Simulated A/C_i curves compared favorably with data (Figure 11.14a-c). Ambient CO_2 concentrations of 350 ppm produced C_i of 200--250 ppm. Assimilation rates of the C_4 plants were close to being saturated at 350 ppm CO_2 ambient, due to concentration of CO_2 by PEP carboxylase into bundle sheath cells. The ratio of A_n at 700 ppm to that at 350 ppm CO_2 was 1.04 in *Andropogon gerardii,* 1.03 in *B. gracilis,* and 1.31 in *Agropyron smithii.* The CO_2 compensation points (x-intercepts) were near 0 ppm for C_4 species, and 50 ppm for the C_3 species.

Light responses were accurately simulated (Figure 11.14d-f). The quantum efficiencies (initial slopes of the light response curves) were correct, as were light compensation points (x-intercepts). The C_3 species was nearly saturated at 1500 mmol m^{-2} s^{-1} while the C_4 plants were

not. However, it was necessary to change the maximal electron transport rate J_m to simulate the light response curve of the C_3 plant at 800 ppm CO_2 and 2% O_2.

Simulated and measured temperature response curves compared favorably, despite a wide range of shapes (Figure 11.14g-i). The C_4 plants exhibited higher temperature optima than the C_3 plants (37-38 °C vs 25 °C) as expected. While A_n in the C_3 grass was still active at 5 °C, in the short C_4 grass *B. gracilis* it was much restricted and in the tall C_4 grass *Andropogon gerardii* it was insignificant. Conversely, the C_4 plants were still active at 50 °C while the C_3 plant was not. The temperature optima for photosynthesis were shifted higher under elevated CO_2 concentrations due to differential temperature sensitivities of solubilities and RubP affinities for CO_2 and O_2, in accordance with observations (Long et *al.* 1989). Photosynthetic light responses of the Kenyan C_4 grass Themeda triandra (Kinyamario and 1mbamba 1992) at different canopy heights were compared with model simulations at different leaf N concentrations (Figure 11.15). Leaves higher in the canopy tend to have higher N concentrations. Top canopy leaves were assumed to have maximal N concentrations. The favorable comparisons supported model predictions of maximal photosynthetic rates of this species, as well as responses to light and N .

The complete GRASS-CSOM model was tested against biomass dynamics and primary productivity data from the CPER and the Nairobi sites (Figure 11.16a, b). Both live and dead aboveground biomass dynamics were well simulated, with a few exceptions. Highly unusual data patterns such as at CPER in 1973 could not and possibly should not have been simulated by the model. Correlations between observed and predicted values for green shoots (Figure 11.17a, b) were highly significant, although the r^2 value was low for the CPER data, due to several outliers. For CPER, 46% of the model predictions fell within ±25% of the observed data value, while for Nairobi 46% fell within the ±25% interval. However for Nairobi, many predicted values were only just outside the ±25% limits. Predictions of aboveground net primary production (ANPP) and peak live shoot mass were more precise (Figure 11.18a, b). Over 90% of the variance in ANPP and 56% of the variance in peak biomass were explained by the model. There was a slight tendency to overpredict ANPP at low values, as reflected by the positive y-intercept.

Figure 11.14 Comparison of observed (points) and simulated (lines) responses of net assimilation (A_n) to leaf internal CO_2, light (PAR) and temperature (T). Three grass species are compared. Observed data for *B. gracilis* (C_4) are from Monson *et al.* (1983) *(A/Ci* from warmgrown plants, temperature and light responses mean of cool- and warmgrown plants). Data for *Andropogon gerardii* (C_4) are from Polley *et al.* (1992) *(A/C$_i$* PAR curves) and from A. Knapp *(T* curve, pers. comm., see Chen *et al.* 1993). Data for

Figure 11.14 (*continued*) *Agropyron smithii* (C_3) are from Monson *et al.* (1983) *(A/C_i curve and 340 ppm CO_2 PAR curve), and Monson *et al.* (1982) (temperature response, and 800 ppm CO_2 PAR curve). *B. gracilis* measured at PAR 2000, *T* 30°, RH 80%, and no water or temperature stress. *Agropyron smithii* measured at 25°, PAR 2000, and no water or N stress. *Andropogon gerardii A/C_i* and PAR curves determined at RH 40%, *T25°,* PAR 1400, *T* 37°, soil water 1 MPa, N 1.8%, and *T* curve at RH 40%, PAR 1000, soil water 1 MPa, N 2%

Figure 11.14 (continued)

Figure 11.15 Light response curves of the African grass *T, triandra* at different leaf N levels, meant to represent leaves at different canopy positions. Observed data (points) from Kinyamario and Imbamba (1992)

Simulated plant responses between GRASS and CENTURY were compared for a semiarid temperate steppe (CPER) and a tropical savanna (Kenya) across several years of simulated and observed study. We found that the two models behaved in similar fashion across a number of properties, including prediction of seasonal monthly live biomass, annual ANPP, and peak live biomass. For each of these properties, the differences between the two models in comparing the regression analysis between simulated and observed data from the two sites were found to be nonsignificant in correlation coefficient, slope, or intercept. The simulated monthly results of CENTURY indicate a bimodal bias in predicting live green plant biomass for the CPER site. The CENTURY model underpredicts live green biomass at the low levels of observed live green biomass and overpredicts live green biomass at higher levels. The Kenya simulations for CENTURY did not show this bias, nor did GRASS for either site.

Figure 11.16 Comparison of observed and GRASS-simulated aboveground biomass dynamics at two sites. Large points, solid line = observed and simulated green shoots. Small points, dashed line = standing dead shoots. Observed CPER data from IBP/ CPER-LTER data bank. Observed Nairobi data from D. Hall *et al.* and J. Kinyamario (pers. comm.)

Figure 11.17 Correlations between observed and GRASS-simulated green biomass observations. Lines represent equality of simulated and observed data. Dashed lines indicate ±25% of observed data. Data sources as in Figure 11.4

Figure 11.18 Correlations between observed and GRASS-simulated aboveground production (a) and peak live aboveground biomass (b) ● CPER nitrogen + irrigated; (X) CPER irrigated Z CPER nitrogen; ■ CPER control; ▲ Nairobi. CPER data from 1970-75, Nairobi from 1988-89. Data sources as in Figure 11.4.

11.7 SUMMARY

The comparison of observed and simulated live peak biomass and plant production had r^2 values of 0.45 and 0.70. The CENTURY error terms were generally less than ±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 ±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 fitted to observed data showed that the CENTURY model was 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 ±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. Comparisons of ecosystem models such as CENTURY with physiologically based models such as GRASS, across a gradient of sites, will provide a better framework to understand the processes controlling the sensitivity of grasslands to environmental change.

11.8 ACKNOWLEDGEMENTS

11.9 REFERENCES

Abrams, M. D., Knapp, A. K. and Hulbert, L. C. (1986) A ten-year record of aboveground biomass in a tallgrass prairie: effects of fire and topographic position. *Am. J. Bot.* **73**, 1509-1515.

Anderson, J. M. (1991) The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecol. Appl.* **1**, 326-347.

Archer, S., Schimel, D. S. and Holland, E. A. (1994) Mechanisms of shrubland expansion: land use, climate or CO_2? *Clim. Change* **29**, 91-99.

Ball, J. T., Woodrow,I. E. and Berry, J. A. (1987)A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins, I. (Ed.) *Progress in Photosynthesis Research,* pp. 221-224. Vol. IV. Martinus Nijhoff, Dordrecht.

Bónis, K., Mészáros, E. and Putsay, M. (1980) On the atmospheric budget of nitrogen compounds over Europe. *Idójárás* **84**, 57-68.

Briggs, J. M., Seastedt, T. R. and Gibson, D. J. (1989) Comparative analysis of temporal and spatial variability in aboveground production in a deciduous forest and prairie. *Holarct. Ecol.* **12**, 130-136.

Burke, I. *C.,* Yonker, C. M., Parton, W. J., Cole, C. V., Flach, K. and Schimel, D. S. (1989) Texture, climate, and cultivation effects on soil organic matter context in U .S. grassland soils. *Soil Sci. Soc. Am. J.* **53**, 800-805.

Chen, D. and Coughenour, M. B. (1994) GEMTM: a general model for energy and mass transfer of land surfaces and its application at the FIFE sites. *Agric. For. Meteorol.* **68**, 145-171.

Chen, D., Coughenour, M. B., Knapp, A. K. and Owensby, C. E. (1993) Mathematical simulation of C_4 grass photosynthesis in ambient and elevated *CO_2. Ecol. Model.* **73**, 63-80.

Christie, E. K. and Detling, J. K. (1982) Analysis of interference between C_3 and C_4 grasses in relation to temperature and soil nitrogen supply. *Ecology* **63**, 1277-1284.

Coughenour, M. B. (1984) A mechanistic simulation analysis of water use, leaf angles, and grazing in east African graminoids. *Ecol. Model.* **26**, 203-230.

Eddy, J. A., Malone, T. F., McCarthy, J. J. and Rosswall, T. (Eds) (1991) *Global Change Systems for Analysis, Research and Training (START*). IGBP Report No.15, Stockholm.

Esser, G. (1986) The carbon budget of the biosphere-structure and preliminary results of the Osnabruck Biosphere Model. *Veroff Naturf Ges. zu Emden von* 1814 **7**, 1-160.

Farquhar, G. D., von Caemmerer, S. and Berry, J. A. (1980) A biochemical model of photosynthetic *CO_2* assimilation in leaves of C_3 species. *Planta* **149**, 78-90.

Gupta, S. C. and Larson, W. E. (1979) Estimating soil water retention characteristics from particle size distribution, organic matter content and bulk density. *Water Resour. Res.* **15** (6), 1633-1635.

Hall, D. O. and Scurlock, J. M. O. (1991) Climate change and productivity of natural grasslands. *Ann. Bot.* 67 (suppl.), **49**-55.

Hao, W. M., Liu, M. and Crutzen, P. J. (1990) Estimates of annual and regional releases of CO_2 and other trace gases to the atmosphere from fires in the tropics. In: Goldammer, J.G. (Ed.) *Fire in the Tropical Biota,* pp. 440-462. Ecological Studies 84. Springer- Verlag, Berlin.

Holland, E. A., Parton, W. J., Detling, J. K. and Coppock, D. L. (1992) Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flows. *Am. Natur.* **140**(4),685-706.

Kinyamario, J. I. and Imbamba, S. K. (1992) Savanna at Nairobi National Park, Nairobi. In: Long, S.P., Jones, M. B. and Roberts, M. J. (Eds) *Primary Productivity of Grass Ecosystems,* Chapter 2. Chapman & Hall, London.

Knapp, A. K., Hamerlynk, E. P. and Owensby, C. E. (1993) Photosynthetic and water relations responses to elevated CO_2 in the C_4 grass *Andropogon gerardii. Int. J. Plant* Sci. **154**, 459-466.

Lauenroth, W. K. (1978) Grassland primary production: North American grasslands in perspective. In: French, N. (Ed.) *Perspectives in Grassland Ecology,* pp. 3-21. Springer- Verlag, New York.

Lauenroth, W. K. and Sala, O. E. (1992) Long-term forage production of North American shortgrass steppe. *Ecol. Appl.* **2**, 397-403.

Lieth, H. (1972) Modelling the primary productivity of the world. UNESCO, Paris. *Nature and Resource* **8**, 5-10.

Linacre, E. T. (1977) A simple formula for estimating evaporation rates in various climates, using temperature data alone. *Agric. Meteorol.* **18**,409-424.

Long, S. P ., Garcia Moya, E., Imbamba, S. K., Kamnalrut, A., Piedade, M. T. F ., Scurlock, J. M. O., Shen, Y. K. and Hall, D. O. (1989) Primary productivity of natural grass ecosystems of the tropics: a reappraisal. *Plant Soil* **115***, 155-166.

Long, S. P., Jones, M. B. and Roberts, M. J. (1992) *Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics.* Chapman & Hall, London. 267 pp.

McGuire, A. D., Melillo, J. M., Joyce, L. A., Kicklighter, D. W., Grace, A. L., Moore, B.III and Vrsmarty, C. J. (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Glob. Biogeochem. Cyc.* **6**, 101-124.

Menaut, J. -C. and César, J. (1979) Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology* **60**,1197-1210.

Monson, R. K., Littlejohn, R. 0. Jr and Williams, G. J. III (1983) Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. *Oecologia* **58**,43-51.

Monson, R. K., Stidham, M. A., Williams, G. J.III and Edwards, G. E. (1982) Temperature dependence of photosynthesis in *Agropyron smithii Rydb. Plant Physiol.* **69**, 921- 928.

OIES (Office for Interdisciplinary Earth Studies) (1991) *Arid Ecosystems Interactions: Recommendations for Drylands Research in the Global Change Research Program.* OIES Report 6, Boulder.

Ojima, D. S., Parton, W. J., Schimel, D. S. and Owensby, C. E. (1990) Simulated impacts of annual burning on prairie ecosystems. In: Collins, S. L. and Wallace, L. (Eds) *Fire in the North American Prairies,* pp. 118-132. Univ. of Oklahoma Press, Norman.

Ojima, D. S., Schimel, D. S., Parton, W. J. and Owensby, C. E. (1994) Long- and short-term effects of fire on nitrogen cycling in tall grass prairie. *Biogeochemistry* **24**, 67-84.

Parton, W. J. (1978) Abiotic section of ELM. In: G. S. Innis (Ed) *Grassland Simulation Model,* pp. 31-53. Ecol. Studies, Vol. 26, Springer-Verlag, Inc., New York.

Parton, W. J. (1984) Predicting soil temperatures in a shortgrass steppe. *Soil Sci.* **138**, 93-101.

Parton, W. J., Cole, C. V., Stewart, J. W. B., Ojima, D. S. and Schimel, D. S. (1989a) Simulating regional patterns of soil C, N, and P dynamics in the U.S. central grasslands region. In: Clarholm, M. and Bergstrom, L. (Eds) *Ecology of Arable Land,* pp. 99-108. Kluwer Academic Publishers, Dordrecht.

Parton, W. J., McKeown, B., Kirchner, V. and Ojima, D. (1992) *CENTURY Users' Manual.* Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.

Parton, W. J., Sanford, R. L., Sanchez, P.A. and Stewart, J.W.B. (1989b) Modelling soil organic matter dynamics in tropical soils. In: Coleman, D. C., Oades, J. M. and Uehara, G. *(Eds)Dynamics of Soil Organic Matter in Tropical Ecosystems,* pp.153-171. NifTAL Project, Univ. of Hawaii Press, Honolulu.

Parton, W. J., Schimel, D. S., Cole, C. v. and Ojima, D. S. (1987) Analysis of factors controlling soil organic matter levels in great plains grasslands. *Soil Sci. Soc. Am. J.* **51**, 1173-1179.

Parton, W. J., Schimel, D. S., Ojima, D. S. and Cole, C.V. (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: Bryant, R. B. and Arnold, R. W. (Eds) *Quantitative Modelling of Soil F orming Processes.* Soil Sci. Soc. Am. J. Spec. Publ. ASA, CSSA and SSA, Madison, Wis. (in press).

Parton, W. J., Singh, J. S. and Coleman, D. C. (1978) A model of production and turnover of roots in shortgrass prairie. *J. Appl. Ecol.* **47**, 515-542.

Parton, W. J., Stewart, J. W. B. and Cole, C. V. (1988) Dynamics of C, N, P and S in grassland soils: a model. *Biogeochemistry* **5**, 109-131.

Polley, H. W., Norman, J. M., Arkebauer, T. J., Walter-Shea, E. A., Greegor, D. H. Jr and Bramer, B. (1992) Leaf gas exchange of *Andropogon gerardii Vitman, Panicum virgatur* , L., and Sorgastrum nutans (L.) *Nash* in a tallgrass prairie. *J. Geophys.Res.* **97**, 18, 837-18,444.

Ryan, M. (1991) The effects of climate change on plant respiration. *Ecol. Appl. 1,* 157-167.

Sala, O. E., Parton, W. J., Joyce, L. A. and Lauenroth, W. K. (1988) Primary production of the Central Grassland Region of the United States. *Ecology* **69**, 40-45.

Sanford, R. L. Jr, Parton, W. J., Ojima, D. S. and Lodge, D. J. (1991) Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modelling. *Biotropica* **23**, 364-372.

Schimel, D. S., Kittel, T. G. F. and Parton, W. J. (1991) Terrestrial biogeochemical cycles: global interactions with the atmosphere and hydrology. *Tel1us,* Spec. Issue AB **43**, 188-203.

Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B. and Hall, F. G. (1992) Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sens. Environ.* **42**, 187-216.

Wedin, D. A. and Tilman, D. (1990) Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* **84**, 433-441.

11.10 APPENDIX

Site-specific parameters relating to plant and soil physiology, and management regimes used for short-term model runs

Site-specific parameters found in the SITENAME.DAT file may be divided into a number of categories: (a) basic site identification (e.g. SITLAT , SITLNG);

(b) 'minimum input' data required to run the CENTURY model;

(i) environmental information such as PRECIP, TMN2M, TMX2M;

(ii) physical features such as SAND, SILT, CLAY;

(c) parameters relating mostly to plant and soil physiology.

Parameters from categories (b ii) and (c) are listed below for all the grassland sites reported here, with notes on the differences between sites.