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# Temperate Grasslands

José M Paruelo

Universidad de Buenos Aires, Buenos Aires, Argentina

*Temperate grasslands have been the biome most affected by one of the main dimensions of the global change: land cover modification. The replacement of grasslands by agricultural fields have local, regional, and global consequences, including loss of soil fertility, soil erosion, reduction of biological diversity, hydrological changes, climate alteration and modification of atmospheric composition. Field and laboratory experiments are beginning to show a positive response, both in total biomass production and water use efficiency for the dominant species of temperate grasslands to the increase of atmospheric carbon dioxide (CO<sub>2</sub>). Simulation analyses indicated that climate change by itself increased net primary production in most of the grassland regions of the world and reduced soil carbon stocks everywhere. The combined effect of climate change and elevated CO<sub>2</sub> increased net primary production in all the sites studied and reduced carbon losses by half.*

Temperate grasslands are an important biome in Eurasia (Palearctic realm,  $7.5 \times 10^6$  km<sup>2</sup>), North America (Nearctic realm,  $2.7 \times 10^6$  km<sup>2</sup>) and southern South America (Neotropical realm,  $1.1 \times 10^6$  km<sup>2</sup>), also occupying small areas in Africa, Australia and New Zealand. At least three physiognomic types are considered grasslands in temperate regions: meadows, prairies, and steppes. Species of the Poaceae family are dominant or co-dominant in these physiognomic types. Grasslands occur in between forest and deserts. The boundaries among these biomes are not clear, and transitional areas develop among them, scattered trees or shrubs are then a common feature in grassland areas. The relative importance of the woody components in grassland is often the consequence of the disturbance regime.

Grasslands played an important role in human history because the centers of origin of the most important cultivated plants (wheat, barley, peas, etc.) and livestock (goats, sheep, cattle) are located in them. Humans dramatically modified grassland areas and the sub-humid portion of this biome has been almost completely transformed by agriculture.

## GENERAL CHARACTERISTICS OF TEMPERATE GRASSLANDS

### Climate and Soils

Grasslands occur over a broad range of temperatures. Mean annual temperature (MAT) of grassland areas range between  $-3^\circ\text{C}$  in the Mongolian and Russian steppes and  $20^\circ\text{C}$

in the tallgrass prairies of Texas (USA) and the desert grasslands of Northern Mexico. A large proportion of grasslands have a continental climate, showing much larger seasonal temperature differences than areas under maritime influence. The range of mean annual precipitation (MAP) where grasslands can be found varies from 150–1500 mm.

Grasslands are not evenly distributed in the climatic space defined by the ranges of MAT and MAP presented above. Grasses are not dominant where temperatures are high and precipitation low (close to the  $20^\circ\text{C}$  and 150 mm corner). At this extreme, grasslands become replaced by shrublands or deserts. At the coldest and wettest extreme, forests are the dominant biome. The distribution of grasslands in the climatic space is related to the magnitude of the water deficit. Grasslands show a ratio of mean annual precipitation and potential evapotranspiration (PET) lower than 1. The MAP/PET ratio is close to 0.3 for dry steppes and to 0.6 for sub-humid prairies.

Grassland soils are among the most productive under agricultural use. High productivity derives mainly from the high content of organic matter. Mollisols is the dominant soil order in this biome.

### Biotic Characteristics and their Environmental Controls

An important structural characteristic of temperate grassland is that most of the carbon is stored below ground, in soil organic matter and plant roots. This large accumulation of carbon results from low decomposition rates relative to net primary production. The total amount of soil organic carbon decreases with MAT and increases with MAP (Burke *et al.*, 1989). Fine textured soils retain more organic matter than coarse textured soils (Burke *et al.*, 1989).

Despite the dominance of just one family, Poaceae, grasslands show marked differences in species composition. Over continental scales, a structural comparison of grasslands based on species composition is precluded by the differences in floras among the different biogeographical realms. Such comparison is possible, though, at the plant functional level (PFT). Five main PFTs can be identified in grassland areas: C<sub>3</sub> grasses, C<sub>4</sub> grasses, shrubs, forbs and succulents. The first three account for most of the biomass and show a clear pattern across environmental gradients. The relative abundance of C<sub>4</sub> grasses increases with MAP, MAT, and the proportion of precipitation falling in summer. C<sub>3</sub> grasses are more abundant as MAT decreases and in areas with a high proportion of precipitation falling in winter. The relative abundance of shrubs increases in dry areas with most of the precipitation falling in winter.

Above-ground net primary production (ANPP) is a key attribute of grassland ecosystems and the main entrance of energy to the ecosystem. Characterization of the climatic controls of ANPP is essential to understand the impact

of global changes on this biome. A positive, linear relationship between ANPP and MAP has been documented for many grasslands around the world (McNaughton *et al.*, 1993). The slope of the relationship between ANPP and MAP in grassland ecosystems ranges between 0.48 and  $0.64 \text{ g C m}^{-2} \text{ mm}^{-1}$ . Epstein *et al.*, (1997) showed a negative relationship between ANPP and MAT when MAP was held constant. Soil texture, through its effect on soil water holding capacity, also showed a significant relationship with ANPP (Sala *et al.*, 1988; Epstein *et al.*, 1997). Below-ground net primary production is equivalent or slightly greater than ANPP. Annual net primary production (below and above-ground) may vary then, from less than  $100 \text{ g m}^{-2}$  in a semi-arid shortgrass steppe to almost  $1000 \text{ g m}^{-2}$  in a tallgrass prairie (Paruelo *et al.*, 1999). Compared to other biomes, grasslands' above-ground biomass is low. Shrublands may have 10 times more biomass than grasslands and evergreen forest up to 100 times more (Chapin, 1993). Differences in ANPP among biomes, however, are not so extreme as in the case of biomass (Chapin, 1993). As a consequence, the ratio ANPP/biomass is higher in grasslands than in any other biome.

McNaughton *et al.* (1993) showed that biomass and consumption of wild herbivores were positively and exponentially related to ANPP. The exponential form of these relationships suggests that the proportion of the ANPP consumed by herbivores increased with ANPP. The efficiency of energy transfer between trophic levels (animal production/net primary production) is higher in grasslands than in forests.

The disturbance regime affects carbon gains in grasslands. Fire reduces ANPP in the driest portion of a precipitation gradient (Oesterheld *et al.*, 1999). In subhumid grasslands fire generally increases ANPP, except in dry years (Knapp *et al.*, 1998). In these grasslands, fire removes large amounts of above-ground dead material, increasing light and soil nutrient availability (Knapp and Seastedt, 1986). In dry years this effect is less important than the reduction in evapotranspiration promoted by the detritus layer (Knapp *et al.*, 1998). Grazing may increase or reduce ANPP depending on the evolutionary history of grazing, MAP, and levels of consumption (Milchunas and Lauenroth, 1993). Over a broad range of grasslands, Oesterheld *et al.* (1999) found that, on average, grazing by large vertebrates slightly reduced ANPP.

Grassland biogeochemistry is largely controlled by precipitation, temperature and soil texture. Decomposition rates are more affected than ANPP by temperature. Given the same amount of precipitation, the consequence of the effect of temperature on decomposition is a higher accumulation of organic carbon in cold than in warm areas. Species composition, through litter quality, has a significant influence on decomposition rates and nutrient immobilization.

## THE IMPACT OF GLOBAL CHANGE ON TEMPERATE GRASSLANDS

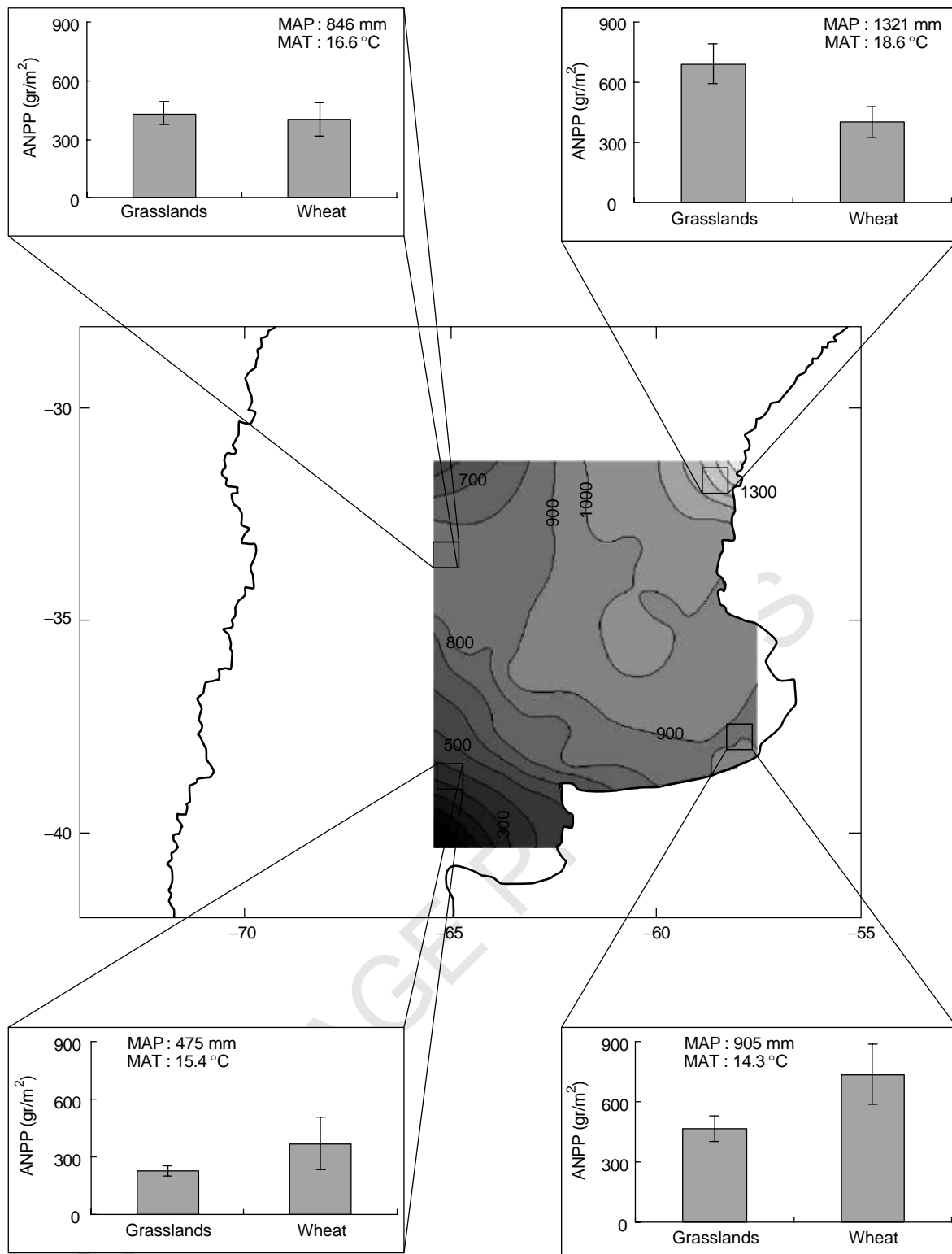
### Land Use

Land cover changes associated with agriculture and grazing by domestic herbivores have had an enormous impact on the structure and functioning of grasslands. Agricultural practices have reduced soil carbon stocks by 35% in the US Central Grasslands during the last 50 years (Burke *et al.*, 1989). Based on carbon isotopic analyses, Wilson (1978) estimated that pioneer agriculture (1860–1890) in temperate areas of Australia, New Zealand, North and South America contributed one and a half times the amount of carbon dioxide ( $\text{CO}_2$ ) produced by all the fossil fuels burnt before 1950. This reduction of soil carbon stocks results from an increase in decomposition rates due to plowing and a reduction of carbon inputs to the soil due to the low below-ground biomass of annual crops and to exports of above-ground biomass.

Land use pattern has a critical influence on mesoscale atmospheric processes, and hence on local climate (Pielke *et al.*, 1997). Mosier *et al.* (1991) reported significant changes in trace gas fluxes associated with cultivation of a semi-arid grassland: agriculture increases the release of methane ( $\text{CH}_4$ ) and nitrous oxide ( $\text{N}_2\text{O}$ ), two greenhouse gases. These additions of  $\text{CO}_2$  and other trace gases to the atmosphere may represent significant feedbacks to global climate change.

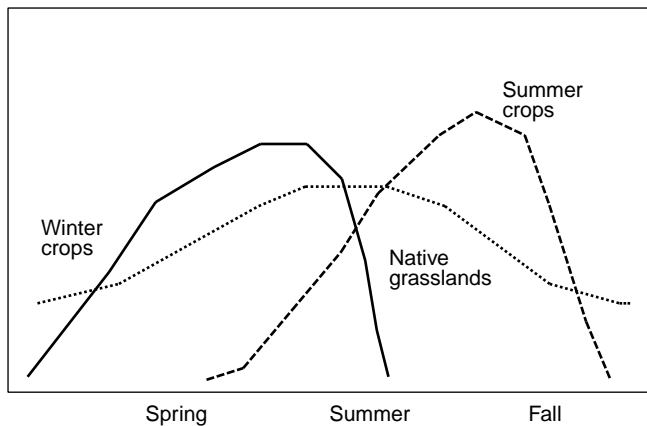
It is not clear to what extent agricultural practices modify total carbon gains. In the Pampas of Argentina, agriculture may increase or decrease above-ground net primary production relative to the native grasslands depending the environmental conditions (Figure 1). The difference in primary production between grasslands and wheat fields was higher in the wettest portion of the Pampas. In warm areas, grasslands were more productive than wheat fields. The opposite happened in the coolest part of the region.

Total carbon gains should be lower for agricultural fields than for native grasslands because below-ground production is one order of magnitude lower for crops than for grasslands. Land use may modify not only total carbon gains but also the seasonal dynamics of leaf area index and intercepted radiation. Figure 2 show the idealized course of the fraction of radiation intercepted by the canopy for different land covers. Curves were drawn from data provided by spectral indices derived from meteorological satellites (Advanced Very High Resolution Radiometer – National Oceanographic and Atmospheric Agency (NOAA/AVHRR)). Land use modifies both the intra annual range of the fraction of intercepted radiation and the timing of maximum interception. These phenological changes modify the partitioning between latent and sensible heat and, consequently, they may affect the dynamics of the boundary layer of the atmosphere.



**Figure 1** ANPP for wheat and grasslands sites located in the climatic extremes of the Pampa grasslands of Argentina. For wheat fields ANPP was estimated from grain yields (Argentine agricultural census) and harvest index. Wheat ANPPs are the average of 10 years. Small bars showed the temporal standard deviation. Grassland ANPPs are the average of estimates derived from four different models for the relationship ANPP–MAP (Sala *et al.*, 1988; McNaughton *et al.*, 1993; Paruelo *et al.*, 1999 (two models)). Small bars corresponded to the standard deviation of the estimates derived from the different models. Isopleths correspond to mean annual precipitation.

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**Figure 2** Seasonal dynamics of the fraction of radiation intercepted by the canopy from three land cover categories in the Argentine Pampas. Intercepted radiation is an estimator of ANPP. Curves were derived from normalized difference vegetation index data from NOAA/AVHRR satellites.

Land use has increased the rate of species extinction not only by replacing natural ecosystems, but also by changing the disturbance regime. Leach and Givnish (1996) showed that 8–60% of the original plant species of remnant prairie sites were lost after 50 years due to landscape fragmentation or fire suppression. Changes in species diversity and composition have direct effects on the functioning of grasslands, affecting their productivity and stability.

The introduction of domestic herbivores promotes structural and functional changes in grasslands. A common effect of overgrazing in grasslands is shrub encroachment (Archer, 1994). The increase in shrub cover in grass steppes of Patagonia due to overgrazing (León and Aguiar, 1985) altered water dynamics, increased albedo, reduced primary production and herbivore biomass (Aguiar *et al.*, 1996). Bryant *et al.* (1990) and Nasrallah *et al.* (1994) reported changes in surface temperature associated with overgrazing in southwestern USA.

### Atmospheric Composition

Early experiments and photosynthetic theory suggested a differential response of  $C_3$  and  $C_4$  grasses to changes in atmospheric concentration of  $CO_2$ .  $C_3$  and  $C_4$  plants differ in their metabolic pathways of  $CO_2$  fixation. In  $C_3$  plants the first product of the photosynthetic  $CO_2$  fixation is a phosphorylated three-carbon compound. In  $C_4$  plants the first product is a four-carbon acid.  $C_3$  and  $C_4$  plants differ also in their leaf anatomy. Two different groups of photosynthetic cells are found in  $C_4$  plants: mesophyll cells and bundle sheath cells. The latest are surrounding the leaf vascular bundles and separate them from the mesophyll cells.  $C_4$  grasses present a  $CO_2$  concentration mechanism in the bundle sheath cells that increases the effective concentration of  $CO_2$  at the carboxylation site. Such a  $CO_2$

pumping mechanism would saturate photosynthesis at current  $CO_2$  levels. Therefore, it has been suggested that this plant functional group would not show a significant growth response to increases in atmospheric  $CO_2$  concentrations. However, a meta-analysis by Wand *et al.* (1999) indicates that the response of wild  $C_3$  and  $C_4$  grasses to elevated  $CO_2$  concentrations was surprisingly similar.

At the leaf level, an increase in atmospheric  $CO_2$  reduces stomatal conductance and increases net photosynthesis. A consequence of these changes is an increase in water use efficiency (WUE). Specific leaf area and nitrogen concentration are, in general, lower under elevated  $CO_2$  concentrations. At the individual level these changes result in an increase in both above and below-ground biomass and in the number of tillers (Wand *et al.*, 1999). The mentioned analysis showed an overall increase in total biomass of 44% in  $C_3$  species and of 33% in  $C_4$  species.

Studies using open top chambers allow one to explore changes at the population, community, and ecosystem level. These changes result not only from the effect of elevated  $CO_2$  on plant production but also from major changes in soil water dynamics associated with changes in water use efficiency. Jackson *et al.* (1994) working in Mediterranean grasslands in California showed increases in density, seed production, and survival of the dominant grass *Avena barbata* under elevated  $CO_2$ . Changes in phenology associated with a delayed senescence have been reported in  $C_4$  tallgrasses (Owensby *et al.*, 1997). In the tallgrass prairie of eastern Kansas (USA) an eight year long open top chamber experiment provided no evidence for a replacement of the dominant  $C_4$  grasses by  $C_3$  grasses or forbs under elevated  $CO_2$  concentrations (Owensby *et al.*, 1993). In these grasslands the balance between  $C_3$  and  $C_4$  grasses seems to be more sensitive to the main disturbances (fire and grazing) than to  $CO_2$  concentration. Elevated  $CO_2$  decreased dominance in sub-humid temperate grasslands (Potvin and Vasseur, 1997). Potvin and Vasseur (1997) showed a higher effect of elevated  $CO_2$  on early successional species growth, which prevented the dominance of late successional ones.

Combining field data and simulation models, Jackson *et al.* (1998) showed that the direct effect of  $CO_2$  on water use efficiency and total biomass production on Mediterranean grasslands affected water dynamics at the ecosystem level. Under elevated  $CO_2$ , plant transpiration was lower. Low transpiration at the beginning of the growing season increased soil water content and deep percolation. Studies based both on field experiments and on model simulations suggest that the observed increase in WUE at the ecosystem level would compensate for increases in potential evapotranspiration associated with climatic changes driven by greenhouse gases. Biogeochemistry models (BIOME-BGC, Century and Terrestrial Ecosystem Model) simulated net primary production responses to doubled atmospheric  $CO_2$  for grasslands that range from 1–20% increase.

## Climate

Changes in climate are difficult to isolate from changes in CO<sub>2</sub> concentrations. Climate modifications not linked to the increase of greenhouse gases may occur, however, as a result of land use changes (Nasrallah *et al.*, 1994; Pielke *et al.*, 1997). General circulation models simulate changes in temperature in temperate grasslands ranging between +2.3 and +6.2 for a doubled CO<sub>2</sub> scenario (Houghton *et al.*, 1992). Changes in mean annual precipitation may range from -2.6% up to 17.5%, depending on the GCM and type of grassland considered. For the Central Grasslands of USA, an increase of 1 ° Celsius in mean annual temperature represents an increase in potential evapotranspiration of 50 mm.

Two main approaches have been used to explore the effect of climate on grasslands: warming experiments and simulation exercises using climate change scenarios. Experimentally heated plots in montane meadows showed significant differences in the timing and magnitude of net carbon fluxes (Saleska *et al.*, 1999). The reduction of primary production resulted from a combined effect of a reduction in soil moisture and a shift in plant community composition. Alward *et al.* (1999) showed that the observed increase in nocturnal minimum temperatures in a semi-arid steppe was correlated with a reduction in the net primary production of the dominant grass species, and with increased abundance and production of exotic species and C<sub>3</sub> forbs.

Model simulations indicated that climate change, by itself, increased net primary production in most of the grassland regions of the world and reduced soil carbon stocks everywhere. The combined effect of climate change and elevated CO<sub>2</sub> increased net primary production in all the sites studied and reduced carbon losses by half (Parton *et al.*, 1995).

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