
5 Carbon Budgets of Temperate Grasslands and the Effects of Global Change

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5.1 INTRODUCTION

Temperate grasslands account for a large fraction of the vegetation of the earth (Coupland 1992). Large expanses of temperate grasslands and derivative croplands are located at mid latitudes in Asia, North, and South America (Singh *et al.* 1983) (Figure 5.1). In North America, the grasslands include the central grassland region, which ranges along a precipitation gradient from the semiarid shortgrass steppe to the subhumid tallgrass prairie, and a temperature gradient from subtropical to boreal. In South America, temperate grasslands encompass large units, such as the pampa grasslands on the mesic end, and the patagonian steppe on the xeric end of the gradient (Soriano *et al.* 1991). Large expanses of temperate grasslands also occur in Asia, stretching from the Ukraine to the Peoples' Republic of China. There are also smaller units in Europe, Australia, and Southern Africa.

Temperate grasslands are located in one of the regions where the impact of global climate change is predicted to be large (Mitchell *et al.* 1990). Most global circulation models (GCMs) predict for a double CO₂ scenario an increase in temperature between 4 and 6 °C for the regions of the world where temperate grasslands are now located. The climate change impact is predicted to be larger only in the region where boreal forests and arctic tundra are now located. The interaction between the large area encompassed and the expected magnitude of the predicted climate change suggests that changes in the carbon budgets of temperate grasslands may have an important impact upon the earth's atmosphere.

Climate change is only one of the components of a set of global-scale en-





Figure 5.1 Map of the temperate grasslands of the world, adapted from Coupland (1992)

vironmental changes affecting ecosystems. Global change includes changes in the composition of the atmosphere such as the observed increases in the concentration of CO₂, methane, and CFCs. These changes in atmospheric composition may have direct impacts upon vegetation, with or without climate change. Global change also includes changes in land use which are driven by economic, demographic, and social forces.

A major feature of global change is that climate, atmospheric composition and land use are not independent factors but they are strongly interactive. For example, changes in land use, such as from grassland to cropland, may be important contributors to changes in atmospheric composition (Burke *et al.* 1991). This change, in turn, may modify the climate which could then speed up or slow down the shift in land use. This, again, would likely affect the emissions of greenhouse gases.

The objective of this chapter is to evaluate the carbon budgets of present temperate grasslands and to assess the possible effects that global change may have. To accomplish our objective we will first discuss how carbon is distributed among different compartments and how the size of these carbon pools is associated with major environmental variables. This is a static view of the carbon budget. Second, we will assess the import inputs and outputs and their controls. Finally, we will evaluate how the three factors driving global change may affect the carbon budget of temperate grasslands.

5.2 A STATIC VIEW OF THE CARBON BUDGET

A simple scheme of the partitioning of carbon among compartments indicates the relative size of carbon pools in temperate grasslands, the major inputs and outputs and their controls (Figure 5.2). Carbon is fixed from the atmosphere by means of photosynthesis which, at the ecosystem level, is called gross primary production (GPP). We represented in the diagram just net primary production (NPP), because it is the variable for which data are available. Carbon is translocated from above- to belowground parts of the plants and in the opposite direction depending upon seasonality and grazing. Herbivory is the flow from plant parts to herbivores. This flow is particularly large in grasslands. Unlike forests, where loss of biomass to herbivores is usually less than 10%, grasslands are frequently characterized by herbivory rates of 25–50% or more of aboveground NPP (McNaughton 1976, 1985; Lauenroth and Milchunas 1992; Milchunas and Lauenroth 1993) and perhaps 25% of the belowground productivity (Coleman 1976; Scott *et al.* 1979; Ingham and Detling 1984; Lauenroth and Milchunas 1992).

Above- and belowground plant parts are transferred into the soil organic matter pool as they become senescent. There is also a flow from herbivores to soil organic matter. We followed the CENTURY model scheme (Parton *et al.* 1987)

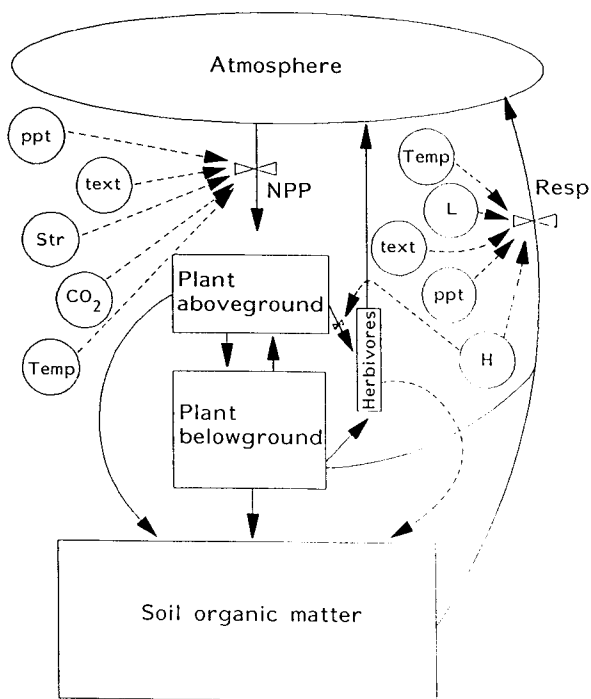


Figure 5.2 A scheme of the C budget of temperate grasslands. State variables are plant aboveground, plant belowground, herbivores, and soil organic matter. The major C flows represented in this diagram are net primary production (NPP), and belowground respiration (Resp). Control variables are precipitation (ppt), soil texture (text), community structure (Str), CO_2 concentration in the atmosphere (CO_2), air temperature (Temp), land use (L), and human intervention (H)

by including soil microorganisms in the soil organic matter compartment. Soil organic matter can be divided further into different compartments according to their turnover rates. We chose not to divide this compartment because of the scarcity of data with that level of detail, and the difficulty of physical characterization of such kinetic pools. Finally, major carbon losses in grasslands occur as a result of respiration from plants, animals and microorganisms (decomposition).

Some patterns are evident across temperate grasslands. Most of the carbon in grasslands is located belowground in the soil organic matter compartment and in the belowground plant compartment (Atjay *et al.* 1979; French *et al.* 1979; Parton *et al.* 1987). The location of the major carbon store belowground provides temperate grasslands with many of their unique characteristics.

During the International Biological Program in the late 1960s and early 1970s, a large data base was collected across temperate grasslands. For North American grasslands, the size of the aboveground plant compartment is correlated with

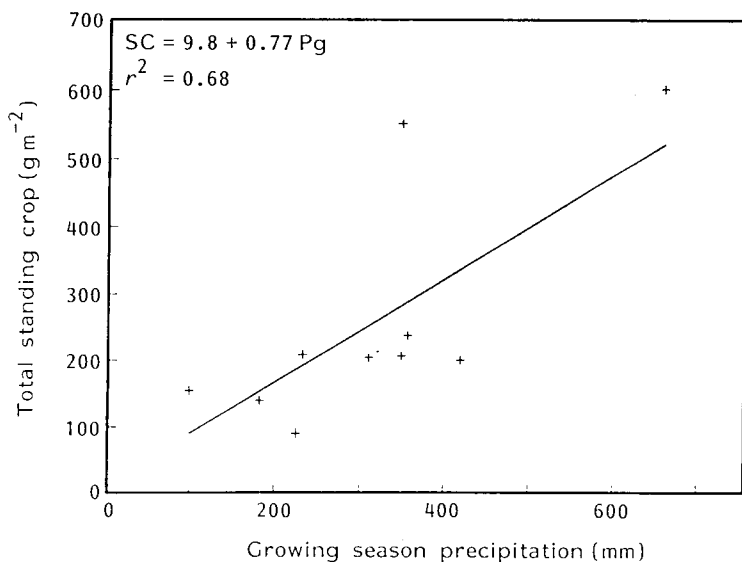


Figure 5.3 Relationship between aboveground total standing crop (SC) and growing season precipitation for North American grasslands (after Sims *et al.* 1978)

growing season precipitation (total standing crop = $9.78 + 0.77P$, $R^2 = 0.68$) (Figure 5.3) (Sims *et al.* 1978).

Plant belowground biomass is most closely related to annual air temperature. We collated data from North and South America encompassing a range of precipitation from 150 to 1000 mm yr⁻¹ and a range of mean annual temperature from 3 to 15 °C. We found that temperature accounted for a large fraction of the variability in root biomass among sites (Figure 5.4) (root biomass = $1996.7 - 94.7t$, $R^2 = 0.74$) (Sims *et al.* 1978; Doll and Deregibus 1986; Soriano *et al.* 1987).

Burke *et al.* (1989) analyzed 500 grassland soil profiles and 300 cropland soil profiles distributed across the central grassland region of North America in an attempt to identify large-scale controls of soil organic carbon. They found that the amount of carbon in the soil was mainly explained by temperature, land use, and precipitation (Figure 5.5a). Temperature was the variable which had the strongest effect upon total soil carbon. Soil organic carbon decreased with increasing mean annual temperature. Moreover, the relationship between carbon in the soil and temperature has a quadratic term, and therefore the accumulation of carbon decreases sharply as a consequence of a small increase in temperature. The authors use this as evidence that decomposition is a major control over soil carbon. Precipitation also explained a significant fraction of the variance in soil carbon, with soil organic carbon increasing with precipitation up to 800 mm

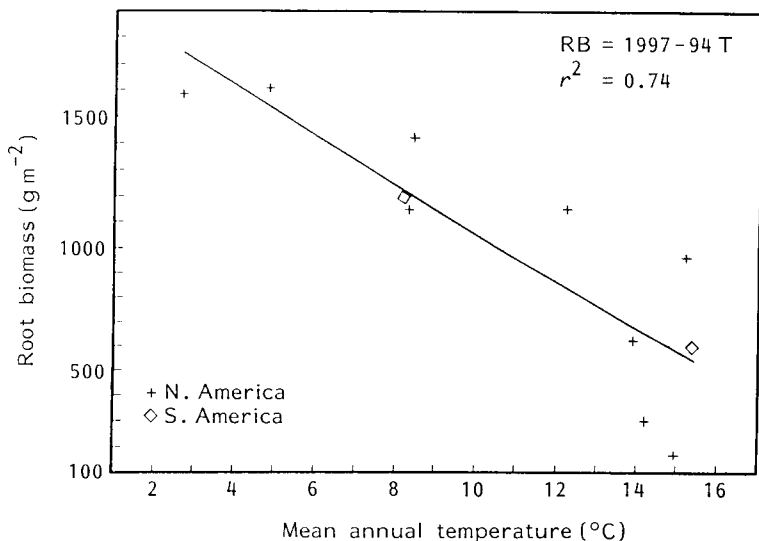


Figure 5.4 Relationship between root biomass (RB) and mean annual temperature for sites from North and South America

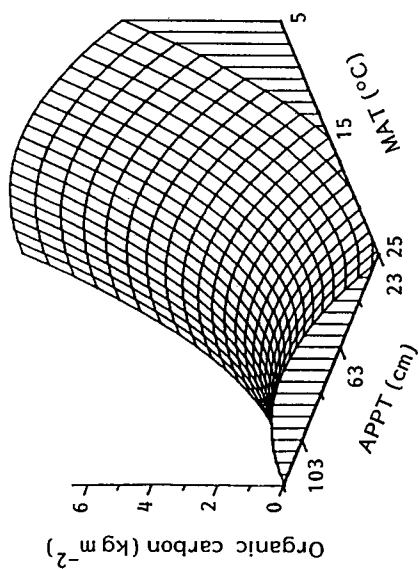
annual precipitation, then leveling off. This is likely due to the influence of precipitation in increasing the inputs into soil organic matter, NPP.

The authors fit similar regression models to grassland and cropland soils, and they assumed that the difference between the two models was the effect of tillage. In this way they were able to estimate the effect of cultivation upon carbon loss. In general, absolute organic carbon loss increased with total soil organic carbon content (Figure 5.5b).

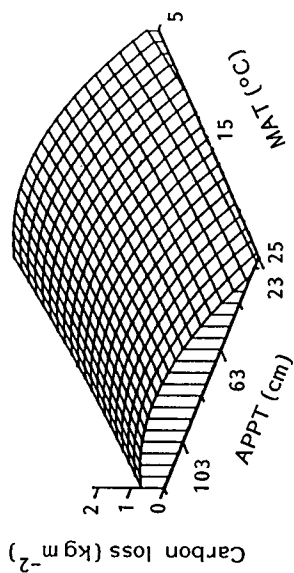
The biomass of herbivores that an ecosystem can sustain depends directly upon aboveground net primary production (ANPP) (McNaughton *et al.* 1989). The relationship between herbivore carrying capacity and primary production is exponential. It indicates that, for example, arid grasslands support less animal biomass per unity primary production than mesic grasslands. This relationship encompasses a range of ecosystems which goes beyond that of grasslands, from deserts to forests (McNaughton *et al.* 1989).

5.3 A DYNAMIC VIEW OF THE CARBON BUDGET: INPUT AND OUTPUT FLOWS

To this point we have analyzed a snapshot of the carbon budget of temperate grasslands. We will next analyze the carbon inputs and outputs. This is an attempt to build our understanding of the carbon dynamics to provide a basis for suggesting responses to potential global change.



(a)



(b)

Figure 5.5 Predicted response surface of soil organic carbon (a) and carbon loss as a result of tillage (b) to variation in mean annual temperature (MAT) and annual precipitation (APPT) for loamy soils (after Burke *et al.* 1989)

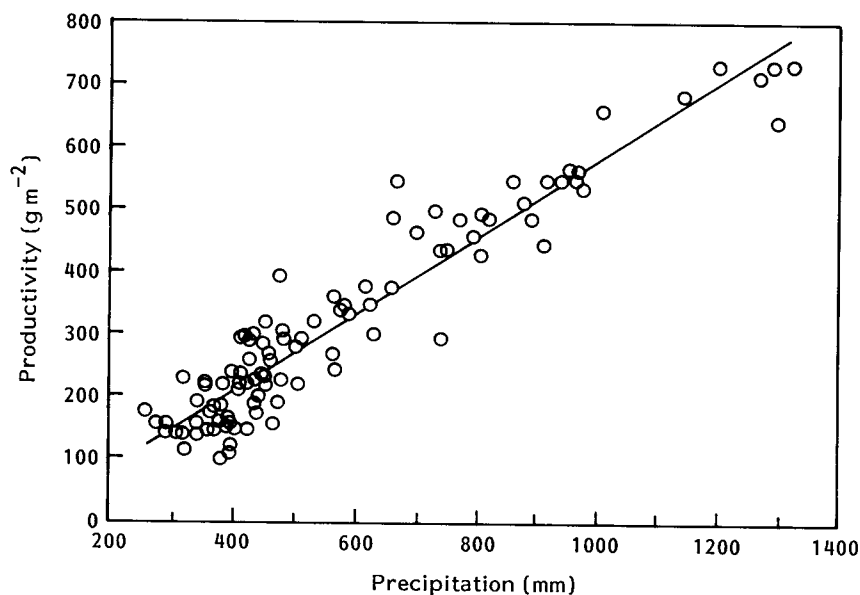


Figure 5.6 Relationship between average aboveground annual NPP and average annual precipitation for 100 ecological regions within the central grassland region of the USA (after Sala *et al.* 1988b)

5.3.1 Net primary production

There is a clear relationship between ANPP and annual precipitation. A linear model has proved to describe this relationship very well. For example, in the central grassland region of North America, 90% of the variance in production of 100 major ecological units was accounted for by annual precipitation (Sala *et al.* 1988b) (Figure 5.6). When the same model was independently fit to data from South America and Africa, there were very small differences in the parameters of the model (Figure 5.7). This gives us some confidence that this is likely to be a universal model for temperate grasslands. Others have found similar results over a wider range of semiarid and arid ecosystems (Walter 1979; Le Houérou 1984).

At a more detailed scale, soil information needs to be included to explain a similar fraction of the variability in ANPP. In central North America, water-holding capacity interacted with annual precipitation to explain ANPP (Figure 5.8). The statistical model was developed using data from a broad range of sites. The data provided an empirical test of the inverse texture hypothesis (Noy Meir 1973). This hypothesis states that production in dry regions should be greater on coarse-textured (low water-holding capacity) soils than on fine-textured (high water-holding capacity) soils. In contrast, in humid regions, production should be greater on fine-textured soils than on coarse-textured soils. Precipitation and

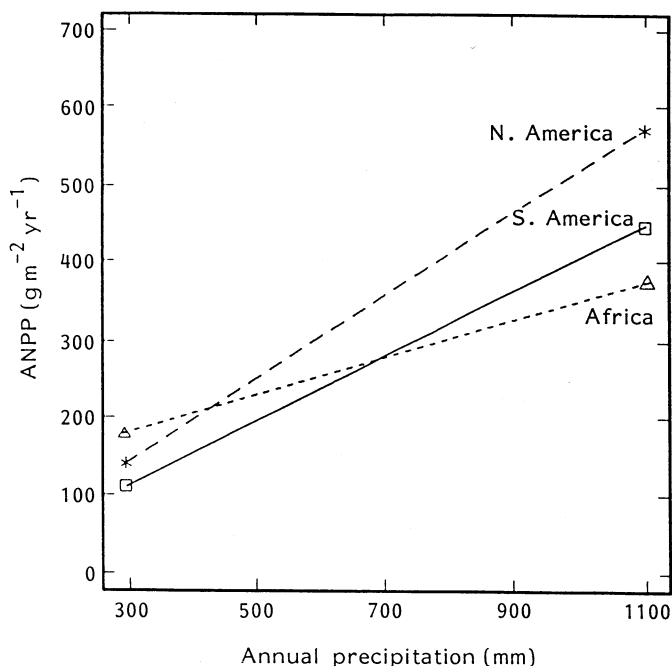


Figure 5.7 Relationship between average aboveground annual NPP and average annual precipitation for the central grassland region of the USA (Figure 5.6), South America and Africa

soil water-holding capacity interact through changes in soil water dynamics. In dry regions, important losses of soil water occur via bare soil evaporation. Bare soil evaporation is lower in sandy soils than loamy soils because water penetrates deeper. In humid regions, substantial water losses can occur via deep percolation, which is relatively low in soils with high water-holding capacity. Therefore, in arid regions, sandy soils with low water-holding capacity have more water available for plant growth than soils with higher water-holding capacity. The opposite pattern occurs in humid regions.

So far we have explored the relationship between primary production and environmental factors across sites. Based upon the assumption that space and time are interchangeable, we might speculate that the effect upon primary production of changes in precipitation resulting from climate change will be depicted by these same models. However, when we analyzed a 52-yr production time series for the shortgrass steppe in north-central Colorado, USA, we found that the relationship between production and precipitation across time was different from the relationship between production and precipitation across space (Figure 5.9) (Lauenroth and Sala 1992). The temporal model had a slope

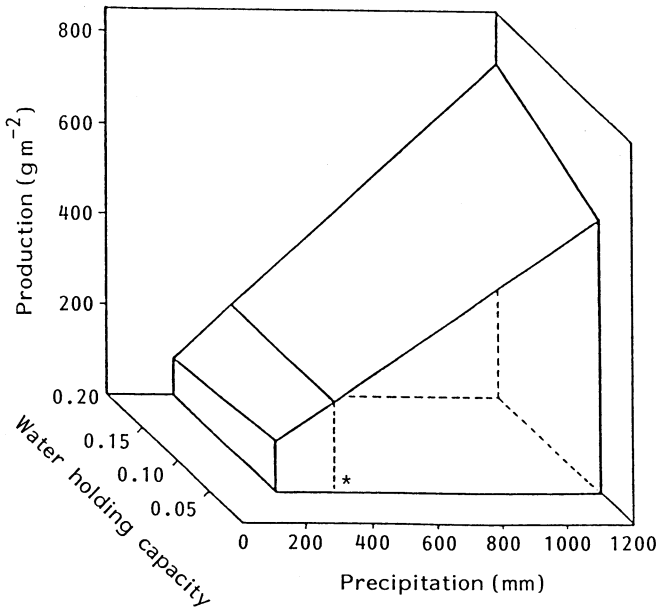


Figure 5.8 Relationship between aboveground NPP, soil water holding capacity, and mean annual precipitation for 9498 sites across the central grassland region of the USA (after Sala *et al.* 1988b)

much smaller than the spatial model. The spatial model compared the average production to average precipitation for different sites whereas the temporal model compared the production and precipitation for different years but always for the same site.

Structural vegetation constraints to primary production and time lags in responding to favorable conditions suggest an explanation for the difference in slope between the two models. In the spatial model each data point represents a site with a different vegetation structure; that is, a particular species composition, plant density, plant cover, and root pattern. By contrast, in the temporal model, it is the same community that responds to changes in water availability. Changes in structure as a result of increases or decreases in water availability involve different processes ranging from leaf expansion, tillering, germination and establishment of new individuals up to migration of new species or ecotypes. These processes have characteristic time constants, some of them exceeding the growing season. We suggest that availability of roots and leaves to capture energy, water, and nutrients can constrain the ecosystem response to increases in water availability.

The difference between spatial and temporal models indicates the difficulty of exchanging space for time. Predictions of the effects of climate change on ANPP, based upon regional models, may contain important sources of previously

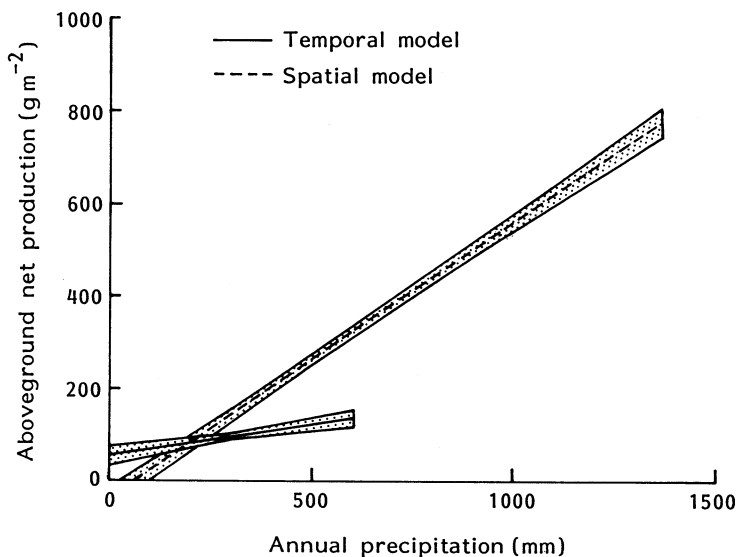


Figure 5.9 Relationship between aboveground NPP and annual precipitation for a regional model (Sala *et al.* 1988b) for the central grassland region of the USA and for the long-term model for the Central Plains Experimental Range in North central Colorado, U.S. (Lauenroth and Sala 1992). Shaded areas represent 95% confidence intervals

unrecognized error. Spatial models depict equilibrium, or at least slowly changing, conditions. The use of such models under scenarios of rapidly changing climatic conditions will result in large errors in estimates of ANPP.

As noted earlier, the regional and long-term analysis pointed out that precipitation was the major environmental correlate of ANPP. Temperature did not account for a significant fraction of the variability in primary production in either the spatial (Sala *et al.* 1988b) or the temporal (Lauenroth and Sala 1992) analysis. There are a number of possible explanations for this finding. There are photosynthetic responses to temperature at the plant level, which apparently are dampened at the ecosystem level. Precipitation and temperature tend to be correlated temporally. Wet days, months, or years tend to be cooler than their dry counterparts. Spatially, the situation is much more complex, and correlations can be positive or negative. The small variability among years in temperature and in potential evapotranspiration relative to the variability in precipitation also affect the predictive power of temperature in the temporal model. Precipitation was almost twice as variable (c.v. = 31%) as potential evapotranspiration (c.v. = 18%) (Sala *et al.* 1992). On the contrary, this explanation does not appear to be valid for the regional model which encompassed a broad range of temperature from the US–Mexico border to the US–Canada border, and in which temperature also was not significant. This analysis suggests that water

availability is the most frequent limiting factor of primary production in temperate grasslands. Its availability in time and space is the single most important factor determining primary production in temperate grasslands.

The discussion to this point has dealt exclusively with aboveground production. The portion of total production that is accounted for by the belowground organs of grassland plants (BNPP) is substantial, equaling or exceeding aboveground production (Coleman 1976; Fogel 1985). A problem encountered by attempts to characterize estimates of BNPP for grasslands or any other ecosystem type is that estimates are few and subject to a large amount of uncertainty (Singh *et al.* 1984; Sala *et al.* 1988a; Milchunas and Lauenroth 1992). While estimates of BNPP for temperate grasslands range from two to three times ANPP (Sims and Singh 1978), estimates based upon the turnover of roots labeled with ^{14}C suggest a relationship between BNPP and ANPP of approximately 1:1 (Dahlman 1968; Milchunas and Lauenroth 1992).

5.3.2 Decomposition

Decomposition rates in temperate grasslands are strongly controlled by temperature, soil texture, and litter quality (Jenkinson 1977; Sorenson 1981; Schimel *et al.* 1985). Decomposition rates rapidly increase with temperature (Jenny 1980). Meentemeyer (1984) constructed maps of decomposition rates (k) for North America, and reported that decomposition rate decreased from the warm and wet southeastern corner of the continent to the cool and dry north-central part of Canada.

The control of decomposition by temperature suggests an explanation for the relationship between root biomass and temperature (Figure 5.4). Most studies of root biomass do not distinguish between dead and live roots. Consequently, dead roots will persist in the soil longer in cool sites where decomposition is slower than in warm sites. We hypothesize that the high root biomass of cool sites is the result of a high proportion of dead roots.

Fine-textured soils generally have slow decomposition rates (Sorenson 1981). Therefore, landscape and regional locations which are net deposition sites for fine soil materials tend to accumulate soil organic matter rapidly. This is attributed to the high surface tension of soils with high clay contents, and subsequent physical and chemical protection of organic matter from decomposers. This important control by soil texture causes strong small- and large-scale (spatial) variations in soil carbon associated with parent material and topography in temperate grasslands (Schimel *et al.* 1985; Yonker *et al.* 1988). Plant litter quality is also an important control over decomposition rates and nutrient availability in grasslands (Wedin and Tilman 1990). Meentemeyer (1978) found that lignin content accounted for part of the variability in decomposition. Although decomposition rates increase with increasing water availability (Meentemeyer 1978), they are much more responsive to changes in temperature, as demonstrated by regional patterns.

5.3.3 Differential controls of production and decomposition

In synthesis, we found that temperature, on balance, seems to influence decomposition more than NPP, and precipitation, on balance, seems to influence production more than decomposition. Regional assessments of soil organic matter suggest that soil organic carbon accumulation is controlled more by output (decomposition) than by input (primary production).

We suggest that the differential response of production and decomposition to temperature and precipitation may be related to the adaptations of decomposing organisms for low-moisture environments. A number of investigators have found that decomposition in desert and semi-desert environments is not limited by moisture availability (Santos *et al.* 1984; Whitford *et al.* 1986, 1988). These authors suggest two explanations for the continued decomposer activity at low water availability, with little or no response to increases in moisture. First, microflora and fauna associated with decomposition in dry areas are exceptionally well-adapted to low moisture conditions. Such adaptations include migration, mucilaginous compounds that protect microorganisms from desiccation, and transport of water across fungal hyphae. The second explanation for high decomposer activity in low-moisture environments is related to the upward transport and condensation of water vapor at the soil surface (Santos *et al.* 1984). Finally, it has been suggested that in environments dominated by pulse availability of moisture, the fluctuations in microclimate may be much more important controls over decomposition than average values of moisture (Whitford *et al.* 1981; Sala and Lauenroth 1982; Schimel and Parton 1986).

5.4 THE POSSIBLE EFFECTS OF GLOBAL CHANGE UPON THE CARBON BUDGET

5.4.1 Land use change

The greatest changes in the carbon budgets of the temperate grasslands as a result of management are related mainly to cultivation. Transformation of grasslands to croplands can result in a net carbon flux to the atmosphere. Historically, all cropland management practices resulted in carbon losses and depletion of soil organic matter (SOM). Tillage increases decomposition by breaking soil aggregates and allowing previously protected material to be exposed to decomposers, and by placing surface residues in contact with the soil (Tieszen *et al.* 1982; Elliott 1986; Doran and Werner 1990). In addition, the shift from perennial to annual plant species, and the removal of a portion of the aboveground biomass during harvest may decrease inputs into SOM. Losses of SOM are nearly exponential in the first 10–20 years of cultivation (Haas *et al.* 1957). A combination of modelling and historical data analysis suggested (Burke *et al.* 1991) that the emissions that occurred as a result of land use change in the central grasslands of North America

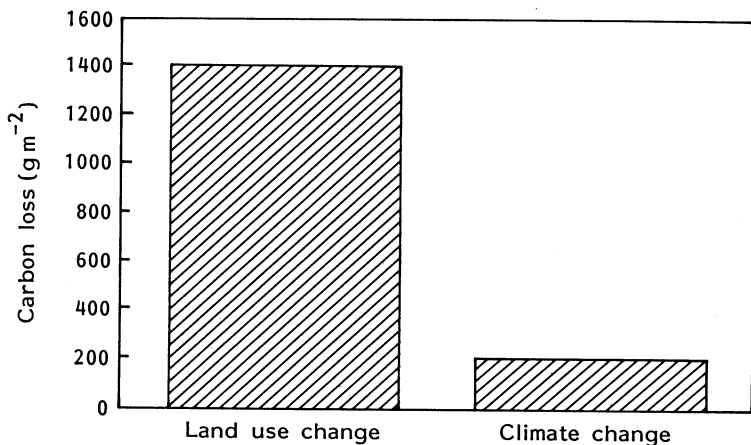


Figure 5.10 The effect of tillage and climate change on carbon losses from the central grassland region of the USA (after Burke *et al.* 1991)

were much larger than those which may occur as a result of the increase in temperature as predicted by the GISS global circulation model (Figure 5.10). Direct effects of CO₂ and changes in precipitation were not considered. Using the CENTURY ecosystem model, Burke *et al.* (1991) estimated that after 50 years of climate change, there will be a net loss of carbon ranging from 50 to 350 g m⁻². In contrast, an historical analysis of field data indicated a carbon loss between 800 and 2000 g m⁻² as a result of cultivation since settlement of the plains. The authors indicated that, on a regional basis, past effects of cultivation have been much more important than the expected climate change as a control upon carbon emissions. The simulated climate effect resulted in emissions of 1.4 Tg C yr⁻¹ for the entire region, which is smaller than the 18 Tg C yr⁻¹ associated with the estimated large-scale effects of historical cultivation.

Concern over losses of SOM and net carbon release to the atmosphere has resulted in new research on cultivation practices over the past several decades. This new research has had conservation of SOM as one of its objectives and has resulted in crop production methods that either minimize tillage, or eliminate it altogether. Preliminary results suggest that these new methods have the potential to conserve or, in some cases, increase soil carbon storage. These new methods decrease or eliminate several of the negative effects of cultivation on ecosystem carbon balance (Wood *et al.* 1990).

A recent trend in many developed countries of converting cropland back to the original ecosystem will create a new and potentially large category of recovering or successional ecosystems. In the temperate grassland regions in the northern hemisphere, such conversions will have important effects on regional carbon

budgets. The long-term significance of the conversion of cropland to grassland will depend upon regional, national, and worldwide surpluses of agricultural products.

5.4.2 Atmospheric composition change

The response of temperate grasslands to an increase in the atmospheric concentration of CO_2 is predicted to have a strong interaction with the availability of nutrients and water (Mooney *et al.* 1991). There has been evidence of enhanced photosynthesis in C_3 plants with elevated atmospheric CO_2 . Elevated CO_2 has two effects: upon the photosynthesis mechanism itself and upon stomatal conductance. An increase in external CO_2 concentration results in an increase in internal CO_2 concentration of C_3 plants, which leads to a higher rate of sucrose formation. The duration of the enhancement of photosynthesis as a result of increased CO_2 concentrations is variable among species. Some species show long-term increases in photosynthesis while others show a short-term increase and then a return to levels associated with ambient CO_2 concentrations. Carbon dioxide enhancement also reduces stomatal conductance and consequently transpiration water loss. Since transpiration is reduced and photosynthesis is enhanced or at least maintained, an increase in CO_2 concentration results in an increase in the amount of carbon fixed per unit of water transpired. The improvement of water use efficiency is the physiological explanation for why the largest response to CO_2 enhancement may occur in water-limited systems. Most of the predictions for the differential response of ecosystems to CO_2 are based upon our current understanding of the response of individual plants to CO_2 , water, and nutrient availability. However, ecosystem level experiments to identify these response patterns are absolutely necessary since in several cases plant level patterns are not translated into ecosystem level patterns (Snaydon 1991).

In nutrient-poor environments, the shortage of nutrients may mask the response in growth to CO_2 enhancement. Some experiments have shown a decrease in the nitrogen content of plants growing under elevated CO_2 conditions. On the map of relative response to CO_2 , temperate grasslands are located in the central region, which suggests that we may expect a moderate response to CO_2 enhancement. Currently few data are available from field experiments on temperate grasslands with elevated levels of CO_2 . Those that have been conducted report fewer responses than had been predicted from extrapolations from laboratory experiments (Knapp *et al.* in prep).

5.4.3 Climate change

There is agreement among climate change predictions from GCMs that an increase in greenhouse gases will result in a temperature increase (Mitchell *et al.*

1990). Discrepancies are associated with the timing, the magnitude, and the spatial distribution of the increase. Our analysis suggests that an increase in temperature will likely result in a reduction of the SOM pool in temperate grasslands as a result of an increase in decomposition rates. Two studies have conducted simulations of the effects of such climate change on North American temperate grasslands (Schimel *et al.* 1991; Burke *et al.* 1991). The studies used the same simulation model, but different climate change scenarios. Simulated decomposition rates increased in response to rising temperatures, and carbon emissions to the atmosphere thus increased.

The effect of an increase in temperature upon primary production is likely to be small. A larger impact may occur via increased potential evapotranspiration and a relative reduction of available water. In the simulations of Schimel *et al.* (1991), increased decomposition resulted in increased nitrogen mineralization which stimulated NPP in the more mesic grasslands. Such interactions are difficult to assess without experimental evidence.

Predictions regarding change in precipitation and soil moisture vary among regions and GCMs. Most models predict a decrease in precipitation for the temperate northern hemisphere grasslands and an increase for the southern hemisphere temperate grasslands. Increases in precipitation, depending upon magnitude, will have a high probability of increasing primary production and carbon input to soils. This may or may not compensate the increase in carbon losses resulting from the relatively more certain temperature increase. For those regions in which a reduction in precipitation is predicted, a decrease in inputs will occur simultaneously with an increase in the outputs. It will clearly drive these grasslands into a negative carbon balance.

The relative importance of the three factors driving global change may vary with time. We suggest that the maximum change in land use in temperate grasslands has already occurred. Most of the areas with some crop-production potential have been transformed into croplands. Although the increase in greenhouse gases has been documented, their importance may continue to increase for the next several decades. The effect of climate change will likely be observed last because of the time lags built in the climate system.

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