CHAPTER **15**

Modeling Soil C Responses to Environmental Change in Grassland Systems

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Introduction

This chapter focuses on the dynamics of soil organic C (SOC) in the carbon (C) cycle in grasslands. Recent years have seen much discussion of the potential impact of altered environmental conditions on storage of C in grasslands and other natural ecosystems (Parton et al., 1995; Ojima 1993 a, b; Hunt et al., 1991; VEMAP, 1995). This chapter discusses how potential changes in climatic factors like precipitation and air temperature, induced by greenhouse gases, may alter C dynamics in grasslands, and it considers the effect of increased atmospheric CO_2 and the combined effect of increased CO_2 and altered climatic conditions.

This chapter also includes a review of the literature about the direct effect of atmospheric CO_2 on grasslands; a general description of the factors that control soil C dynamics; and an analysis of the results of modeling the effects of environmental change on grassland dynamics. The modeling section reviews other grassland models but provides detailed results from the CENTURY ecosystem model (Parton et al., 1987) and primarily highlights results for the U.S. Great Plains region. The CENTURY model has been tested extensively, using observed soil C and plant production data from grasslands around the world (Burke et al., 1991; Parton et al., 1993; Gilmanov et al., 1997), with the most extensive testing completed for the U.S. Great Plains region.

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Factors that Control Soil Carbon Dynamics

One of the unique features of grasslands is in the distribution of C, with over 95% of it in soil organic matter (SOM). Aboveground plant organs typically account for 40 to 200 g C/m^2. Total root C (0- to 30-cm depth, 80% to 90% of the total roots) ranges from 200 to 400 g C/m^2, while soil C levels (0 to 100 cm) range from 3000 to 20,000 g C/m^2.

The typical depth distribution of C in plant root material and SOM for a short-grass steppe, and grasslands in general, is striking in its rapid decrease with depth (Fig. 15.1) (Mosier, unpublished data). Most SOM forms as a result of decomposition of dead grass roots and resultant stabilization through the microbial biomass into organic matter (OM). This stabilized OM, combined with resistant OM from plant material with a high lignin content and material protected within soil aggregates, makes up a relatively large pool of OM with a slow turnover time. The decrease in soil organic content (SOC) with increasing soil depth results from an exponential decline in root biomass and associated litter and exudates moving down through the profile.

For most grasslands, over 90% of the live roots are in the top 30 cm of the soil (Yonker at al., 1991, Gill et al., 1999), and 92% of the variability in surface (5 cm) total soil C can be explained by a total root biomass covariant (Kelly et al., 1996). The relationship between live plant and SOM C is similar for most grasslands, although the trend is toward a lower root:shoot ratio in more productive grasslands (20% increase from a short grass steppe to a tall grass prairie) and a higher root biomass in cold grassland systems (Kelly et al., submitted).

An important structural feature of grasslands is a rapid increase in the age of SOM with increasing soil depth (see Fig. 15.1c). Radiocarbon testing estimated that SOM's age (conventional ^{14}C age) for a native site in Iowa increases from less than 100 years in the 0- to 10-cm layer to over 1500 years at 50 cm (Harden, unpublished data). The details of how soil C's age increases with depth are understood poorly. Possible factors include decreasing soil temperature with depth, increasing soil anaerobic conditions with depth, and slow movement of resistant OM down the soil profile. Since the older soil C at depth highly resists change, we focus here on potential changes in SOM in the top 20 to 30 cm of the soil, resulting from changes in atmospheric CO_2 and climatic factors.

Figure 15.2's simplified flow diagram of soil C dynamics in grasslands, based on the CENTURY ecosystem model, shows controls on SOM. The major factors that control soil C dynamics include C inputs to the soil, the abiotic decomposition factor (DEFAC), and soil texture. Plant production, which is a function of climate and soil nutrient availability, controls C inputs to the soil. Grazing and fire also may alter inputs. Soil temperature and soil water status control the abiotic decomposition index (DEFAC) (Fig. 15.3), with decomposition increasing with increasing soil temperature and more favorable soil water status.
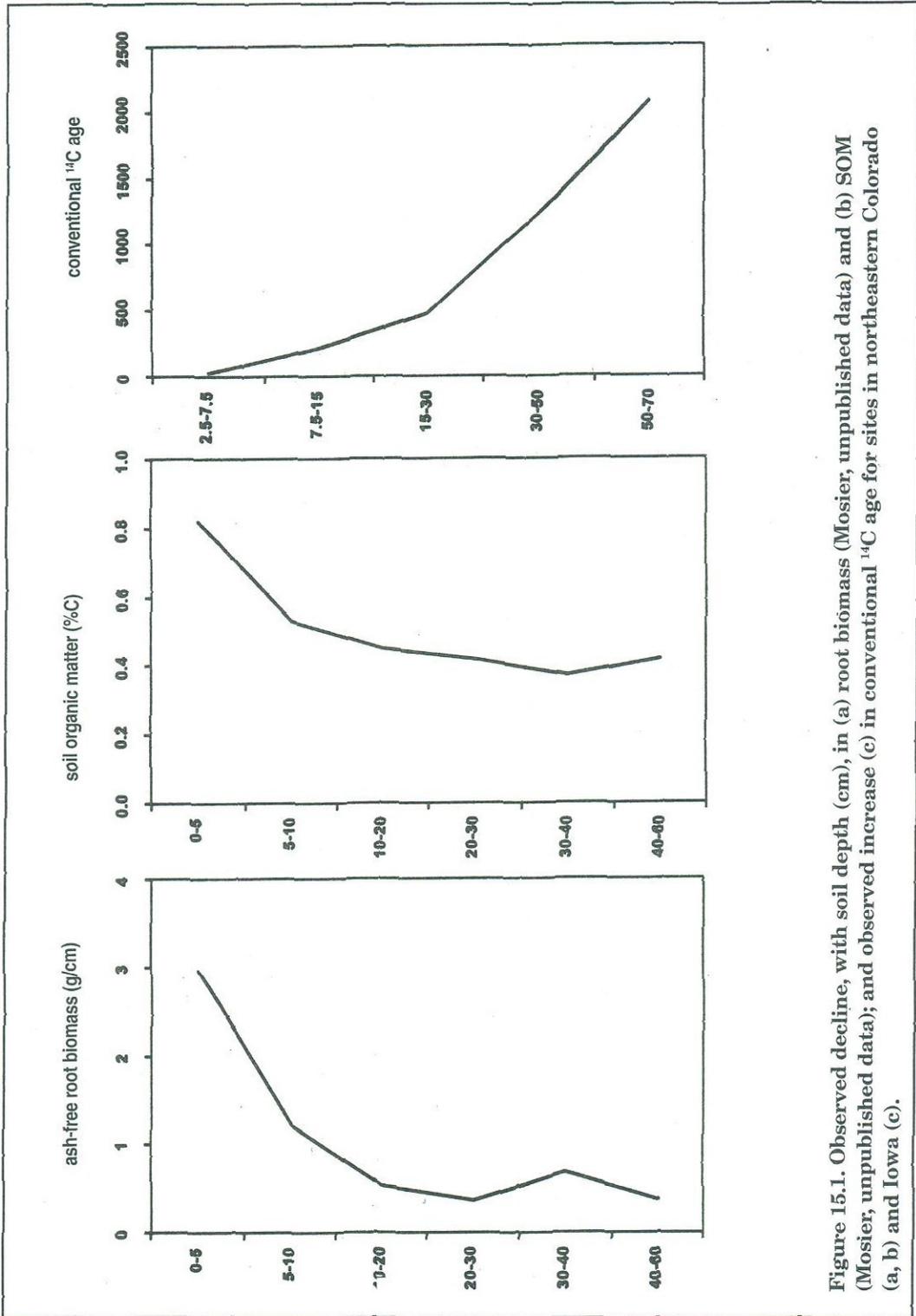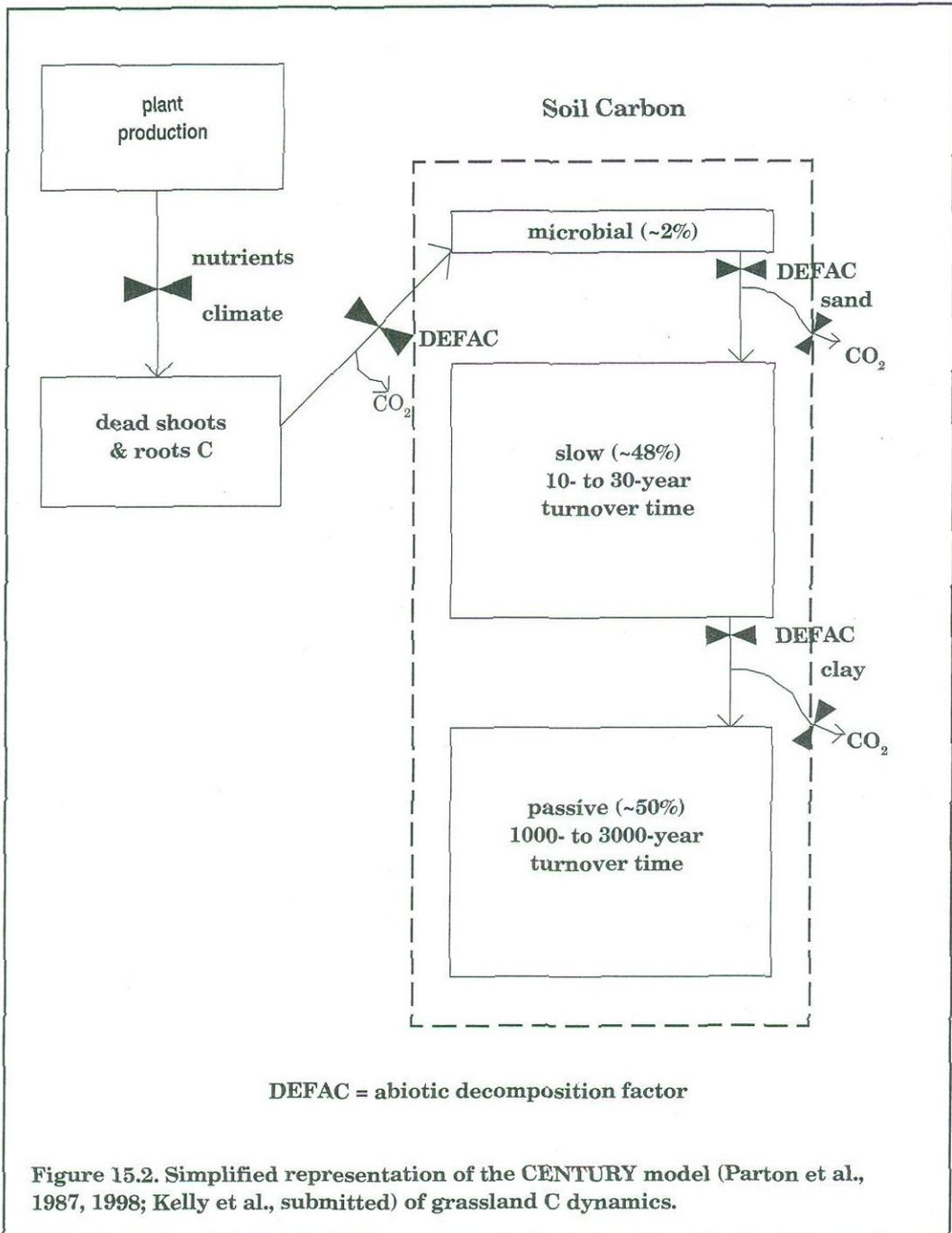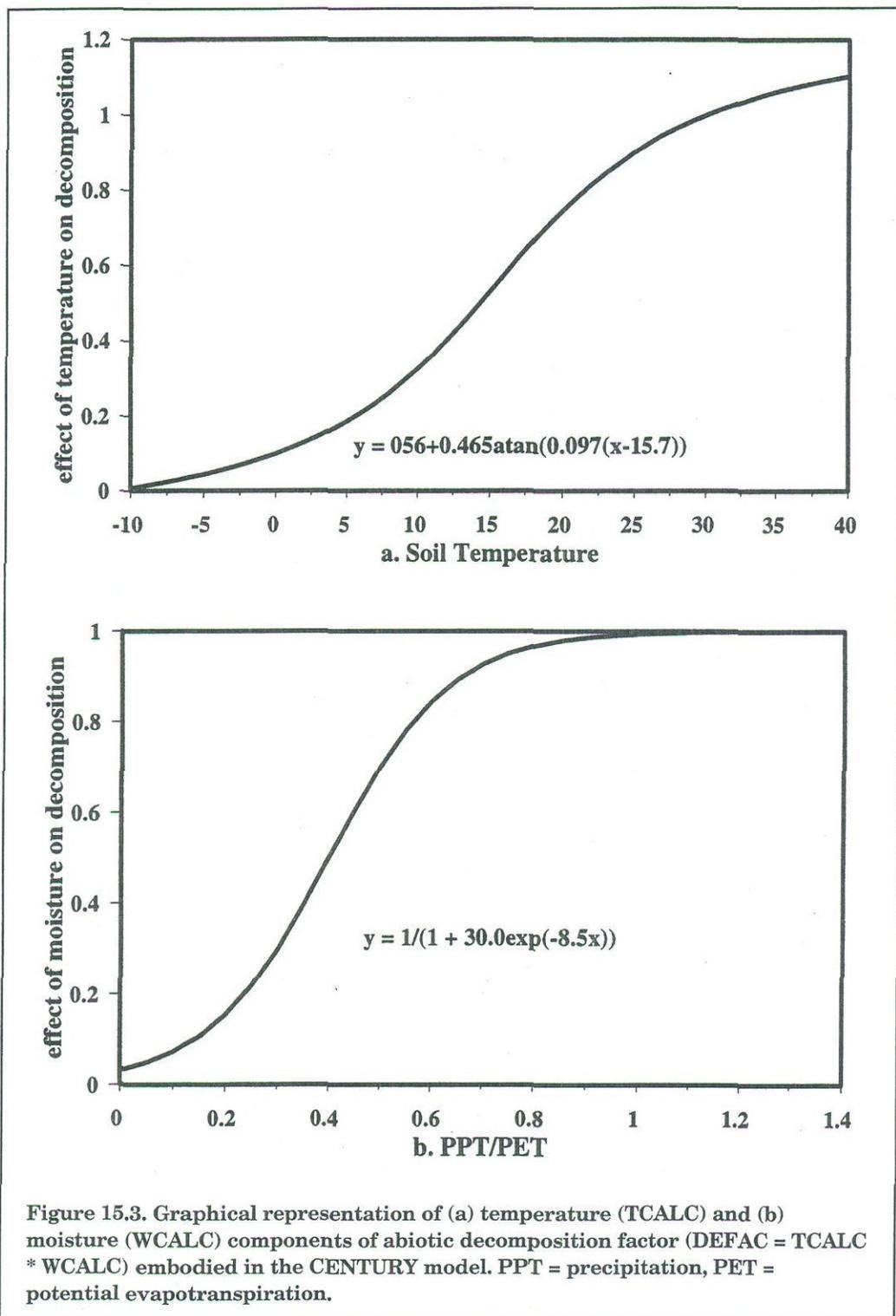
Figure 15.1. Observed decline, with soil depth (cm), in (a) root biomass (Mosier, unpublished data) and (b) SOM (Mosier, unpublished data); and observed increase (c) in conventional ^{14}C age for sites in northeastern Colorado (a, b) and Iowa (c).

Figure 15.2. Simplified representation of the CENTURY model (Parton et al., 1987, 1998; Kelly et al., submitted) of grassland C dynamics.

$$y = 056+0.465atan(0.097(x-15.7))$$

a. Soil Temperature

$$y = 1/(1 + 30.0exp(-8.5x))$$

b. PPT/PET

Figure 15.3. Graphical representation of (a) temperature (TCALC) and (b) moisture (WCALC) components of abiotic decomposition factor (DEFAC = TCALC * WCALC) embodied in the CENTURY model. PPT = precipitation, PET = potential evapotranspiration.

The soil temperature curve CENTURY uses (Fig. 15.3a) shows that decomposition is most rapid at relatively low soil temperatures (Q_{10} = 4 at 5°C vs. Q_{10} = 1.6 at 25°C). The greatest increase in decomposition occurs as the ratio of available water to potential evapotranspiration rate increases from 0.2 to 0.6, with little impact for ratios above 0.6.

Like other widely used models of C dynamics (van Veen and Paul 1985; Jenkinson 1990), CENTURY divides the total SOM into multiple pools to account for different C to N ratios and rates of turnover. The SOM in CENTURY is divided into three different pools, with approximately 2%, 48%, and 50% of the soil C in the microbial, slow, and passive pools, respectively. In a 50- to 100-year time period, the most important changes in soil C result from changes in the microbial and slow pools, because they are coupled more tightly to the ambient environment than are chemically stabilized passive materials.
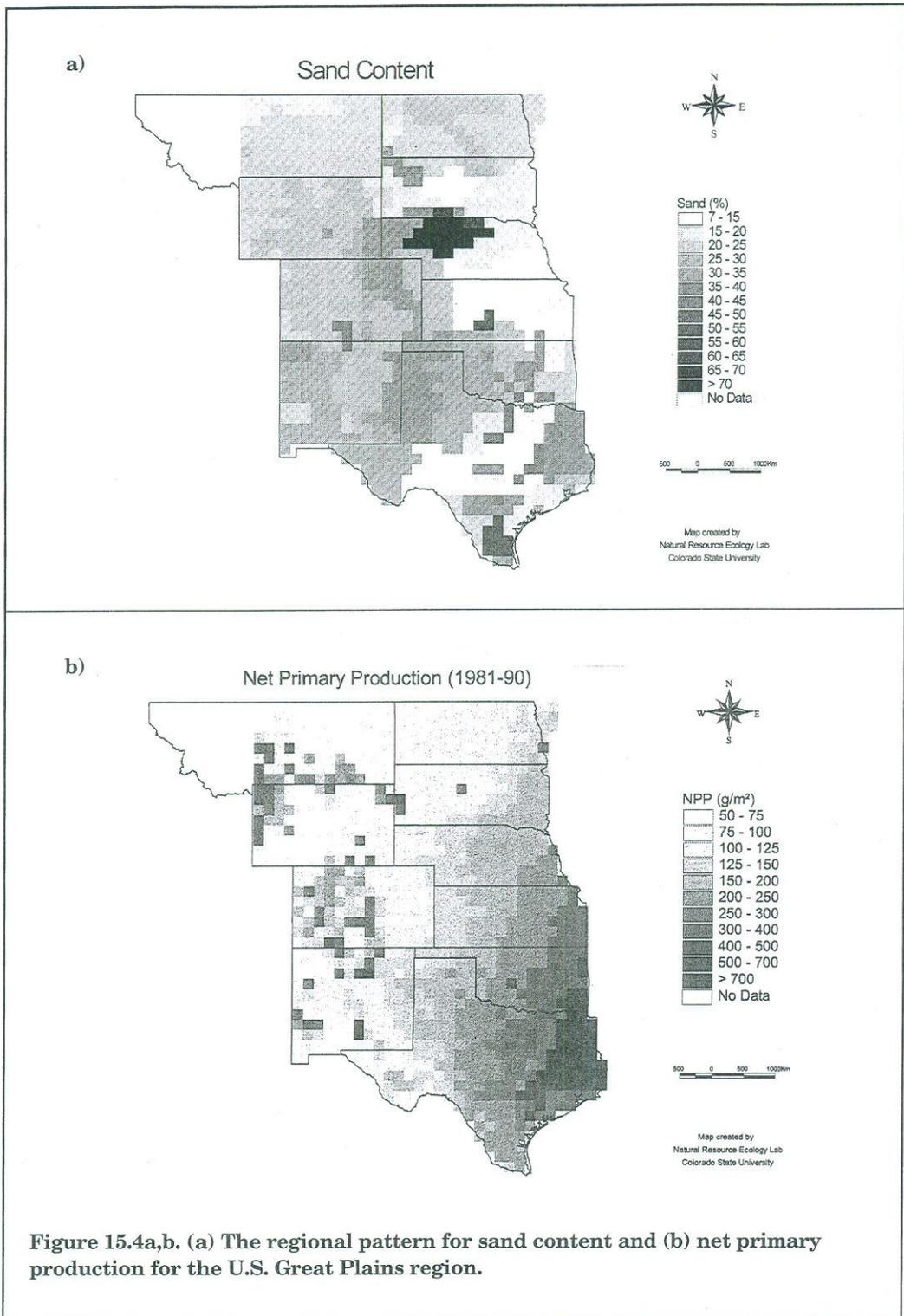
Soil texture has an important impact on physical and chemical protection of OM, with higher levels of OM and physical-chemical protection occurring in soils with high clay and silt content. Holding other factors constant, higher respiration losses for sandy soils result in lower soil C levels, while clay soils have low respiration loss and high soil C levels.
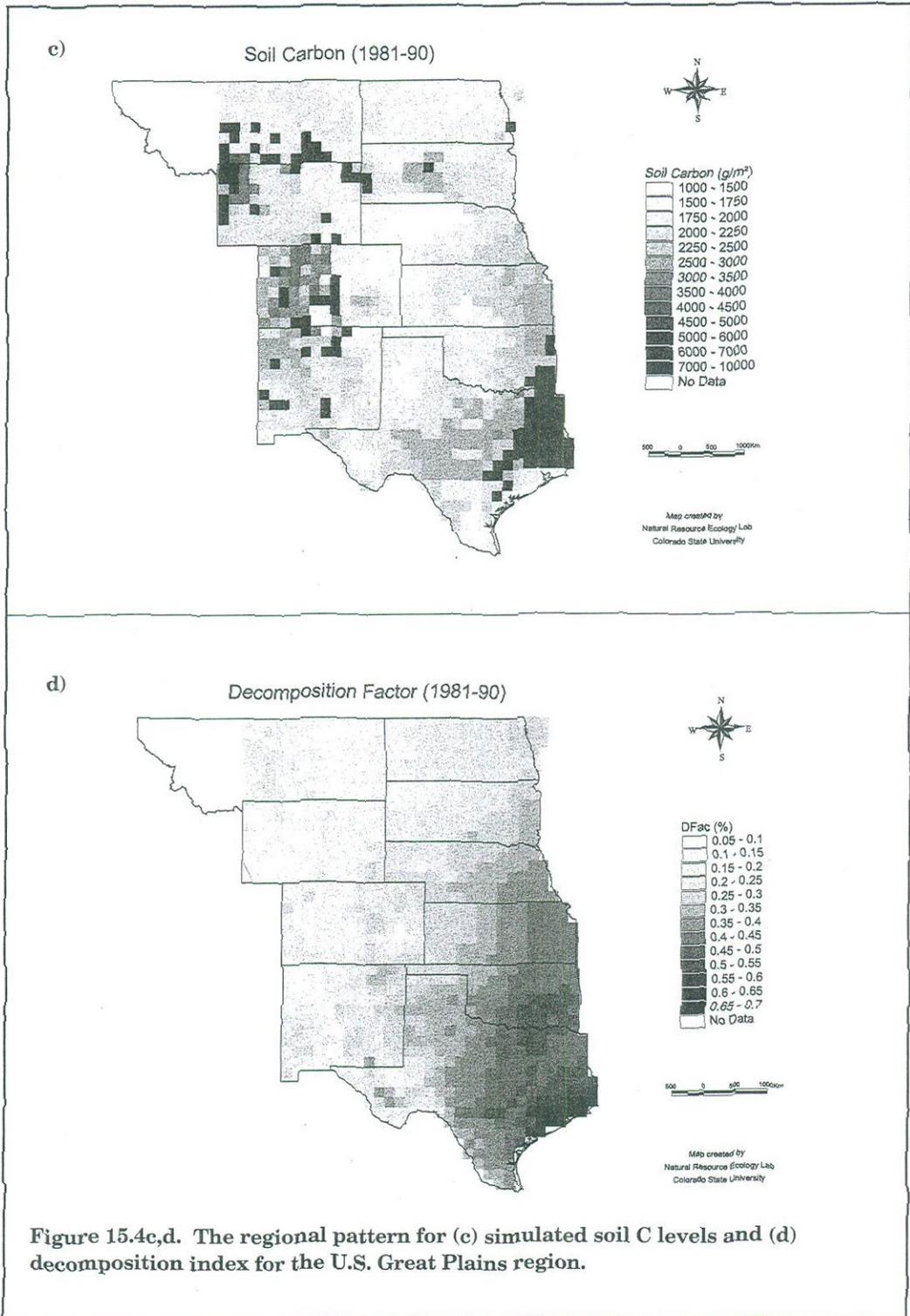
We used CENTURY's simulated patterns of soil C, plant production, and abiotic decomposition index (Fig. 15.4a,b,c,d) to demonstrate the controls on soil C levels for the U.S. Great Plains region. These model experiments were conducted using the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) 0.5 x 0.5 degree-scale database of climate and soils (Kittel et al., 1995) as input to a version of CENTURY designed to run across a grid (Schimel et al., 1996, 1997).

The CENTURY model has been tested extensively using observed soil C and plant production data for the Great Plains region (Burke et al., 1991; Sala et al., 1988). Schimel et al. (1998 VEMAP validation paper) demonstrated that the model accurately represents regional patterns of soil C in the U.S.

Comparison of the simulated patterns of NPP and DEFAC show that each has its highest values in the Southeastern U.S., and values decrease as you move northwest across the Great Plains. For CENTURY VEMAP simulations, a high correlation was observed between net primary productivity (NPP) and DEFAC for the U.S. (unpublished data). Comparison of VEMAP sand content data with simulated soil C numbers shows that soil C patterns in the Great Plains correlate with sand content (higher soil C with low sand content [unpublished data]).

A detailed analysis of these simulated patterns shows that soil C tends to increase with increasing plant production, but the increase is not direct, since decomposition rates are also greater in the high productivity zones. Burke et al. (1989) showed that, while mean annual temperature and annual precipitation have a substantial impact on observed soil C (more soil C with higher precipitation and lower soil temperatures), soil texture exerts dominate control on regional patterns in soil C content.

a)

Sand Content

Sand (%)
- 7 - 15
- 15 - 20
- 20 - 25
- 25 - 30
- 30 - 35
- 35 - 40
- 40 - 45
- 45 - 50
- 50 - 55
- 55 - 60
- 60 - 65
- 65 - 70
- > 70
- No Data

500   0   500   1000Km

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b)

Net Primary Production (1981-90)

NPP (g/m²)
- 50 - 75
- 75 - 100
- 100 - 125
- 125 - 150
- 150 - 200
- 200 - 250
- 250 - 300
- 300 - 400
- 400 - 500
- 500 - 700
- > 700
- No Data

500   0   500   1000Km

Map created by
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Figure 15.4a,b. (a) The regional pattern for sand content and (b) net primary production for the U.S. Great Plains region.

The Potential of U.S. Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect

c)

Soil Carbon (1981-90)

Soil Carbon (g/m²)
1000 ~ 1500
1500 ~ 1750
1750 ~ 2000
2000 ~ 2250
2250 ~ 2500
2500 ~ 3000
3000 ~ 3500
3500 ~ 4000
4000 ~ 4500
4500 ~ 5000
5000 ~ 6000
6000 ~ 7000
7000 ~ 10000
No Data

500   0   500   1000Km

Map created by
Natural Resource Ecology Lab
Colorado State University

d)

Decomposition Factor (1981-90)

DFac (%)
0.05 - 0.1
0.1 - 0.15
0.15 - 0.2
0.2 - 0.25
0.25 - 0.3
0.3 - 0.35
0.35 - 0.4
0.4 - 0.45
0.45 - 0.5
0.5 - 0.55
0.55 - 0.6
0.6 - 0.65
0.65 - 0.7
No Data

500   0   500   1000Km

Map created by
Natural Resource Ecology Lab
Colorado State University

Figure 15.4c,d. The regional pattern for (c) simulated soil C levels and (d) decomposition index for the U.S. Great Plains region.

Impacts of Atmospheric Carbon Dioxide on Grasslands

An important consideration in evaluating grasslands' ability to sequester C must be how increased atmospheric CO_2 affects the C cycle, both through its influence on plant photosynthesis and associated plant processes and through the subsequent cycling of that C through the entire plant-soil system. This section reviews some of the latest findings on these effects of CO_2, primarily in grassland systems.

C_3 plants

CO_2 is the C substrate for photosynthesis in plants. For plants using the C_3 pathway, a group comprising approximately 95% of the world's plant species, atmospheric concentrations of CO_2 are, at present, well below levels required for photosynthetic saturation (Drake et al., 1997).

Increasing atmospheric CO_2 concentrations, which have risen from approximately 270 ppm in pre-industrial times to over 360 ppm today, are expected to increase both photosynthesis and productivity in plants. However, the degree of stimulation of photosynthesis due to increased atmospheric CO_2 depends on a complicated interaction of CO_2 with nutrients, water, and climate, particularly temperature and light (Poorter, 1993). Large differences exist among species in their capacity to respond to elevated CO_2, but an average productivity increase is 37% in plants subjected to growth at CO_2 concentrations approximately twice the present atmospheric levels of 360 ppm (Poorter, 1993).

C_4 plants

Unlike that of C_3 plants, photosynthesis in C_4 plants is nearly saturated at present atmospheric CO_2 concentration, suggesting little potential growth responses to rising CO_2 levels. Plants with the C_4 photosynthetic metabolism represent a much smaller group than C_3 plants, less than 5% of the world's species.

Grasses of this group, however, are particularly important in the world's tropical and subtropical grasslands (Ehleringer et al., 1997). Despite a photosynthetic apparatus that is nearly saturated at present ambient CO_2 concentrations, Wand and Midgley (1999) reported that production increased an average 15% in C_4 grasses when grown at doubled CO_2 concentrations, a response strikingly similar to the 23% average enhancement noted for C_3 grasses.

Some grassland studies indicate that CO_2 enrichment may result in comparable growth enhancements between C_3 and C_4 plants (Hunt et al., 1996; Morgan et al., 1998) or, on occasion, even greater growth responses in C_4 than C_3 grasses (Owensby et al., 1993). The significant growth enhancement in C_4 plants under

elevated CO_2 is due primarily to indirect effects of CO_2 on plant-water relations, although some evidence shows a direct photosynthetic enhancement in some C_4 grasses (Ghannoum et al., 1997; LeCain and Morgan, 1998).

Stomata are sensitive to CO_2 and tend to close as CO_2 concentrations rise (Drake et al., 1997), irrespective of photosynthetic class. In grasslands, this change in stomatal conductance can reduce canopy level evapotranspiration (Ham et al., 1995), retard the rate of soil water depletion (Kirkham et al., 1991; Owensby et al., 1993; Jackson et al., 1994; Morgan et al., 1998), enhance plant and soil water relations (Knapp et al., 1994; Morgan et al., 1994, 1998; Wilsey et al., 1997), and lengthen the growing season (Chiarielle and Field, 1996).

Grasslands almost always are characterized by periods of water shortage (Campbell et al., 1997), and these periods may be especially important in the large responses of C_4 grasses to CO_2. Therefore, CO_2 enrichment should increase water use efficiencies and NPP of most grasslands, and these responses will likely be expressed more readily in arid and semi-arid regions.

Acclimation

Many studies indicate that, over time, plants' physiological traits, like photosynthesis, tend to acclimate to CO_2 enrichment, leading to a lessened effect over time (Drake et al., 1997; Sage, 1994). This downward regulation is particularly common in environments in which essential nutrients for plant growth, like N, are limiting (Morgan et al., 1994; Sage. 1994). Nevertheless, even when acclimation is apparent, growth still generally is enhanced above the rate of present ambient CO_2 concentrations (Drake, 1996).

Acclimation which occurs in suboptimal soil environments, investigated mostly in regard to low available N (Canadell et al., 1996), suggests that reduced sensitivity of plants to CO_2 over time may be due to the inability of soil nutrients to keep pace with enhanced growth under elevated CO_2. However, good evidence shows that plants grown at elevated CO_2 become more efficient in use of N through changes in their metabolism (Berntson and Bazzaz, 1996; Conroy, 1992; Drake et al., 1997). Both soil and plant metabolic responses are likely to figure into plants' acclimation to CO_2 enrichment.

Above- and belowground growth

In most grasslands, the proportion of plant biomass in perennial belowground organs dominates the vegetative compartment (Tate and Ross, 1997). While CO_2 may vary considerably in how it affects partitioning of growth between above- and belowground plant organs, in most natural ecosystems, particularly when nutrients and/or water are limiting, CO_2 enrichment appears to cause increased parti-

tioning of biomass to belowground organs (Canadell et al., 1996; Morgan et al., 1994; Owensby et al., 1993; Rogers et al., 1994, 1996).

Soil water

The above discussion indicates a strong probability that the flow of NPP and C into soils will be enhanced in future CO_2-enriched grasslands. However, the storage and cycling of that C is less certain. A myriad of complex direct and indirect responses of plants and soils to elevated CO_2, and their interactions, over time, ultimately will determine the effects on grassland soil C.

In general, elevated CO_2 will affect the dynamics of C cycling through its impact on soil water and through increased rhizodeposition (Cardon, 1996). CO_2-induced enhanced efficiency of water use, due to stomatal closure, will be especially important in characteristically water-limited grasslands. Altered stomatal conductance may affect the dynamics of wetting and drying of grassland soils, resulting in periods of enhanced soil water content. Soil water content is an important driver of soil microbial activities, so these responses to elevated CO_2 will be important for soil C and N cycling (Hungate et al., 1996; Hunt et al., 1991).

Soil microbes

Root symbionts like mycorrhizae and N-fixing organisms represent an additional potential C sink to consider in CO_2 enriched environments. One might expect that these sinks would be important in helping plants adapt in future CO_2-enriched atmospheres, and evidence from several studies supports this (Canadell et al., 1996; Diaz, 1996).

Changes in mycorrhizae or N-fixation capacity may be due either to alterations in the specific infection rate or fixation activity, or simply to larger root systems (Canadell et al., 1996). Increases in NPP tend to be greater in nodulated and mycorrhizae-infected species (Diaz, 1996), suggesting a potentially greater response to elevated CO_2 than that of species with no associated symbionts. This greater response is expected, given the importance of mycorrhizae in nutrient acquisition and plant water relations (Allen, 1991) and the generation of available N through fixation.

The ability of grassland soil resources to sustain from CO_2 enrichment, in the long term, and the enhanced productivity observed in short-term studies, will depend on the complex interactions among soil biology, hydrology, and plants' responses. While researchers generally agree that elevated CO_2 will increase inputs of labile C compounds into SOM and that soil microbial biomass also will be enhanced (Berntson and Bazzaz, 1996), they also hypothesize that soil microbes

may enhance (Zak et al., 1993) or constrain (Díaz et al., 1993) NPP responses to elevated CO_2.

Changes in grassland plant communities from CO_2 enrichment are likely to affect important ecosystem driving factors like soil water availability, available N, or C inputs and to interact in ways that are difficult to predict from our present knowledge, which has come mostly through studies of single plant species over short time periods. Modeling can provide a useful tool for extrapolating beyond our experimental boundaries and for exploring the likely long-term consequences of CO_2 enrichment on grassland C cycling.

Modeling the Impacts of Environmental Change on Grassland Dynamics

This section examines modeling studies that simulate the potential impacts of environmental changes on grassland dynamics. A recent review by Parton et al. (1996) shows how grassland models have been used extensively during the last 25 years to evaluate changes in grassland dynamics resulting from altered climatic conditions, elevated atmospheric CO_2 levels, and different grassland management practices (e.g., grazing intensity, seasonality of grazing, fertilization, changes in grass species, etc). Here we focus on more recent (post-1990) studies that evaluate the effects of climatic change, increased atmospheric CO_2, and the combined effect of CO_2 and climatic change on grassland dynamics.

The ecosystem variables we consider include plant production, soil C storage, soil water status, and abiotic factors affecting decomposition (DEFAC). We primarily present results from the CENTURY model (Parton et al., 1993) but also include a review of other modeling studies. Most studies before 1995 evaluated the effect of altered climatic conditions, while studies after 1995 include the combined effects of increased atmospheric CO_2 and altered climatic conditions. We present new results from the daily time-step version of the CENTURY model (DAYCENT) (Parton et al., 1998) for sites in Colorado and Kansas, and results from a recent CENTURY transient climate change run (1990 to 2100) using the Hadley Centre for Climate Prediction and Research General Circulation Model (GCM [*http://www.meto.govt.uk/sec5/CR_div/index_climate.html*]).

CENTURY 1.0

Schimel et al. (1990) used an earlier version of the CENTURY model (Version 1.0; Parton et al., 1987) to simulate the ecosystem-level impacts of different GCM-predicted climatic changes for selected sites in the U.S. Great Plains. Simulation studies indicate that climate change scenarios result in increased plant produc-

tion and N cycling, while SOM storage decreases. Predicted increases in air temperature (2 to 4°C) have the largest impact on system response. The increase in N availability causes plant production to increase, but this increase in C inputs to the soil is insufficient to compensate for increased decomposition of SOM.

These results were improved upon in a later paper (Schimel et al., 1991) which evaluated climate change impacts across the Great Plains using the Goddard Institute for Space Studies' (GISS [Hansen et al., 1984]) GCM double CO_2 scenarios. The model's results showed that plant production increased and soil C decreased for most of the region, with the exception of Texas and Oklahoma, where plant production decreased by >10% as a result of increased drought stress.

Burke et al. (1991) did a more detailed analysis of GISS climatic change impacts for the southern Great Plains and found results similar to Schimel et al.'s (1991). They showed that the 50-year simulated decreases in soil C (100 to 300 g C/m) were small compared to the observed decreases in soil C resulting from agricultural land use changes (cultivation-induced decreases of 1000 to 2000 g C/m^2).

Jenkinson

Jenkinson's (1990) SOM model was used to evaluate the impact of increasing air temperature (3°C) on soil C levels for the natural ecosystems of the world. His simulated C losses were much greater than the values CENTURY simulated. These larger losses probably occurred because he did not include the temperature-induced increase in N availability on plant production and the resultant increase of C inputs into the soil.

CENTURY 4.0

Version 4 of the CENTURY model (Parton et al., 1993) has been tested using observed plant production and soil C and N data from tropical and temperate grasslands. It was used to assess the potential impact of different GCM projections on plant production, soil C levels, and DEFAC for all of the major grasslands in the world (Ojima et al., 1993a; Parton et al., 1995).

Projected changes in climate from the $2XCO_2$ GCM scenarios occurred as a 50-year linear increase (no change after 50 years), and the direct impacts also were considered. The major direct effects of increasing atmospheric CO_2 are decreasing water loss due to transpiration (stomatal conductance decreasing with increasing atmospheric CO_2) and increase in the C:N ratio of live plant shoots (Owensby et al., 1998; Ojima et al., 1993a). Increasing atmospheric CO_2 generally resulted in an increase in soil C storage (Table 15.1) for global grassland systems except the dry savannas. This primarily results from the CO_2-induced increase in plant pro-

Table 15.1. Simulated change in aboveground plant production, represented as an average change during a 50- to 75-year period following initiation of altered climate conditions and CO_2 levels (doubling in 50 years).

Sites	Land Cover Area (Mha)	Current Plant Production (gC/m²/yr)	% Change in Plant Production				
			2xCO_2	CCC CC	CCC 2xCO_2 and CC	GFDL CC	GFDL 2xCO_2 and CC
Extreme continental steppe	209.5	59.7	29.4	−24.8	−2.3	−27.7	−3.3
Dry continental steppe	294.3	36.4	11.0	−17.3	4.0	7.9	34.6
Humid temperate	395.8	133.8	16.9	13.4	34.1	11.6	31.5
Mediterranean	16.1	78.8	15.3	25.1	25.1	7.0	27.0
Dry savanna	510.9	54.6	15.0	22.1	22.1	−1.0	16.2
Savanna	799.0	190.9	13.0	14.1	14.1	6.7	21.4
Humid savanna	170.8	339.6	9.9	8.1	8.1	2.4	14.6

Climate change scenarios were derived from the Canadian Climate Center (CCC) and the Geophysical Fluid Dynamics Laboratory (GFDL) GCM 2 x CO_2 simulations (Ojima et al., 1993). CC = climate change. Following Table 2, Environmental Change in Grasslands (Parton et al., 1994).

duction (Table 15.2). Increased CO_2 also increases DEFAC (causes wetter soil conditions), but the increase in production is greater than the increase in DEFAC.

The Canadian Climate Centre (CCC) (Boer, McFarlane, and Lazare, 1992) and Geophysical Fluid Dynamics Laboratory (GFDL) (Manabe and Wetherald, 1990; Wetherald and Manabe, 1990) climate change scenarios result in a decrease in soil C for the majority of the grassland biomes, with large decreases (>10%) for the dry and extreme continental steppe systems. This decrease for most grasslands results in more rapid increase in DEFAC than in plant production with the climate change scenarios.

The larger decrease for the continental steppe systems results from large increases in DEFAC and substantial decreases in plant production (as great as 25%) resulting from increased drought stress (higher temperatures and reduced precipitation). Adding the CO_2 effect to the climate change runs results in decreased soil C losses and increased plant production. The combined effect of increased atmospheric CO_2 and climate change is a net loss of 0.2 Pg soil C, compared to 0.4 Pg for climate change alone.

Table 15.2. Simulated change in soil C, represented as an average change during a 50- to 75-year period following initiation of altered climate conditions and CO_2 levels (doubling in 50 years).

Sites	Land Cover Area (Mha)	Current Soil C (Pg to 20 cm)	% Change in SOM				
			$2xCO_2$	CCC CC	CCC $2xCO_2$ and CC	GFDL CC	GFDL $2xCO_2$ and CC
Extreme continental steppe	209.5	12.65	1.42	−11.64	−12.21	−9.08	−9.05
Dry continental steppe	294.3	7.72	1.03	−13.16	−12.92	−14.11	−13.10
Humid temperate	395.8	28.89	2.45	−4.39	−1.95	−4.19	−2.12
Mediterranean	16.1	0.25	2.94	−9.23	−6.44	−9.14	−6.23
Dry savanna	510.9	12.79	−0.09	−0.37	0.04	0.49	1.03
Savanna	799.0	39.46	3.44	−1.61	1.62	−1.13	2.31
Humid savanna	170.8	3.76	8.55	−4.36	3.56	−3.44	5.59

Climate change scenarios were derived from the Canadian Climate Center (CCC) and the Geophysical Fluid Dynamics Laboratory (GFDL) GCM 2 x CO_2 simulations (Ojima et al., 1993). CC = climate change, Pg = 10^6 g. Following Table 3, Environmental Change in Grasslands (Parton et al., 1994).

TEM 4.0

The Terrestrial Ecosystem Model (TEM version 4), a process-based ecosystem model (Raich et al., 1989; McGuire et al., 1992, 1993, 1996a,b; Melillo et al., 1993, 1995), is similar to the CENTURY model in many ways and includes the interactive feedback of nutrient availability and climate on plant production and the direct effects of atmospheric CO_2 on plant production. The global model results (Melillo et al., 1993) show that climate change alone causes decreased soil C levels and increased plant production. Adding the direct effect of increasing atmospheric CO_2 substantially reduces the loss of soil C and increases plant production.

VEMAP

The VEMAP model comparison (VEMAP 1995) compared biogeochemistry models to evaluate the impact of CO_2-induced GCM climate change on ecosystems' dynamics in the continental U.S., using a .5x.5 degree grid. The models were set up to use the same land use, climatic change scenarios, and current climatic conditions. The biogeochemistry model's results for the grassland regions in the Great Plains showed that soil C and plant production would increase for the central and northern Great Plains, but plant production and soil C storage tended to decrease for the southern Great Plains. This general pattern was most pronounced for the TEM and CENTURY models' results using the GFDL and the United Kingdom Meteorological Office [UKMO (Wilson and Mitchell 1987)] GCM scenarios.

DAYCENT Model Carbon Dioxide Results

The major factors that have been included in models that consider direct CO_2 effects are:

1. stomatal conductance response
2. alteration of photosynthetic rate
3. changing allocation to roots vs. shoots, and
4. modified nutrient content of live leaves.

DAYCENT (Parton et al., 1996; Kelly et al., submitted) has been used extensively *to simulate the effects of increased atmospheric* CO_2 *concentration on* system C dynamics, and it allows the user to prescribe the magnitude of each of these effects. We conducted an illustrative set of simulations for two sites representative of two climatic extremes of the U.S. Great Plains.

Konza Prairie Research Natural Area, a tall grass prairie Nature Conservancy site in central Kansas, is characteristic of subhumid grasslands lying at the eastern edge of the Great Plains grasslands. The Central Plains Experimental Range located in northeast Colorado is a short grass steppe lying at the northern boundary of Great Plains grasslands. Identical effects of CO_2 doubling were applied for each site.

Both grasslands are dominated by C_4 grasses which can respond to CO_2 (Hunt et al., 1996; Morgan et al., 1994, 1998a,b; Owensby et al., 1993b), including with limited direct photosynthetic enhancement at elevated CO_2 (Morgan et al., 1994; LeCain and Morgan, 1998). However, since growth enhancements in these grasslands under elevated CO_2 appear driven primarily by improved water relations via stomatal closure (Kirkham et al., 1991; Morgan et al., 1994, 1998a,b; Owensby et al., 1993), and also because photosynthetic acclimation of C_3 prairie grasses severely limits their photosynthetic response to elevated CO_2 (Morgan et al., 1994, and unpublished data), we assumed for modeling purposes that CO_2 enrichment reduced stomatal conductance by 30% but had no effect on photosynthesis.

We also assumed that root:shoot ratios increased 50% under elevated CO_2, given the hypothesis that CO_2 enrichment leads to increased root:shoot ratios in N-limited systems like the short grass steppe, as a plant mechanism for achieving balanced growth (Hunt et al., 1998; Morgan et al., 1994; Rogers et al., 1994, 1996). The live ratio of C:N was increased by 30% to reflect the common observation of reduced tissue N concentration of plants grown in CO_2-enriched atmospheres (Hunt et al., 1996; Morgan et al., 1994; Owensby et al., 1993a; Read et al., 1997).

For each site, we created a long-term equilibrium simulation at ambient CO_2 levels before the 50-year post-doubling test period. Models for both sites showed a slight increase in total production over the experimental 50-year period. The increase in production was almost entirely belowground, annually averaging 41% and 26% greater than an ambient CO_2 control for Konza and CPER, respectively,

over the 50-year post-doubling period (Fig. 15.5a). Concomitant with the increase in production was an increase in total SOM, averaging 6% and 2% higher than ambient CO_2 control for Konza and CPER, respectively (Fig. 15.5b).

As total SOM increased, the modeled chemical composition of the SOM also changed over time, toward a higher ratio of C:N. This change in OM quality may have long-term implications for ecosystem productivity. The lower quality implies a lower overall capacity to supply mineral N to the system.

The abiotic decomposition factor (DEFAC) was increased for both CPER (12%) and Konza (11%). The dynamics of the change in DEFAC are particularly interesting (Fig. 15.6). While the difference between ambient and doubled CO_2 simulation results for Konza remained relatively constant over time (CV = 21%), results for CPER were far more variable (CV = 71%).

The greater overall variability for CPER is due to both greater interannual variation and to a change in modeled response at 28 years after CO_2 doubling. Overall, the enhancement of DEFAC by high CO_2 decreases, and the amplitude of the interannual variation increases (including single-year decreases in DEFAC to levels lower than simulated under ambient CO_2). Thus it appears that, in years with relatively low precipitation, DEFAC may be lower under high CO_2 conditions than at ambient levels.

New VEMAP Results

The most recent VEMAP model comparisons use the transient GCM results from the HEDLEY CENTRE and CCC models. CENTURY's simulations of NPP, soil C, and DEFAC after 50 years of climatic change (2050 values minus 1980 levels) using the HEDLEY CENTRE GCM show soil C storage tending to increase in the southern and central Great Plains and decrease in the northern Great Plains (Fig. 15.7a,b,c).

The decrease in soil C in the northern Great Plains primarily results from the increase in DEFAC resulting from increased soil temperatures. In the central Great Plains, soil C content increased because of increased plant production combined with a small increase in DEFAC. In the southern Great Plains, soil C increased slightly as a result of a big decrease in DEFAC (drier conditions reduced DEFAC) and a decrease in plant production. The HEDLEY CENTRE GCM results indicate that precipitation was increasing by 25% for most of the Great Plains and this increase resulted in higher NPP for most of the region. These results show the differential impact of climatic changes on plant production and DEFAC and the combined effect of both factors on soil C levels.

A summary of the observed data and model results shows that the major factors which affect grassland soil C levels are soil texture, decomposition rates, and C input to the soil. Some of the initial modeling work assessing climate change
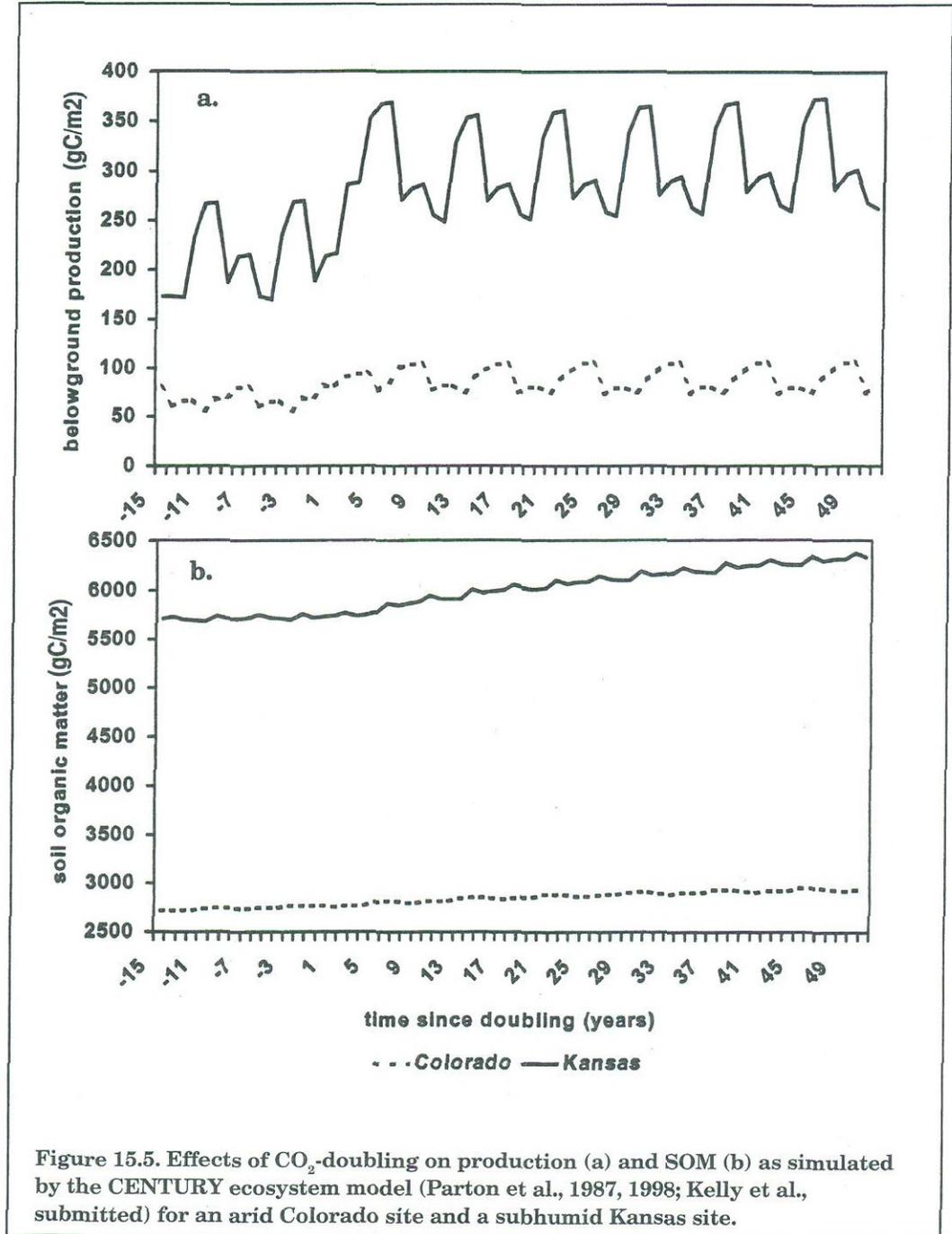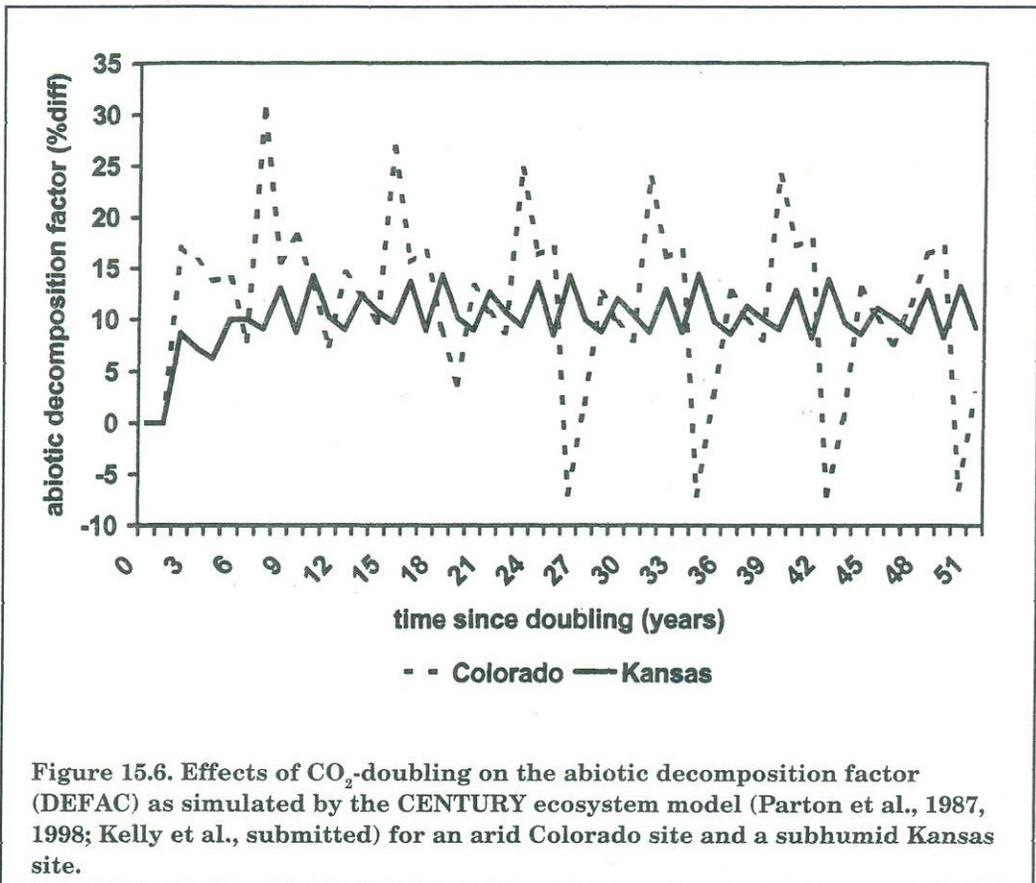
Figure 15.5. Effects of CO_2-doubling on production (a) and SOM (b) as simulated by the CENTURY ecosystem model (Parton et al., 1987, 1998; Kelly et al., submitted) for an arid Colorado site and a subhumid Kansas site.
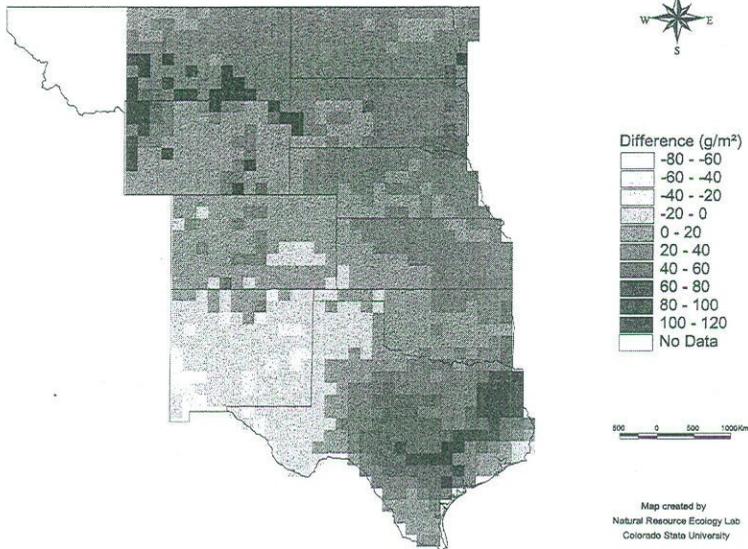
suggested that grassland soil C levels could decrease as much as 5 to 10% with 2X CO_2 climate change scenarios, with most of the decrease due to increases (2 to 4°C) in the soil temperatures. The more recent model's results, which include the direct impact of increased atmospheric CO_2 on plant growth, suggest the earlier estimates of C loss were exaggerated and that, for the U.S. Great Plains, soil C levels may increase slightly, although soil C may decrease in the North.

Increasing atmospheric CO_2 concentration enhances grassland plant production and allocation of C to the root system. These factors are primarily responsible for the predicted increases in soil C. Another possible factor in new GCM scenarios is the predicted increase in precipitation associated with the increase in air temperature, which may result in increased plant production and inputs of C to the soil.

Figure 15.6. Effects of CO_2-doubling on the abiotic decomposition factor (DEFAC) as simulated by the CENTURY ecosystem model (Parton et al., 1987, 1998; Kelly et al., submitted) for an arid Colorado site and a subhumid Kansas site.

a) NPP Difference (2050 - 1980)

Difference (g/m²)
-80 - -60
-60 - -40
-40 - -20
-20 - 0
0 - 20
20 - 40
40 - 60
60 - 80
80 - 100
100 - 120
No Data

500   0   500   1000Km

Map created by
Natural Resource Ecology Lab
Colorado State University

b) DeFac Difference (2050 - 1980)

Difference
-0.06 - -0.04
-0.04 - -0.02
-0.02 - 0
0 - 0.02
0.02 - 0.04
0.04 - 0.06
0.06 - 0.08
> 0.08
No Data

500   0   500   1000Km

Map created by
Natural Resource Ecology Lab
Colorado State University
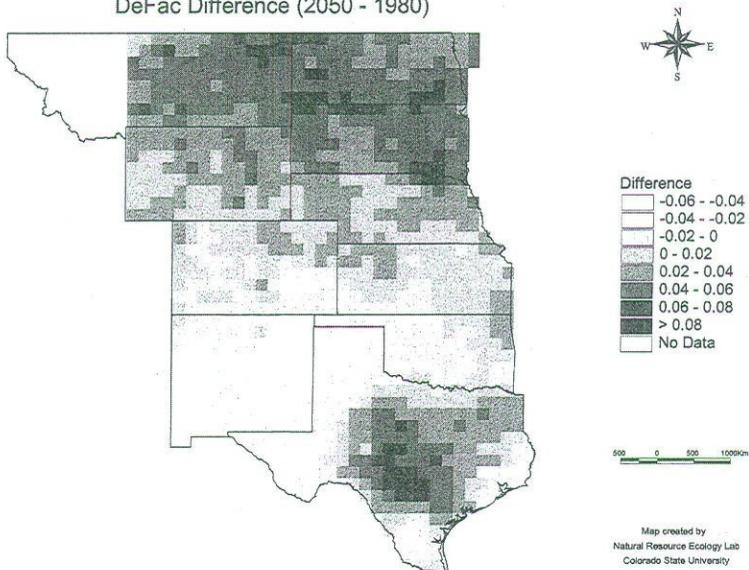
Figure 15.7a,b. Simulated changes in (a) net primary production and (b) decomposition index (DEFAC) under the Hedley Centre transient GCM scenario for 50 years of climate change.

Figure 15.7c. Simulated changes in (c) soil carbon levels under the Hedley Centre transient GCM scenario for 50 years of climate change.
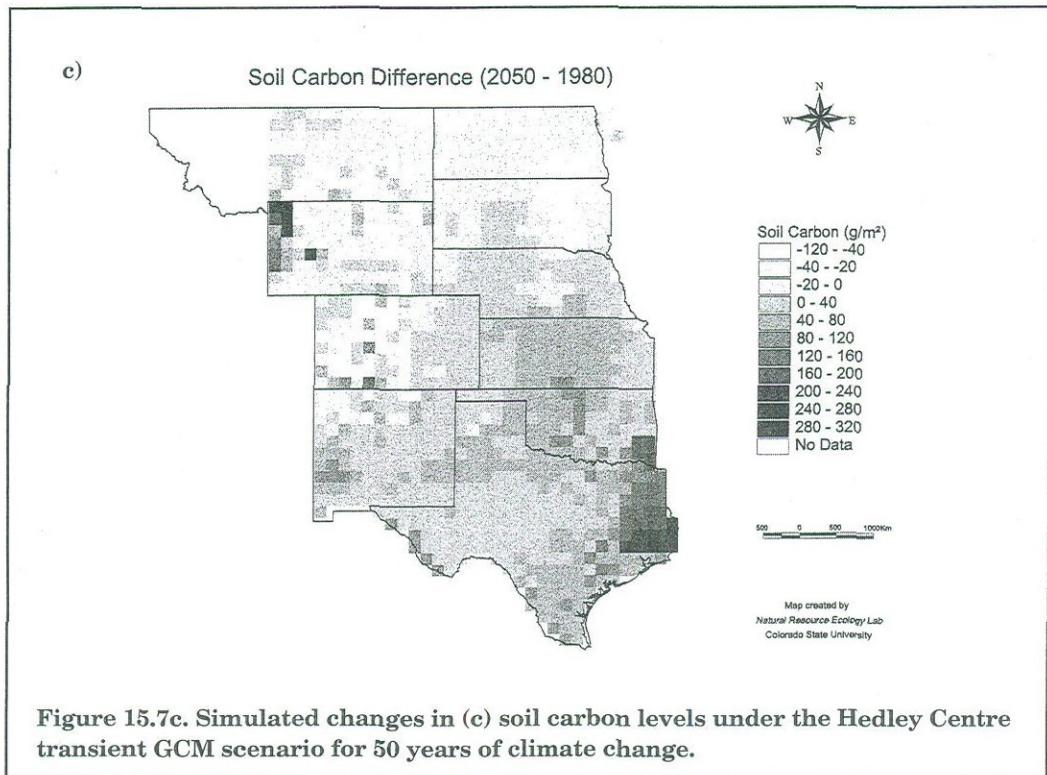
Conclusion

Current field research and modeling studies suggest that key research efforts should evaluate the effects of the interactions between potential climatic changes and increasing atmospheric CO_2 concentration. Increasing atmospheric CO_2 for grasslands generally results in increased total plant production, higher root:shoot ratios, reduction of transpiration water loss and N content of the live shoots, and increased soil water contents during the growing season. Available soil N generally reduces the response of plants to increased atmospheric CO_2 levels, but whether long-term exposure to higher CO_2 levels will increase N inputs to soil through N fixation remains unclear.

We are just becoming able to evaluate how increased atmospheric CO_2 levels affect plant growth. Current modeling studies have shown both grasslands' sensitivity to the combined impacts of climatic change and increased atmospheric CO_2 concentration, and our lack of knowledge about that sensitivity.

We also know too little about plant communities' potentially complex responses to global change. These responses may include competitive interactions regarding water, nutrients, and light, as well as functional differences in re-

sponses to CO_2, temperature, and water. Functional differences are likely to dominate how these plant communities respond.

Various modeling systems describe what happens to plants' resposes which plant production drives. This simplistic treatment, although vital in the development of modeling studies, ignores changes in species' composition. Also emerging is evidence of a potentially significant response of C_4 grasses to CO_2, including their photosynthetic acclimation (Morgan et al., in review). Tissue quality may decline, resulting in a declining N supply in the system. This implies a potentially important role of legumes in future CO_2-enriched environments. It also underscores our need to understand these processes formally, so that we can describe how plant systems will respond to CO_2 enrichment.

Acknowledgments

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The Potential
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