

## Grassland ecosystems as a biological force in dusty dry regions

Gregory J. Retallack, Department of Geological Sciences, University of Oregon, Eugene, OR 97403-1272, [gregr@darkwing.uoregon.edu](mailto:gregr@darkwing.uoregon.edu)

### Introduction and methods

Two features of paleosols allow a new perspective on the climatic range of grasslands in the geological past: their subsurface horizons of calcareous nodules and their distinctive surface horizons. Soils supporting sod-forming grasses have abundant small (2-5 mm) rounded clods, dark with organic matter intimately mixed with clay. In paleosols, these mollic epipedons are recognized from common small (2-5 mm) rounded soil peds and abundant fine (1-2 mm diameter) root traces. Mollic epipedons of soils are dark brown to black (Munsell hues 7.5YR-10YR and values 2-5) with organic matter, but this dark color is seldom preserved in paleosols because of burial decomposition of organic matter. Mollic epipedons also are clayey enough to take the impression of fingerprints when moistened, even when partly lithified as paleosols. Mollic epipedons are also rich in nutrients, indicated for paleosols by carbonate, plagioclase, or other easily weathered minerals (Retallack, 1997).

Grassland soils of dry regions develop subsurface horizons of calcareous nodules. The depth within the profile to this calcic horizon shows a close relationship to mean annual precipitation (Retallack, 1994). Calcic horizons of soils vary in degree of development from thin wisps of carbonate to thick cemented layers, but those of the nodular stage have been found to be the most reliable indicators of former rainfall. Other problems for interpretation of former rainfall from depth to the calcic horizon in paleosols include erosion of the upper portion of paleosols before burial and changing levels of atmospheric CO<sub>2</sub> in the past. Severe erosion would not leave an horizon thick enough to qualify as mollic nor a soil with a deep calcic horizon. Such paleosols are not significant to this study seeking the first geological appearance of the deepest of these horizons in mollic paleosols. Oligocene and later changes in atmospheric CO<sub>2</sub> were not sufficiently significant (Retallack, 1997) to have altered the relationship between rainfall and carbonate depth (Retallack, 1994). A more serious problem is compaction of paleosols after burial. A standard equation was used to calculate burial compaction of each paleosol from geological estimates of overburden (Retallack, 1997, 1998).

### Results

Surveys have now been completed on three continents of mollic epipedons and calcic horizons in Neogene paleosols, and these are summarized here (Fig. 1). A remarkable observation arising from consideration of these 261 paleosols is that dark, crumb-structured horizons first appear during the early to middle Miocene in paleosols with calcic horizons at depths of 40 cm or less, but crumb-structured horizons above calcic horizons as deep as 1 m do not appear until the late Miocene. This observation can be interpreted as evidence for expansion of grasslands at about 6-7 Ma into wetter climatic regions, so that the ecotone between grassland and woodland was shifted from the 400 mm isohyet to near the 750 mm isohyet encompassing the current area of tall grasslands (Fig. 2). Furthermore, paleosols provide evidence of sod-forming short grasslands in dry regions (less than 400 mm mean annual precipitation well back into the Miocene. Desert rangelands lacking sod-forming

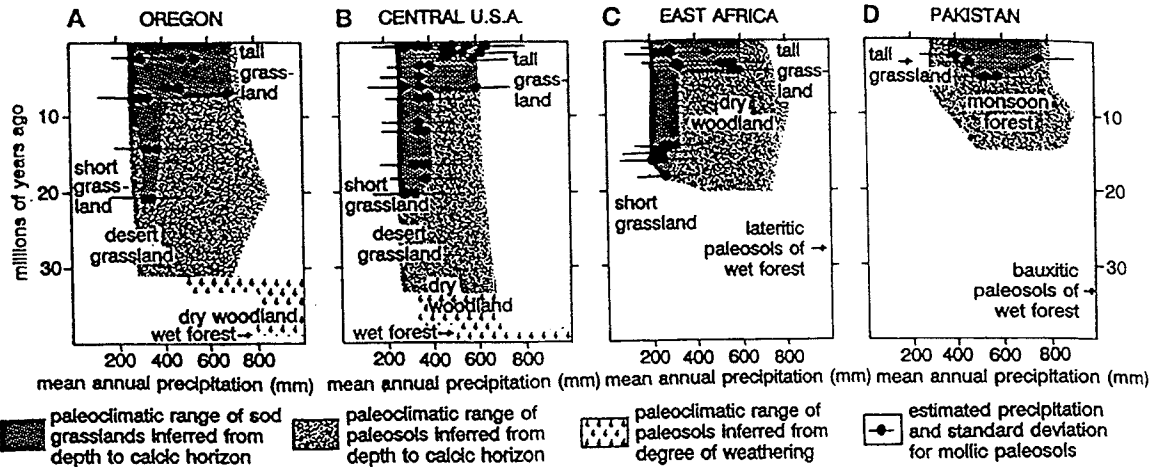


Figure 1. Climatic expansion of sod grasslands through Miocene time in (A) Oregon (Retallack, 1997), (B) North American Great Plains (Retallack, 1997), (C) East Africa (Retallack, 1998) and (D) Pakistan (Retallack, 1998) inferred from mollic epipedons and depth to calcic horizon of paleosols.

grasses may be as ancient as Oligocene in South Dakota, and Eocene in Argentina (Retallack, 1997). Sod-forming grasslands thus replaced pre-existing dry woodlands during Miocene time, dramatically expanding their climatic and geographic range.

Post-Eocene expansion of grasslands can also be inferred from paleontological data. The past 40 million years was a time of evolutionary radiations for a variety of grassland creatures, including grasses, daisies, legumes, dung beetles, bees, colubrid snakes, passerine birds, murid rodents, and ungulate mammals (Retallack, 1997; Cerling *et al.*, 1997). The coarse gritty fodder of grasses provided significant selection pressure for the evolution of high-crowned (hypsodont) teeth in ungulates. Open grassy terrain selected for cursorial limb structure in ungulates. Large, hypsodont, hard-hooved ungulates coevolved with a variety of defenses among grasses: abrasive coatings of silica phytoliths, sod-forming underground systems of roots and rhizomes, telescoped terminal meristems, and intercalary meristems. The Neogene can be viewed as a time of protracted evolutionary arms race between grasses and grazers (Bakker, 1983), during which grassland ecosystems displaced pre-existing dry woodlands of subhumid regions.

## Role for Grasslands in Neogene Global Change

Grasslands may not merely have been products of Neogene climatic cooling. The high organic matter content and fine ped structure of sod-grassland soils are a substantial carbon sink. Territorial expansion of grasslands could have been a significant perturbation to the global carbon cycle. Mollisols are now a less important carbon sink than soils of peat swamps (Histosols) and oligotrophic woodlands (Spodosols). But both Histosols and Spodosols date back at least to the Carboniferous ice age, and these distinctive ecosystems have played important roles in the global carbon cycle since then (Retallack, 1997). Desert soils (Aridisols) like many grassland soils (Mollisols) also sequester carbon in calcareous nodules, but storage of carbonate ( $\text{CO}_3^{2-}$ ) does not greatly alter the balance of  $\text{CO}_2$  and  $\text{O}_2$  in the atmosphere, and Aridisols have a geological record extending well back into the Precambrian. Grassland ecosystems were the new players of the Neogene.

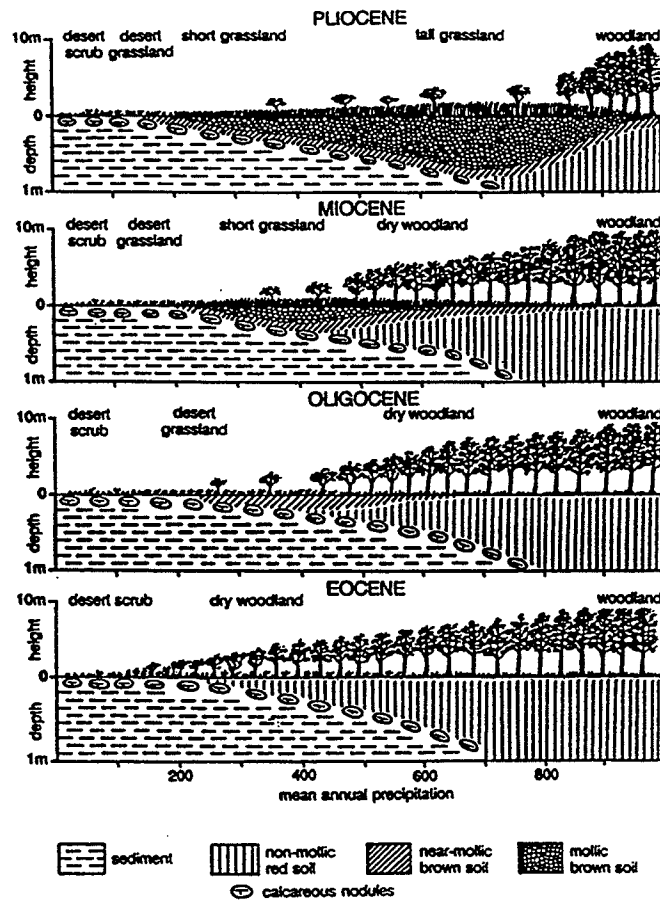


Figure 2. A scenario for the stepwise evolution of grasslands and their soils in the Great Plains of North America (from Retallack, 1997)..

In assessing carbon storage in grassland ecosystems it is well to remember that biomass and productivity increase steadily with mean annual rainfall (Retallack, 1994, 1998). The carbon perturbation created by newly-evolved sod grasslands is in comparison with the dry woodlands that they replaced (Figs 1,2), so appropriate comparisons in the present context are between grassland and woodland vegetation of similar climatic belts. Grasslands have only about a third of the biomass of dry woodlands, but biomass is dwarfed by an order of magnitude more carbon in grassland soils. Grassland and woodland soils may have comparable amounts of organic carbon in the surface 15 cm. Beyond that depth organic carbon values drop off dramatically in woodland soils, but remain high in grassland soils to a meter or more. The fine structure and fertility of grassland soils is in large part due to this large carbon reservoir.

Not all this carbon is permanently stored, because much soil carbon is actively recycled. Total soil carbon may approach near-maximal values on time scales of only  $10^3$  years in well drained eutrophic soils due to carbon recycling within the soil (Chadwick *et al.*, 1994). Grasslands are most greedy carbon hoarders early in ecological succession after disturbance. In addition, grassland paleosols, unlike grassland soils, do not commonly have high amounts of organic carbon (Retallack, 1997). Thus grassland soils cannot be considered a permanent store for organic carbon, but rather a

transient storage on time scales of  $10^3$ - $10^5$  years. The provisional nature of carbon storage in grasslands could have injected an element of instability into Neogene climates.

There is however a permanent consumer of carbon in soils: the export of bicarbonate ions following hydrolytic weathering of soil minerals by carbonic acid. The role of hydrolysis as a carbon sink declines over hundreds of thousands of years as weatherable minerals are depleted from the soil, but it continues long after storage of organic carbon in biomass and soil reaches equilibrium. On coastal terraces in humid northern California some 2-8% of carbon sequestered by grassland soils was consumed by hydrolysis, with the remainder stored as organic carbon. Comparison of these Californian soils with others in arid Wyoming and humid New York, shows that an increasing fraction of carbon is consumed by weathering in humid rather than drier climates, in young rather than old soils, and in soils rich in easily weatherable minerals rather than nutrient-poor soils (Chadwick *et al.*, 1994). Thus grassland Mollisols consume more carbon than woodland Alfisols of subhumid to humid climates, because they are more nutrient-rich and younger.

Another reason for greater carbon consumption by grassland soils is the order of magnitude larger internal surface area and moisture retention of deep mollic epipedons compared with the coarse structure of woodland soils (Retallack, 1997, 1998). Simple geometric constraints of face-centered cubic arrangement give an internal surface area of  $2221 \text{ m}^2 \cdot \text{m}^{-3}$  for balls 3 mm in diameter, compared with  $150 \text{ m}^2 \cdot \text{m}^{-3}$  for cubes 4 cm across. Increased weathering due to the net of fine roots and high internal surface area of Mollisols under grasslands may have been an important new carbon sink.

A new explanation for climatic cooling is now apparent. By this view, grasslands and their soils were a "mollic machine": a newly evolved carbon sink that withdrew carbon dioxide of the earlier Tertiary greenhouse atmosphere. This model does not rely on physical forcing of climate by mountain uplift or changes in ocean currents. Rather it postulates global cooling by biological means of thresholds in the territorial expansion of grasslands and accelerating coevolution of grasses, grazers and other grassland creatures.

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