

# DIVISION S-3—SOIL MICROBIOLOGY AND BIOCHEMISTRY

## Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands<sup>1</sup>

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### ABSTRACT

We analyzed climatic and textural controls of soil organic C and N for soils of the U.S. Great Plains. We used a model of soil organic matter (SOM) quantity and composition to simulate steady-state organic matter levels for 24 grassland locations in the Great Plains. The model was able to simulate the effects of climatic gradients on SOM and productivity. Soil texture was also a major control over organic matter dynamics. The model adequately predicted above-ground plant production and soil C and N levels across soil textures (sandy, medium, and fine); however, the model tended to overestimate soil C and N levels for fine textured soil by 10 to 15%. The impact of grazing on the system was simulated and showed that steady-state soil C and N levels were sensitive to the grazing intensity, with soil C and N levels decreasing with increased grazing rates. Regional trends in SOM can be predicted using four site-specific variables, temperature, moisture, soil texture, and plant lignin content. Nitrogen inputs must also be known. Grazing intensity during soil development is also a significant control over steady-state levels of SOM, and since few data are available on presettlement grazing, some uncertainty is inherent in the model predictions.

**Additional Index Words:** grazing, simulation modeling, soil texture, mineralization, immobilization.

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**A**BUNDANT INFORMATION is available in the soils literature on organic matter and the cycling of C, N, S, and P through organic matter (Stevenson, 1986). Incorporation of concepts of organic matter formation and turnover into simulation models is an excellent means of integrating this information. We have developed a model of rangeland and cropland ecosystems that is designed to simulate the effects of macroenvironmental gradients as a first step toward simulating the effects of climatic change. The model includes the effects of management and soil and plant properties over long periods of time (ca. 50–2000 yr). The model simulates primary productivity, soil nutrient dynamics, and soil water, but focuses on changes in soil organic matter. We focus on organic matter because it integrates changes in production and decomposition over time. Organic matter is central to the cycling of plant nutrients, influences water relations and erosion potential, and is a key factor in soil structure (Tisdale and Oades, 1982). The model simulates both the labile (rapid turnover) and stabilized (slow turnover) fractions, thus simulating the nu-

trient-supplying capacity of the soil organic matter as well as the absolute quantity.

The modeling exercise had several objectives. The first was to simulate the effects of climatic gradients on productivity and soil organic matter over large areas, which is a first step in modeling the effects of climate change. The second was to identify key soil properties that would allow us to simulate differences between soils within a single climatic zone.

A variety of different types of models have been used to represent long-term changes in soil organic N and C. Jenny (1941) used a single-state variable model form to represent the decline of organic C and N in cultivated soils. Campbell et al. (1978) improved upon this approach by dividing soil organic matter (SOM) into two different compartments, which included stable organic matter and labile organic matter with turnover rates ( $1/k$ ) of 53 and 1429 yr, respectively. Paul and Van Veen (1978) and Van Veen and Paul (1981) made further improvements in the SOM models by dividing the plant residue into recalcitrant and decomposable fractions and introducing the concept of physically protected soil organic matter. A critical assumption in their model was that physically protected organic matter has a much lower decomposition rate than nonphysically protected organic matter.

Our soil organic matter formation model (the Century model) incorporates multiple SOM compartments (Anderson, 1979; Jenkinson and Rayner, 1977), simulates decomposition rates that vary as a function of monthly soil temperature and precipitation, and includes both N and C flows. The structure and concepts used in our model are similar to those used by Paul and Van Veen (1978); however, we do not explicitly use the concept of physically protected and nonphysically protected organic matter. In recent years, Pastor and Post (1986) and Aber et al. (1982) have used a modeling approach similar to ours for representing soil C and N dynamics in forest systems.

We estimated as many of the parameters as possible directly from published data using a nonlinear data-fitting procedure (Powell, 1965). We validated the model by comparing simulated soil C and N and aboveground plant production to mapped values at 24 sites on the Great Plains, which span the overall moisture and temperature gradients in this region.

### MODEL DESCRIPTION

#### Soil and Decomposition Submodel

The SOM submodel contains three soil organic matter (SOM) fractions (Fig. 1). They constitute (i) an active fraction (active SOM) of soil C and N consisting of live microbes and microbial products, along with soil organic matter with a short turnover time (1–5 yr); (ii) a pool of C and N (slow SOM) that is physically protected and/or in chemical forms

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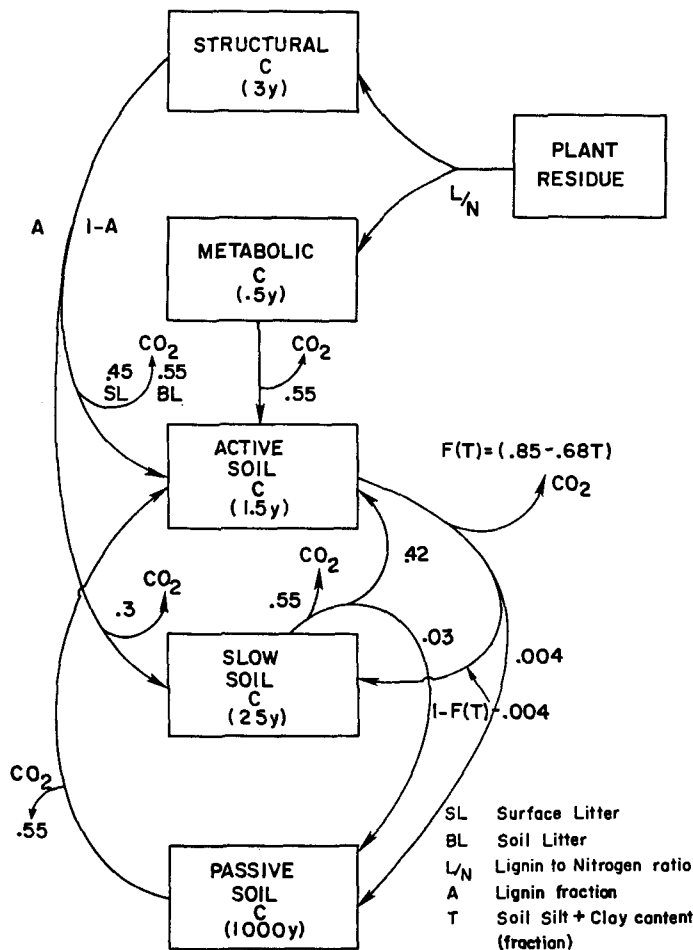


Fig. 1. Flow diagram for the C flows in the Century model.

with more biological resistance to decomposition, with an intermediate turnover time (20–40 yr); and (iii) a fraction that is chemically recalcitrant (passive SOM) and that may also be physically protected, with the longest turnover time (200–1500 yr). Plant residue (shoot and root plant biomass) is divided into structural pools that have 1- to 5-yr turnover times and metabolic pools that have 0.1- to 1-yr turnover times (based on McGill et al., 1981) prior to transfer into SOM pools.

We assume that the lignin-to-N ratio controls the split of plant residue into structural and metabolic material and that all of the plant residual lignin flows into the structural compartment. We also assume that the decay rate of structural material is a function of its lignin content and that the lignin fraction is incorporated into the slow soil pool. This direct flow of lignin into slow soil organic matter is based on data from laboratory incubation of labeled lignin-type material (Stott et al., 1983), which show that very little (<2%) of the lignin is found in microbial biomass, with most (70%) being stabilized in the soil. The release of lignin at a rate that is proportional to its concentration in structural material is based on the assumption that lignin is distributed fairly uniformly through the structural material and is released as the microbes decompose the more labile components of the structural material (e.g., hemicellulose and cellulose).

Decomposition of each of the state variables is calculated using the following equation:

$$dC_i/dt = K_i \cdot M_d \cdot T_d \cdot C_i, \quad [1]$$

where  $C_i$  = the carbon in the state variable;  $i = 1, 2, 3, 4, 5, 6$ , and  $7$  for structural and metabolic soil surface litter,

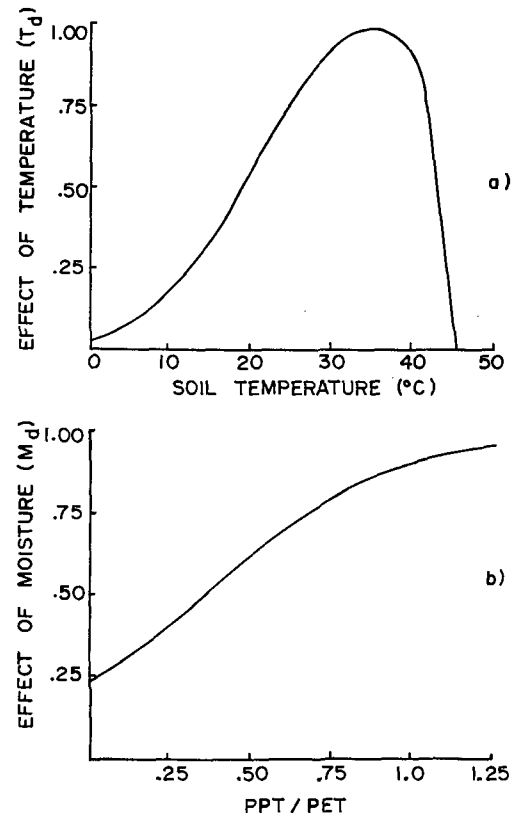


Fig. 2. The effect of soil temperature ( $T_d$ ) and moisture ( $M_d$ ) on monthly decomposition rates.

structural and metabolic soil litter, and active, slow and passive soil fractions;  $K_i$  = the maximum decomposition rate parameter (per week) for the  $i$ th state variable ( $K_i = 0.076, 0.28, 0.094, 0.35, 0.14, 0.0038$ , and  $0.00013$ );  $M_d$  = the effect of the ratio of monthly precipitation (PPT) to potential evapotranspiration rate (PET) on decomposition (see Fig. 2b); and  $T_d$  = the effect of monthly average soil temperature on decomposition (see Fig. 2a).

The effect of soil temperature on decomposition was determined by using a nonlinear data-fitting procedure (Powell, 1965) to determine the parameter value for an equation (generalized Poisson function) that represented the effect of soil temperature on decomposition of labeled cellulose at three different temperatures (10, 20, and 30°C) for a 90-d incubation [data derived from Sorenson (1981)]. The average monthly soil temperature was calculated by averaging the average monthly maximum and minimum soil-surface temperatures, which were calculated as a function of the observed averaged monthly maximum and minimum air temperatures (2 m) and the standing crop plant biomass, using an equation developed by Parton (1984). The effect of the ratio of PPT to PET on decomposition was calculated using daily water budget (Parton, 1978) and soil temperature (Parton, 1984) models and a daily decomposition model to simulate monthly average decomposition rate for a 34-yr simulation run. We then evaluated the best fit curve to represent the effect of the ratio of monthly PPT to PET on monthly decomposition rates. The monthly decay rate was assumed to be proportional to the product of a soil temperature term (see Fig. 2a) and a moisture term (see Fig. 2b).

All of the decomposition rate parameters ( $K_i$ ) for the state variables were constant except for the structural decay rate ( $K_1^s$  and  $K_2^s$ ), which is a function of the lignin content of the structural material, and the active SOM decay rate ( $K_3^s$ ), which is a function of the soil texture. Also note that decay rates for the soil surface litter are 20% lower than the soil litter.

This is based on the assumption that soil moisture content will be less optimal for decomposition near the soil surface (Holland and Coleman, 1987).

The model assumes that all C decomposition flows are a result of microbial activity and that microbial respiration is associated with each of these flows. The model assumes (see Fig. 1) that 55% of the C decomposition flow for soil non-lignin structural C, metabolic C, and slow and passive soil SOM is lost as microbial respiration. Nonlignin surface structural litter has a low respiration loss (45%), since fungi are the primary decomposers of surface litter and more efficiently stabilize C into microbial biomass (Holland and Coleman, in press). Stabilizing lignin into slow SOM is a fairly efficient process with only 30% lost as respiration loss (Stott et al., 1983). The efficiency of stabilizing active SOM into slow SOM is assumed to be a function of soil texture, with sandy soils being less efficient than fine-textured soils (see discussion below).

Twelve 1-yr plant residue incubations in subsoil (Pinck et al., 1950) were used to estimate the effect of the lignin (L) to N ratio on the split plant residue into structural and metabolic components and decay rates for soil structural and metabolic litter ( $K_3$  and  $K_4$ ). The L content of incubated plant residue ranged from <5% for bluegrass (*Poa pratensis* L.) to 17% for corn (*Zea mays* L.) stover, whereas N content ranged from 4.3% for bluegrass to 0.7, 0.6, and 0.4%, respectively, for oak (*Quercus* sp.) leaves, wheat (*Triticum aestivum* L.) straw, and corn stover. To evaluate the parameters, we used a simplified version of the model, where we dropped the passive SOM pool and assumed that the loss of slow C was minimal in a 1-yr incubation, and then evaluated the fit for the specific parameters. Note that the decay rate for active SOM and the efficiency of creating slow SOM from active SOM were determined by an independent data-fitting process. A comparison of the Pinck et al. (1950) data with more recent soil incubation data (Ladd et al., 1981) shows similar results and suggests that controls over decomposition are similar in subsoil and surface horizon soils.

A comparison of the observed and simulated C remaining vs. time for five different plant incubations (Fig. 3a) showed high C losses during the first 8 weeks and low C losses at the end of the incubation. The high-N and low-lignin residues (oats and millet, *Avena sativa* L. and *Panicum miliaceum* L.) decomposed more rapidly than the high-lignin and low-N residue. In general, the difference between the observed data and simulated results was small (<3%).

The split of plant residue into metabolic and structural components is determined as a function of the L/N ratio of the residue, using the following equation:

$$F_M = 0.85 - 0.018 \cdot L/N, \quad [2]$$

where  $F_M$  = the fraction of residue that is metabolic and  $F_S$  = fraction of residue that is structural ( $F_S = 1 - F_M$ ). This equation predicts that as the L/N ratio gets larger,  $F_M$  decreases while  $F_S$  increases. This is consistent with data presented by Melillo et al. (1984), who showed that decomposition of leaf litter was inversely related to the initial L/N ratio of the plant material. The split between structural and metabolic material occurs when the plant residue is transferred into surface or soil litter material. We assume that fractions of the soil mineral N (0.05 and 0.10 for surface and soil litter, respectively) are immobilized and, in effect, modify the L/N ratio. This can stimulate the decomposition of low-N plant residue (Pinck et al., 1950). Uptake of N from the soil does not occur if the C/N ratio is <10 (Pinck et al., 1950). The decomposition rate for surface and soil structural material ( $K_1^s$  and  $K_3^s$ ) are calculated as a function of fraction of structural material that is lignin ( $L_S$ ) and the maximum decay rates ( $K_1, K_3$ ), using the following equations:

$$K_1^s = K_1 \cdot \exp(-3.0 \times L_S), \quad [3]$$

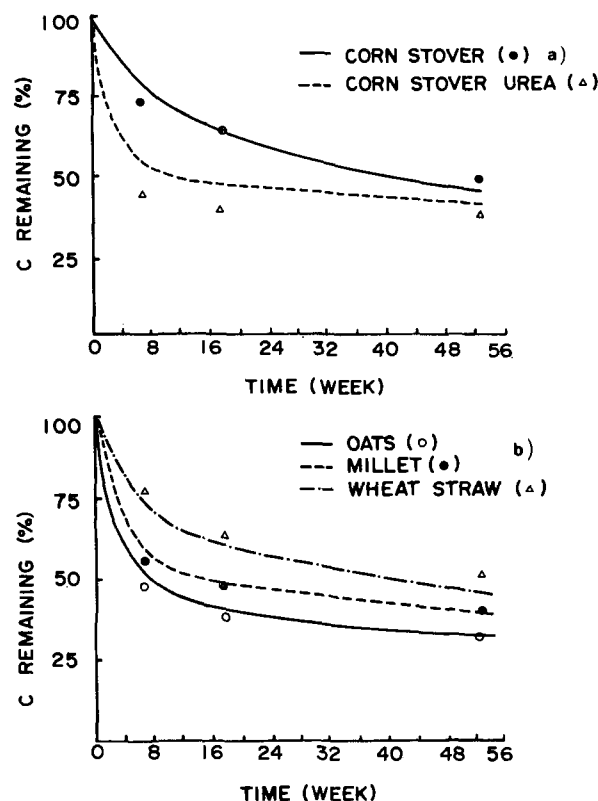


Fig. 3. A comparison of observed and simulated C remaining vs. time for 1-yr incubations of different types of (a) plant material and (b) wheat straw in a sandy and a clayey soil [data from Pinck et al. (1950)].

$$K_3^s = K_3 \cdot \exp(-3.0 \times L_S). \quad [4]$$

These equations cause the structural decay rates to decrease as the lignin content increases and are based on the assumption that as the lignin content increases, the ability of the microbes to decompose the more readily decomposable substrates (cellulose, hemicellulose, etc.) decreases rapidly (Melillo et al., 1982, 1984). The estimated parameter values in Eq. [2], [3], and [4] and the value for  $K_3$  and  $K_4$  were determined by fitting the model to the observed laboratory incubation data (Fig. 3a), whereas values for  $K_1$  and  $K_2$  were determined by assuming that surface residue decomposes ~20% slower than incorporated soil residue.

The model assumes that the lignin content of dead-root biomass ( $L_R$ ) and dead aboveground plant material ( $L_a$ ) changes as a function of the annual precipitation ( $L_a = 2 + 0.12 \cdot \text{PPT}$ ,  $L_R = 26 - 0.15 \cdot \text{PPT}$ ; PPT in cm). The lignin values are based on grassland plant lignin data from the Great Plains (unpublished data from the USIBP Grassland Biome). Shifts in lignin content with precipitation may result from within-species responses and from changes in plant-community composition. Since the model does not explicitly include species characteristics, it does not distinguish between these two types of effects.

The model assumes that soil texture influences the decomposition rate of active SOM ( $K_2^s$ ) and efficiency of stabilizing active SOM into slow SOM ( $E_s$  = fraction of C lost as  $\text{CO}_2$  when active SOM is decomposed and stabilized into slow SOM). The effect of soil texture was determined by fitting the model to Sørensen's (1981) laboratory incubation data of cellulose in soils with different textures. Equation [5] shows the effect of the soil silt plus clay fraction ( $T$ ) on the decay rate of active SOM ( $K_2^s$ ), and Eq. [6] shows the effect of  $T$  on the efficiency of stabilizing active SOM into slow SOM ( $E_s$ ).

$$K_5^2 = K_5 \cdot (1 - 0.75 \cdot T), \quad [5]$$

$$E_s = (0.85 - 0.68 T). \quad [6]$$

Equation [5] shows that the decay rate of active SOM decreases as the silt plus clay content increases. Many other studies show that microbial turnover rates are similarly related to texture (Ladd et al., 1981; Schimel et al., 1985a, b; Schimel, 1986). The  $E_s$  decreases as the silt plus clay content increases, with a resulting increase in the amount of C stabilized in slow SOM for fine-textured soils (high silt and clay content). This model for the stabilization of active SOM into slow SOM has been independently validated using wheat straw (see Fig. 3b) laboratory incubation data (Pinck et al., 1950) and glucose laboratory incubation data (Van Veen et al., 1984).

The decay rate for the slow SOM pool ( $K_6 = 0.0038 \text{ week}^{-1}$ ) was assumed to be equal to the decay rate at the end of (day 360 to day 1600) Sørensen's (1981) long-term cellulose incubation. His data also show that the decay rate at the end of the incubation is the same for different soil textures in spite of the fact that the C level in the sandy soil was 50% lower than the C level in the high-clay soil.

The flows that control the formation of passive SOM and its decay rate ( $K_7$ ) could not be estimated using existing laboratory incubation data because of the long turnover time of passive SOM. The stabilization of active SOM into passive SOM and the stabilization of slow SOM into passive SOM are the flows into passive SOM, and were set equal to 0.4% of the C flow out of active SOM and 3% of the C flow out of slow SOM. The decay rates of passive SOM and the fraction of total SOM in the passive fraction are based on soil carbon-dating data from Martel and Paul (1974), which show that C dates of older soil organic fractions ranged from 800 to 1600 yr and that the old SOM fraction comprises >50% of the total SOM. The actual value of  $K_7$  and the parameters that control the formation of passive SOM were determined by a systematic model-tuning procedure, where the parameters were adjusted to fit observed total SOM levels for several sites ranging from Colorado to eastern Kansas.

### Plant Submodel

The plant production flow model simulates the monthly dynamics of C and N in the live and dead aboveground plant material, live roots, and structural and metabolic surface and soil residue pools. Maximum annual aboveground ( $P_{\max} = \text{g biomass m}^{-2}$ ) and belowground production ( $R_{\max} = \text{g biomass m}^{-2}$ ) without nutrient limitations are calculated as a function of annual precipitation (APPT in cm), using the following equations:

$$P_{\max} = -40 + 7.7 \cdot \text{APPT}, \quad [7]$$

$$R_{\max} = 100 + 7.0 \cdot \text{APPT}. \quad [8]$$

The equation for aboveground production is based on data of Dodd and Lauenroth (1978) and Owensby et al. (1970); root production is based on data from Sims and Singh (1978). The monthly maximum plant production during the growing season (May–September) is equal to annual maximum production divided by the length of the growing season (30 weeks) and is then reduced if there is insufficient mineral N. The C/N ratio of plant material is allowed to float between a maximum value ( $C_{\max}$ ) and a minimum value ( $C_{\min}$ ). The value of  $C_{\max}$  and  $C_{\min}$  change as a function of the APPT, using the following equations, which were estimated using plant-N data from grasslands in the Great Plains (unpublished data from the U.S. IBP Grassland Biome):

$$C_{\max} = 44 + 0.2 \times \text{APPT}, \quad [9]$$

$$C_{\min} = 39 + 0.2 \times \text{APPT}. \quad [10]$$

Plant production is reduced if mineral N is insufficient to produce plant material with a C/N ratio less than or equal to  $C_{\max}$ , and uptake of N will be restricted so that the C/N ratio will not be less than  $C_{\min}$ . Changes in  $C_{\max}$  and  $C_{\min}$  result from both within-species growth responses and changes in species composition, which are not modeled explicitly. Plant lignin content was determined as described in the previous section.

Death of live shoots occur at a base rate of 6% per 30 d, but at plant senescence, 98% of the biomass dies. Dead shoots are transferred to standing-dead material which is transferred to surface litter at a rate of 10% per 30 d. Live root biomass dies at the rate of 4% per 30 d and is transferred directly into soil residue. When standing-dead biomass is transferred to surface litter and live roots die, the residue is split into structural and metabolic material as a function of its initial L/N ratio (see Eq. [2]). Nitrogen flows for the plant model are calculated as functions of the C flows and are equal to the product of C flow times the N/C ratio of the source pool.

### Nitrogen Submodel

The nitrogen model (Fig. 4) has the same structure as the carbon-flow diagram and we assume that most N is bonded to C. We assume that the C/N ratio of structural (150), active (8), slow (11), and passive (11) fractions remains fixed. The C/N ratio for the active SOM is based on typical C/N ratios for microbes and microbial products; the element ratios of structural material were based on results in McGill et al. (1981). The N content of the metabolic pool is allowed to vary as a function of the N content of the incoming plant material, with the plant N not needed to create structural material (C/N of 150) going to the metabolic-N pool.

The N flows were assumed to be stoichiometrically related to C flows and were equal to the product of the C flow rate and the fixed N/C ratio of the state variables receiving the C. Either mineralization or immobilization of N (see Fig. 4) can result from C flow, depending on the initial C/N ratio of material, the C/N ratio of pools receiving the C, and the fraction of the C flow lost as  $\text{CO}_2$  respiration (30–80% of the total C flow).

The model also simulates N inputs due to atmospheric deposition ( $N_a = \text{g N m}^{-2} \text{ yr}^{-1}$ ) and symbiotic plus non-symbiotic  $\text{N}_2$  fixation ( $N_f = \text{g N m}^{-2} \text{ yr}^{-1}$ ) by using Eq. [11] and [12], respectively, which assumes that N inputs are controlled by the annual precipitation

$$N_a = 0.21 + 0.0028 \cdot \text{APPT}, \quad [11]$$

$$N_f = -0.18 + 0.014 \cdot \text{APPT}. \quad [12]$$

Equation [11] is based on annual wetfall atmospheric N deposition data ( $\text{NO}_3^- + \text{NH}_4^+$ ) from the National Atmospheric Deposition sites in the Great Plains from 1979 to 1984. The soil plus plant  $\text{N}_2$  fixation equation (Eq. [12]) was determined by a model-tuning procedure that used observed plant production data from sites in Colorado and Kansas.

Nitrogen loss from grasslands occurs as a result of  $\text{NH}_3$  volatilization (Schimel et al., 1986), leaching, and volatilization of the  $\text{N}_2\text{O}$  and  $\text{N}_2$  resulting from nitrification and denitrification (Mosier et al., 1983). In the model it is assumed that N will be lost as a result of volatilization of N products ( $\text{N}_2$ ,  $\text{N}_2\text{O}$ , and  $\text{NH}_3$ ) and removal of N by cattle (*Bos taurus*) grazing. Leaching is assumed to be negligible for undisturbed grasslands. Volatilization losses are estimated by assuming that 5% of the sum of the N mineralization flows will be lost to the atmosphere, so that N volatilization rates were proportional to gross N-mineralization rates.

Losses of N due to large ungulate grazing are assumed to be equal to 20% of the N uptake by the cattle and include loss via  $\text{NH}_3$  volatilization from feces and urine, and N removed by the cattle. We assume that N returned to the

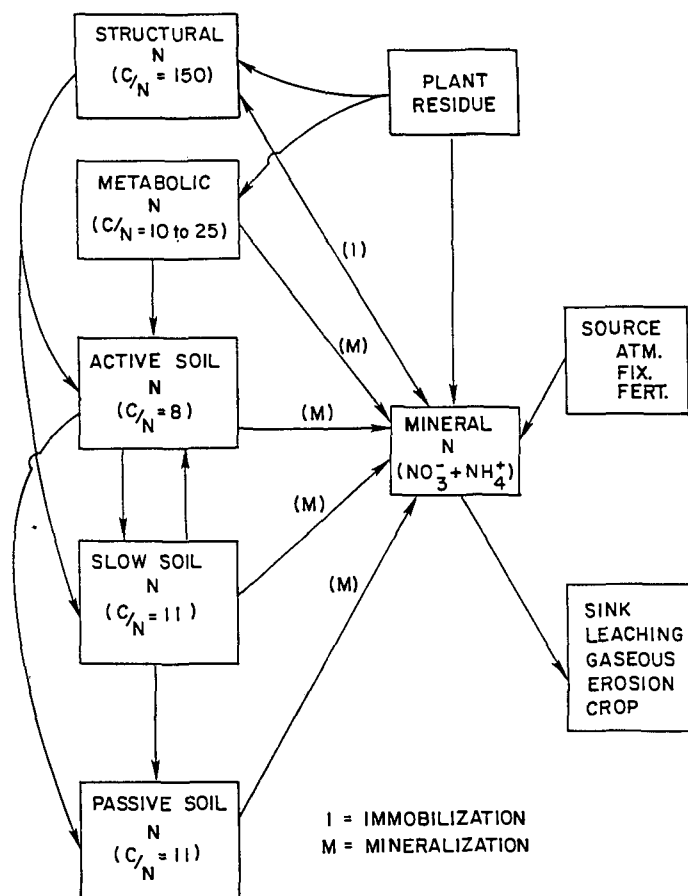


Fig. 4. Flow diagram for the N submodel of the Century model.

system is equally split between urine and feces and that 30% of the C consumed by the cattle is returned to the system with a 25% lignin content (Schimel et al., 1986).

### Model Validation

The model was validated by simulating steady-state soil C and N levels and aboveground plant production for 24 sites in the Great Plains and comparing the simulated values with mapped plant production and soil C and N levels for fine- (25% sand, 30% clay), medium- (50% sand, 22% clay), and sandy- (75% sand, 10% clay) textured soils at these sites. The sites were selected along three east-west transects (see Fig. 5a). Data from a transect from Colorado to eastern Kansas were used to estimate some of the parameters in the model (Fig. 5).

The model was run using the observed maximum and minimum monthly temperature and monthly precipitation as inputs for the model. We further assumed that the grasslands had been grazed during their development at a moderate level, with 16 and 8%, respectively, of the live and standing-dead biomass removed per 30 d from April through September (45% removal of animal aboveground production). Steady-state SOM, C, and N levels were very sensitive to grazing levels, with SOM level dropping by 40% as the simulated grazing level increased from zero to 50% of annual production. The model's sensitivity to changes in the grazing intensity is supported by data from Bauer et al. (in press), which show that preventing grazing for 80 yr caused soil C levels to increase 0.4 to 0.6 kg m<sup>-2</sup>.

Plant production maps (Fig. 5b) and soil C maps for sandy and fine-textured soils (Fig. 6) are shown. The plant production (PROD) map was based on range production data

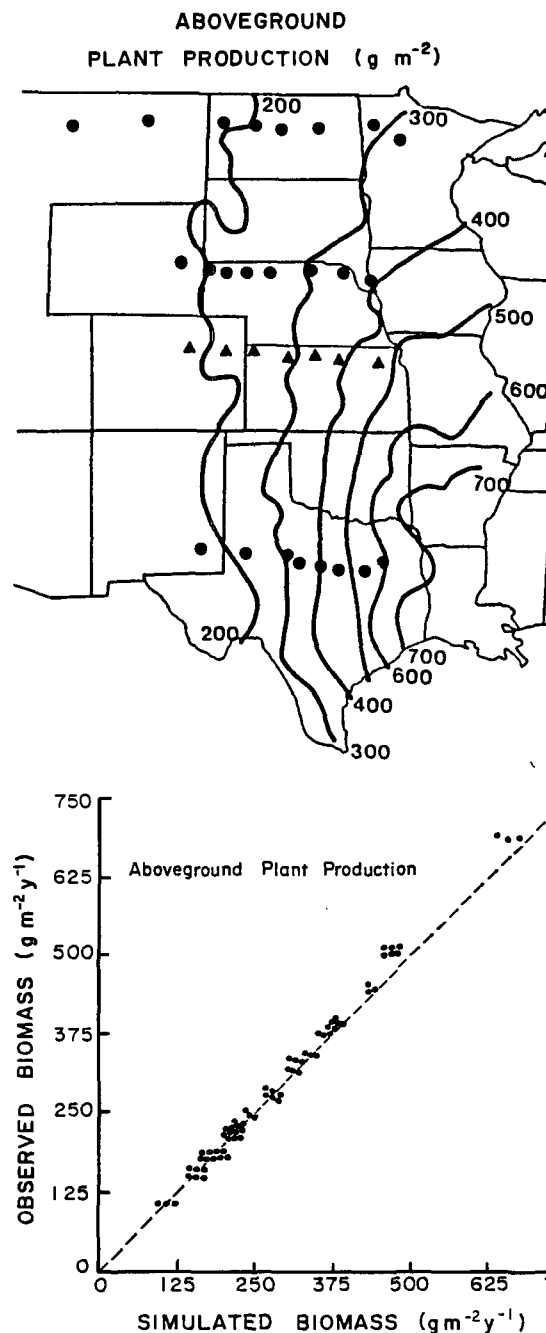


Fig. 5. (a) Mapped aboveground grassland plant production for the Great Plains, and (b) comparison of mapped and simulated aboveground plant production for the 24 validation sites. The dots on plant production maps show the location of validation sites. The triangles show the parameterization sites.

collected by the Soil Conservation Service at 9500 sites in the Great Plains and was generated using a regression equation ( $\text{PROD} = -34 + 6 \times \text{APPT}$ ,  $r^2 = 0.9$ ) to predict plant production at 400 sites in the Great Plains as a function of annual precipitation, and a contouring routine from the S package (Bell Labs, Murray Hill, NJ, USA) to generate the maps.

A similar approach was used to generate the soil C and N maps. We developed regression equations ( $r^2 = 0.49$  for C and  $r^2 = 0.42$  for N;  $n = 560$ ) to predict soil C and N levels as functions of soil texture (silt and clay content) and climatic factors (growing season [April–September] precip-

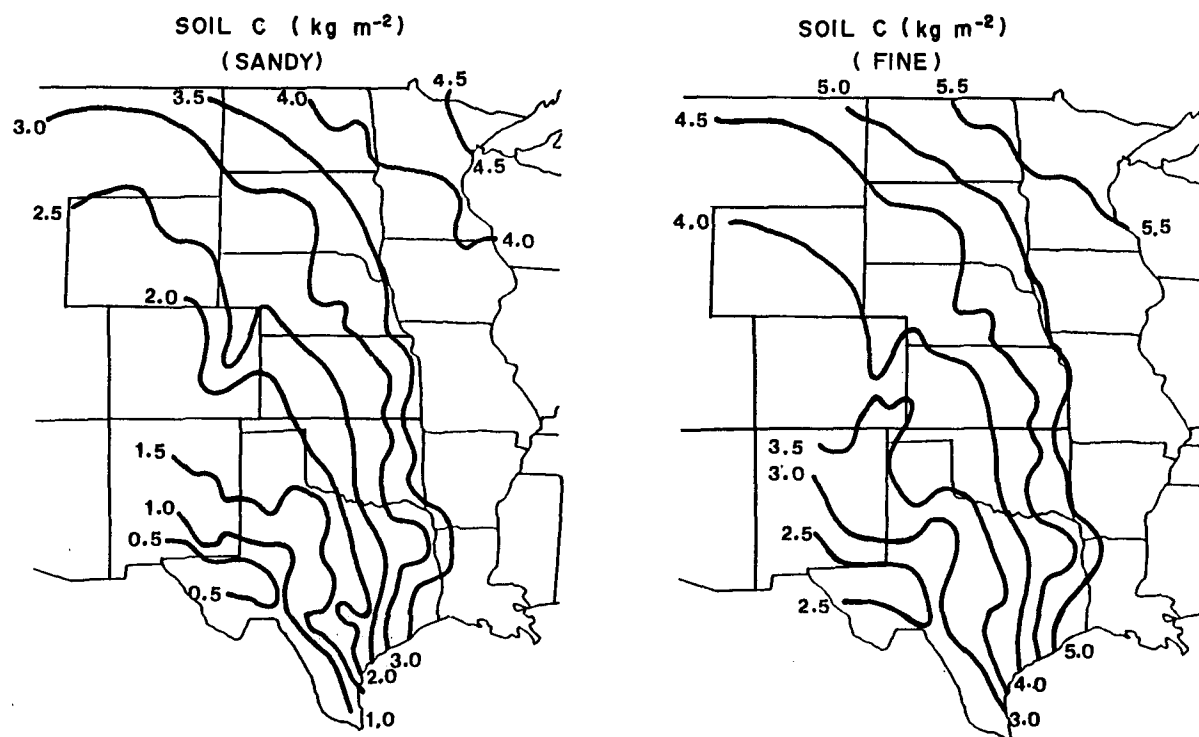


Fig. 6. Soil C levels (0–20 cm) (a) for sandy and (b) fine-textured soils of the Great Plains. Contours are based on regression analysis of SCS pedon data and are potential values for soils of specified textures.

itation and potential evapotranspiration rate, and mean annual temperature) by using soil C and N data from 560 soil pedons in the Great Plains (unpublished data). This equation was used to predict potential soil C and N levels at three soil textures for 400 sites in the Great Plains, which were then used to generate the maps. Figure 7 compares mapped and simulated soil C and N levels for all 24 validation sites and shows regression lines for each soil texture. The model tends to overestimate the soil C and N levels for the fine-textured soils, underestimates the values for sandy soils with the higher C and N levels (i.e., in the more mesic parts of the Great Plains), and does an excellent job of fitting the medium-textured soil. The results show that the model adequately represents the effect of soil texture and climate on soil C and N levels in the Great Plains. The significance of the discrepancies in some soils are unclear because of problems with the equation used to calculate bulk density and, hence, in converting C and N on a mass basis to a volume basis. A major uncertainty is associated with Rawls's (1983) bulk density equation, since it substantially overestimated (5–30%) bulk density in the surface soils (0–20 cm layer). Limited bulk density data from Bauer et al. (1987) showed that the apparent error is a function of soil texture (error is highest for the sandy soils) and was used to modify the Rawl's (1983) bulk density equation.

The model did an excellent job of simulating aboveground plant production (Fig. 5b). The fit is a result of the facts that simulated plant production is highly correlated to simulated N inputs, that N inputs in the model are direct functions of annual precipitation, and that observed plant production was highly correlated with annual precipitation.

### DISCUSSION

This analysis demonstrates that broad regional trends in productivity and organic matter can be adequately modeled using a small set of driving variables. In the current model, only four driving variables are required to characterize a site. Annual precipita-

tion affects the decomposition and production sub-models and controls N inputs. Temperature is a control over the decomposition submodel directly and through estimates of PET. Soil texture is a control over the formation and turnover rates of the active and slow soil organic matter pools. Plant lignin content is an important control over decomposition rate and varies for above- and belowground material as a function of climate. The model represents regional trends in organic matter content with an overall error of about 15% using this set of driving variables. Site-specific data on climate, soil texture, and plant lignin content are readily obtained over large areas, and so the applicability of the model, at least within the Great Plains, is not limited by data availability. Pastor and Post (1986) used the same set of driving variables in a model of forest C and N cycles, suggesting that the utility of this approach is not restricted to grasslands.

The model's ability to predict SOM levels is limited by its sensitivity to several factors for which data is difficult or impossible to obtain. Grazing intensity and N input during soil development exert an important influence over contemporary organic matter levels. There are no sources of data from which to estimate the history of presettlement grazing intensity or N input rate by region within the Great Plains. Although we used reasonable assumptions, uncertainty resulting from site history cannot be eliminated. Pastor and Post (1986) reached similar conclusions about the effects of site history (past forestry practices) on model uncertainty in their model of forest nutrient cycling. These uncertainties set a limit on the precision that may be expected from the Century model's regional predictions. This uncertainty is not unacceptable, given our objectives.

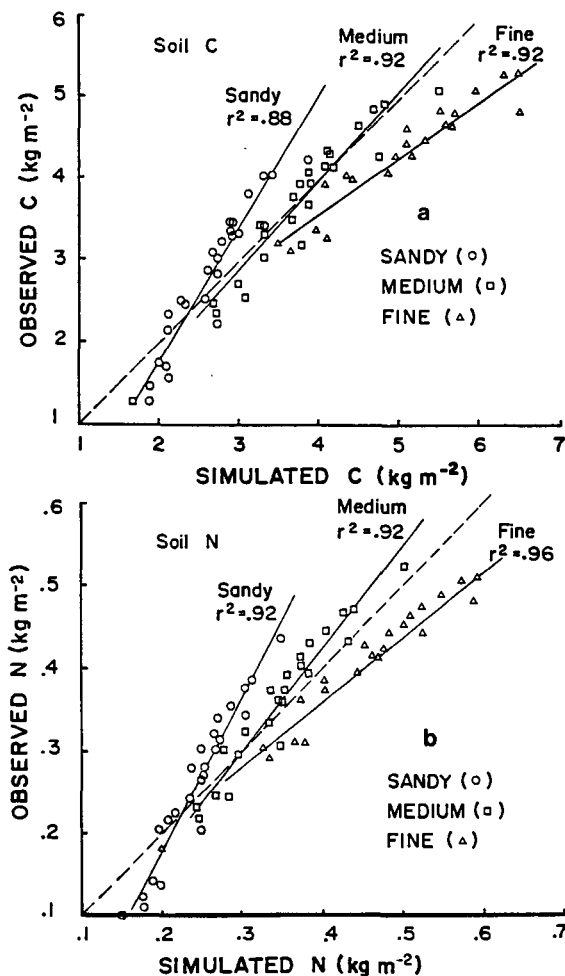


Fig. 7. Comparison of mapped and simulated (a) soil C and (b) N levels for the sandy, medium, and fine-textured soils. The regression lines for each soil texture (solid line) are included on the graphs. The equality line (1:1) is shown as a dashed line.

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### REFERENCES

- Aber, J.D., J.M. Melillo, and C.A. Federer. 1982. Predicting the effects of rotation length, harvest intensity and fertilization on fiber yield from northern hardwood forests in New England. *For. Sci.* 28:31-45.
- Anderson, D.W. 1979. Processes of humus formation and transformation in soils of the Canadian Great Plains. *J. Soil Sci.* 30:77-84.
- Bauer, A., C.V. Cole, and A.L. Black. 1987. Soil property comparisons in virgin grasslands between grazed and nongrazed sites. *Soil Sci. Soc. Am. J.* 51:176-182.
- Campbell, C.A. 1978. Soil organic carbon, nitrogen, and fertility. p. 173-272. *In* M. Schnitzer and S.U. Khan (ed.) *Soil organic matter*. Elsevier Scientific Publ. Co., Amsterdam.
- Dodd, J.D., and W.K. Lauenroth. 1978. Analyses of the response of a grassland ecosystem to stress. p. 43-58. *In* N.R. French (ed.) *Perspectives in grassland ecology*. Springer-Verlag, New York.
- Holland, E.A., and D.C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* 68(2):425-433.
- Jenkinson, D.S., and J.H. Rayner. 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Sci.* 123:298-305.
- Jenny, H. 1941. *Factors of soil formation*. McGraw-Hill, New York.
- Ladd, J.H., J.M. Oades, and M. Amato. 1981. Microbial biomass formed from <sup>14</sup>C, <sup>15</sup>N-labeled plant material decomposition in soils in the field. *Soil Biol. Biochem.* 13:119-126.
- Martel, Y.A., and E.A. Paul. 1974. Effects of cultivation on the organic matter of grassland soils as determined by fractionation and radio-carbon dating. *Can. J. Soil Sci.* 54:419-426.
- McGill, W.B., H.W. Hunt, R.G. Woodmansee, and J.O. Reuss. 1981. PHOENIX, a model of the dynamics of carbon and nitrogen in grassland soils. *Ecol. Bull. (Stockholm)* 33:49-115.
- Melillo, J.M., Aber, J.D., and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621-626.
- Melillo, J.M., R.J. Naiman, J.D. Aber, and A.E. Linkins. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. *Bull. Mar. Sci.* 35(3):341-356.
- Mosier, A.R., W.J. Parton, and G.L. Hutchinsen. 1983. Modelling nitrous oxide evolution from cropped and natural soil. *Environ. Biogeochem. Ecol. Bull. (Stockholm)* 35:229-241.
- Owensby, C.E., R.M. Hyde, and K.L. Anderson. 1970. Effects of clipping and supplemental nitrogen and water on loamy upland range. *J. Range Manage.* 23:341-346.
- Parton, W.J. 1978. Abiotic section of ELM. p. 31-53. *In* G.S. Inniss (ed.) *Grassland simulation model*. Springer-Verlag, New York.
- Parton, W.J. 1984. Predicting soil temperature in a shortgrass steppe. *Soil Sci.* 138:93-101.
- Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2:3-27.
- Paul, E.A., and J. Van Veen. 1978. The use of tracers to determine the dynamic nature of organic matter. *Trans. Int. Congr. Soil Sci.* 11th 3:61-102.
- Pinck, L.A., F.E. Allison, and M.S. Sherman. 1950. Maintenance of soil organic matter: II. Losses of carbon and nitrogen from young and mature plant material during decomposition in soil. *Soil Sci.* 69:391-401.
- Powell, M.J.D. 1965. A method for minimizing a sum of squares of nonlinear function without calculating derivatives. *Comput. J.* 7:303-307.
- Rawls, W.J. 1983. Estimating soil bulk density from particle size analysis and organic matter content. *Soil Sci.* 135:123-125.
- Schimel, D., M.A. Stillwell, and R.G. Woodmansee. 1985a. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology* 66:276-282.
- Schimel, D.S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. *Biogeochemistry* 2:345-357.
- Schimel, D.S., D.C. Coleman, and K.A. Horton. 1985b. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma* 36:201-214.
- Schimel, D.S., W.J. Parton, F.J. Adamsen, R.G. Woodmansee, R.L. Senft, and M.A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochemistry* 2:39-52.
- Sims, P.L., and J.S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover, and efficiencies of energy capture and water use. *J. Ecology* 66:573-597.
- Sørensen, L.H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biol. Biochem.* 13:313-321.
- Stevenson, F.J. 1986. *Cycles of soil carbon, nitrogen, phosphorus, sulphur, micronutrients*. John Wiley & Sons Inc., New York.
- Stott, E., G. Kassin, W.M. Jarrell, J.P. Martin, and K. Haider. 1983. Stabilization and incorporation into biomass of specific plant carbons during biodegradation in soil. *Plant Soil* 70:15-26.
- Tisdale, J.M., and J.M. Oades. 1982. Organic matter and water stable aggregates in soils. *J. Soil Sci.* 33:141-163.
- Van Veen, J.A., and E.A. Paul. 1981. Organic C dynamics in grassland soils. I. Background information and computer simulation. *Can. J. Soil Sci.* 61:185-201.
- Van Veen, J.A., J.H. Ladd, and M.J. Frissel. 1984. Modelling C and N turnover through the microbial biomass in soil. *Plant Soil* 76:257-274.