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Cenozoic Expansion of Grasslands and Climatic Cooling

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ABSTRACT

Mountains, ocean currents, forests, and swamps have played an important role in regulating global climate for hundreds of millions of years, but the truly novel event of the Cenozoic was the evolution and expansion of grasslands, with their uniquely coevolved grasses and grazers. Neogene expansion of the climatic and geographic range of grasslands at the expense of woodlands is now revealed by recent studies of paleosols, fossils, and their stable isotopic compositions. Grasslands and their soils can be considered sinks for atmospheric CO_2, CH_4, and water vapor, and their Cenozoic evolution a contribution to long-term global climatic cooling. Grassland soils are richer in organic matter than are woodland and desert soils of comparable climates, and when eroded, their crumb clods form sediment unusually rich in organic matter. Grasslands also promote export of bicarbonate and nutrient cations to lakes and to the oceans where they stimulate productivity and C burial; this increased productivity and C burial occur because grasslands preferentially exploit fertile young soils in the first flush of weathering and their soils have a crumb structure with much higher internal surface area for weathering than soils of woodlands and deserts. Grasslands also promote regional climatic drying by virtue of their higher albedo and lower transpiration than woodlands of comparable climatic regions. Labile pools of C in grassland soils and their accelerated weathering rates early in soil development may also account for increased climatic instability over the past 40 m.yr. Unidirectional, stepwise, long-term climatic cooling, drying, and climatic instability may have been driven not by tectonic forcing but by the coevolution of grasses and grazers.

Introduction

During the past 40 m.yr., world climate has shown three pronounced trends: it has become cooler, drier, and less stable. Equable Eocene greenhouse climates contrast with Quaternary icehouse climates and dramatically fluctuating ice volumes. Over the same time span, grasslands nudged their way into the array of terrestrial ecosystems (Retallack 1997*b*; Jacobs et al. 1999). One could take the view that grasslands found opportunity in global climatic deterioration driven by Himalayan and American Cordilleran uplifts (Raymo and Ruddiman 1992) or in declining volume of oceanic thermohaline circulation (Flower and Kennett 1994). An alternative view is that grasslands were a biological force in their own right (Retallack 1998), in some ways comparable to the human rise to dominance of planetary resources (Vitousek et al. 1997).

Grasslands have long been considered products of the coevolution of grasses and grazers (Kovalevsky 1873). Few plants other than grasses can withstand the high-crowned, enamel-edged teeth and hard hooves of antelope and horses. Yet these same animals are best suited to the abrasive gritty opal phytoliths and dust of flat, open grasslands. Grasses recover readily from fire and nurture large herbivores such as elephants: both fire and elephants promote grassland at the expense of woodland (Retallack 1997*b*; Jacobs et al. 1999). Grasses suppress insect and fungal attack with secondary metabolites such as cyclic hydroxamic acids (Frey et al. 1997). Grasses create Mollisols, unique soils with fine crumb clods rich in organic matter (Retallack 1997*b*). This article explores possible roles of this uniquely Cenozoic ecosystem for global climatic change over the past 40 m.yr. Were grass-

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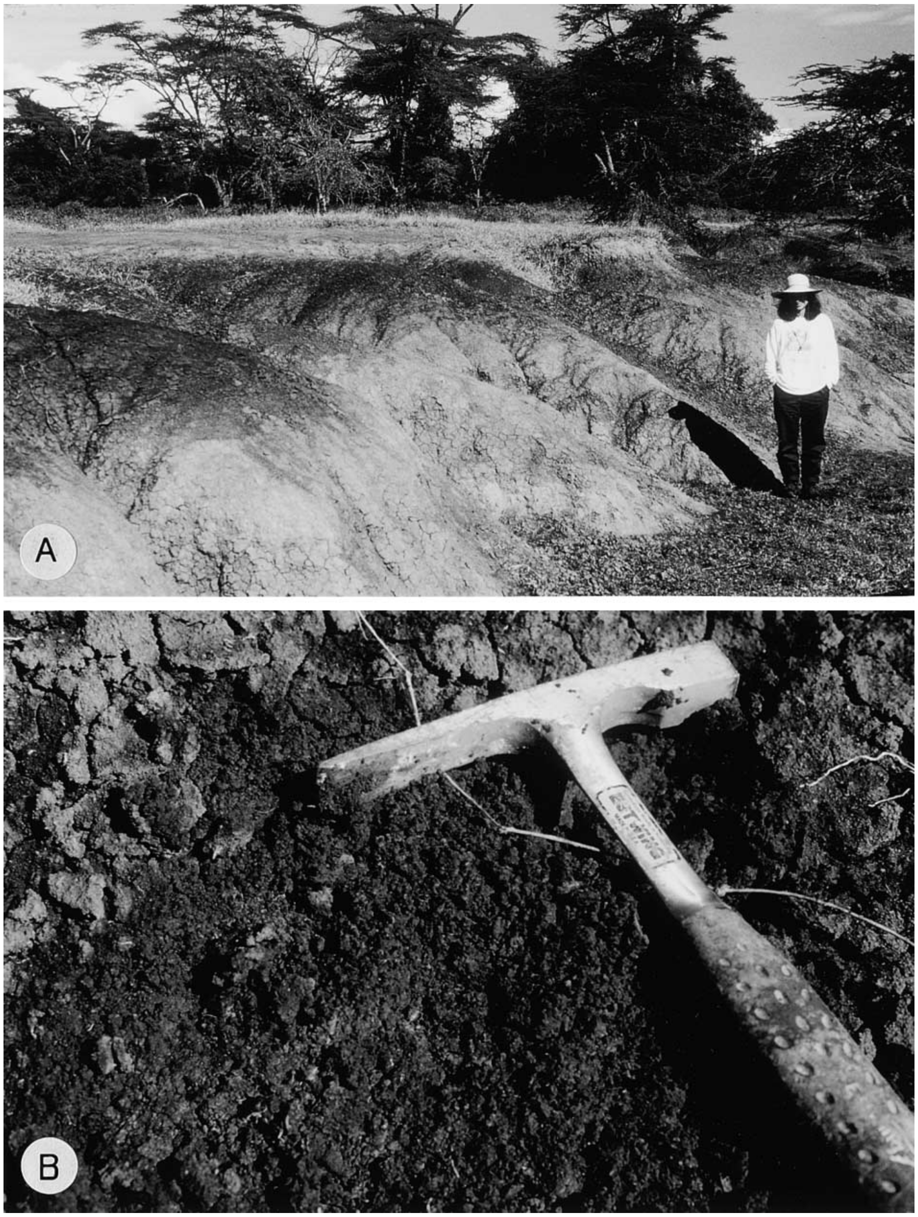

Figure 1. A grassland soil (Udoll or humid climate Mollisol) in Lake Nakuru National Park, Kenya, showing dark, organic surface horizon (*A*, mollic epipedon) and its fine root traces and crumb structure (*B*). Helen Vallianatos (*A*) and hammer (*B*) for scale.

lands with their unique organic-crumb (mollic) soils and biota a "mollic machine" that helped engineer Cenozoic global change?

Evidence for Cenozoic Grassland Expansion

Evidence for ancient grasslands has long been known from fossil grasses and mammals (Kovalevsky 1873). New evidence can be added from the stable isotopic composition of fossil grasses, mammals, and paleosols and from paleosol morphology, petrography, and geochemistry.

Paleosols. 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 dark surface horizons. Soils supporting sod-forming grasses have abundant, small (2–5 mm), rounded clods, dark with organic matter intimately mixed with clay (fig. 1). These crumb peds form a soft, dark surface

Table 1. Paleosols of East Africa Examined for This Study

Locality	Coordinates	Age (Ma)	A horizon	Depth Bk (cm)	Depth of burial (km)	Source
Kariandusi	0°25.773′S, 36°15.050′E	.3	Non	33	.002	1
Kariandusi	0°25.773′S, 36°15.050′E	.4	Near	37	.003	1
Olduvai	3°0′S, 35°21′E	1.1	Mollic	26	.030	2
Olduvai	3°0′S, 35°21′E	1.2	Non	57	.035	2
Olduvai	3°0′S, 35°21′E	1.3	Mollic	55	.040	2
Koobi Fora	4°18′N, 36°15′E	1.3	Non	65	.090	3
Koobi Fora	4°18′N, 36°15′E	1.3	Non	30	.090	3
Olduvai	2°59′S, 35°21′E	1.4	Mollic	25	.045	4
Koobi Fora	4°11′N, 36°25′E	1.5	Mollic	20	.110	3
Koobi Fora	3°55′N, 36°19′E	1.7	Non	60	.180	3
Koobi Fora	4°11′N, 36°25′E	1.8	Mollic	15	.230	3
Koobi Fora	3°57′N, 36°15′E	1.9	Non	100	.195	3
Koobi Fora	4°11′′N, 36°25′E	1.9	Non	110	.195	3
Hadar	11°3′N, 10°26′E	3.2	Mollic	65	.105	5
Hadar	11°3′N, 10°26′E	3.3	Mollic	27	.106	5
Kinangop	0°46.388′S, 36°29.888′E	3.3	Mollic	67	.003	4
Kinangop	0°46.388′S, 36°29.888′E	3.3	Near	43	.003	4
Kinangop	0°47.501′S, 36°31.040′E	3.3	Near	37	.002	4
Kinangop	0°46.388′S, 36°29.888′E	3.4	Non	36	.004	4
Kinangop	0°47.501′S, 36°31.040′E	3.4	Mollic	32	.003	4
Kanapoi	2°18.961′N, 36°3.842′E	3.4	Near	56	.614	6
Kanapoi	2°18.961′N, 36°3.842′E	3.5	Near	51	.615	6
Kanapoi	2°19.158′N, 36°5.143′E	3.6	Non	56	.645	6
Lothagam	2°53.909′N, 36°2.733′E	4.0	Near	47	.621	7
Kanapoi	2°18.304′N, 36°5.184′E	4.1	Mollic	68	.666	6
Kanapoi	2°18.304′N, 36°5.184′E	4.2	Mollic	72	.667	6
Kanapoi	2°17.721′N, 36°5.349′E	4.2	Non	25	.670	6
Kanapoi	2°17.721′N, 36°5.349′E	4.2	Non	34	.671	6
Kanapoi	2°17.403′N, 36°5.282′E	4.2	Non	56	.675	6
Kanapoi	2°17.403′N, 36°5.282′E	4.2	Non	37	.676	6
Lothagam	2°53.909′N, 36°2.733′E	4.9	Non	71	.713	7
Lothagam	2°53.909′N, 36°2.733′E	5.0	Non	52	.715	7
Lothagam	2°54.979′N, 36°3.127′E	5.5	Non	88	.765	7
Lothagam	2°54.058′N, 36°2.815′E	5.6	Near	52	.770	7
Lothagam	2°54.979′N, 36°3.127′E	5.6	Near	52	.770	7
Lothagam	2°54.986′N, 36°3.178′E	5.7	Non	65	.795	7
Lothagam	2°54.793′N, 36°3.198′E	6.0	Non	33	.785	7
Lothagam	2°55.178′N, 36°3.236′E	6.0	Non	59	.825	7
Lothagam	2°55.138′N, 36°3.251′E	6.1	Non	65	.828	7
Lothagam	2°56.416′N, 36°3.563′E	7.5	Non	104	.965	7
Lothagam	2°56.416′N, 36°3.563′E	7.6	Non	116	.966	7
Lothagam	2°56.416′N, 36°3.563′E	7.7	Non	93	.967	7
Fort Ternan	0°13.248′S, 35°20.382′E	13.9	Mollic	19	.625	8
Fort Ternan	0°13.248′S, 35°20.382′E	14.4	Mollic	17	.629	8
Fort Ternan	0°13.248′S, 35°20.382′E	14.4	Mollic	24	.630	8
Koimoroon	0°22.194′S, 35°1.561′E	14.5	Non	22	.100	9
Kaimogool	0°22.280′S, 35°1.597′E	14.5	Non	13	.060	9
Kaimogool	0°22.280′S, 35°1.597′E	14.5	Non	14	.062	9
Kaimogool	0°22.280′S, 35°1.597′E	14.5	Non	15	.063	9
Kaimogool	0°22.280′S, 35°1.597′E	14.7	Near	19	.065	9
Kaimogool	0°22.280′S, 35°1.597′E	14.7	Near	20	.066	9
Kaimogool	0°22.280′S, 35°1.597′E	14.7	Non	27	.070	9
Kaimogool	0°22.135′S, 35°1.650′E	14.7	Near	34	.070	9
Kaimogool	0°22.280′S, 35°1.597′E	14.7	Mollic	10	.072	9
Kaimogool	0°22.280′S, 35°1.597′E	14.7	Non	17	.073	9
Maboko	0°9.814′S, 34°36.362′E	14.7	Mollic	16	.035	10
Maboko	0°9.814′S, 34°36.362′E	14.7	Mollic	18	.034	10
Maboko	0°9.804′S, 34°36.351′E	14.8	Mollic	18	.040	10
Maboko	0°9.804′S, 34°36.351′E	14.8	Mollic	16	.041	10
Maboko	0°9.804′S, 34°36.351′E	14.9	Mollic	12	.043	10
Maboko	0°9.804′S, 34°36.351′E	14.9	Non	24	.044	10

Table 1. (*Continued*)

Locality	Coordinates	Age (Ma)	A horizon	Depth Bk (cm)	Depth of burial (km)	Source
Majiwa	0°8.875′S, 34°36.204′E	14.9	Non	21	.004	9
Kaimogool	0°22.280′S, 35°1.597′E	14.9	Non	18	.064	9
Majiwa	0°8.875′S, 34°36.204′E	15.0	Non	21	.005	9
Rusinga	0°24.315′S, 34°12.582′E	17.7	Mollic	20	1.025	11
Rusinga	0°24.315′S, 34°12.582′E	17.7	Non	34	1.026	11
Rusinga	0°24.315′S, 34°12.582′E	17.7	Non	49	1.040	11
Rusinga	0°25.025′S, 34°9.191′E	17.9	Non	35	1.100	12
Rusinga	0°25.025′S, 34°9.191′E	17.9	Non	28	1.101	12
Rusinga	0°25.025′S, 34°9.191′E	17.9	Non	45	1.102	12
Songhor	0°2.197′S, 35°12.497′E	20.1	Non	42	.700	8
Songhor	0°2.197′S, 35°12.497′E	20.2	Non	98	.701	8

Sources. Most field measurements are by me, but paleosol and other locality information can be found in the following references: 1, McCall et al. 1967; 2, Hay 1976; 3, Wynn and Feibel 1995; 4, Baker et al. 1971; 5, Radosevich et al. 1992; 6, Leakey et al. 1998, Wynn 2000; 7, Leakey et al. 1996; 8, Retallack 1991*a*; 9, Pickford 1986; 10, Feibel and Brown 1991; 11, Retallack et al. 1995; 12, Bestland and Retallack 1993.

Note. Decimal coordinates were obtained in the field using a Garmin GPS 38 and no less than six satellites; nondecimal coordinates are from regional maps.

called a mollic epipedon (Pawluk and Bal 1985). In paleosols, mollic epipedons can be recognized from common, small (2–5 mm), rounded soil peds, in addition to abundant, fine (1–2-mm diameter) root traces (Quade et al. 1995; Retallack 1997*a*, 1997*b*). Many soils and paleosols have crumb peds and fine root traces near the surface, but grassland soils are unique in having a thick horizon dominated by these features (at least 18 cm in friable parent materials and commonly a meter or more) (Soil Survey Staff 1999). Tropical grassland soils were at one time thought to be exceptional in lacking the fine structure and high organic content of temperate grassland soils, but analytical studies have revealed that there are both tropical and temperate Mollisols and mollic epipedons (Deshpande et al. 1971; de Wit 1978; Jager 1982). Mollic epipedons of soils are dark brown to black with organic matter (Munsell hues 7.5–10 yr and values of two to five), although this dark color is seldom preserved in paleosols because of burial decomposition of organic matter (Retallack 1991*a*, 1991*b*). Mollic epipedons also are rich in nutrients, indicated for paleosols by carbonate, plagioclase, or other easily weathered minerals, as well as by molecular weathering ratios of chemical analytical data (Retallack 1997*b*).

Grassland soils of dry regions develop subsurface horizons of calcareous nodules. The depth within the profile to this calcic horizon shows a relationship to mean annual precipitation (Retallack 1994, 2000). 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_2 in the past. Severe erosion would not leave a surface horizon thick enough to qualify either as a mollic epipedon or a soil with a deep calcic horizon. Such paleosols would not be significant to finding the first geological appearance of the deepest of these horizons, as is the intent of this study. Cumulic additions are marked by relict bedding and other textural discontinuities in the profile. Oligocene and later changes in atmospheric CO_2 are not thought to have been sufficient (Pearson and Palmer 2000) 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*a*).

Surveys have now been completed on three continents of mollic epipedons and calcic horizons in paleosols of the past 40 m.yr. Paleosol data from Oregon and the North American Great Plains are presented elsewhere (Retallack 1997*b*). Paleosol data from Pakistan and Nepal were gleaned from Quade et al. (1994, 1995), Retallack (1991*a*, 1995), and Tanaka (1997*a*, 1997*b*). New observations on paleosols from East Africa are presented here, based on my own fieldwork in 1984, 1987, and 1997 (table 1). The aim of these surveys has been to compile observations from as many paleosols as possible of (1) paleosol surface type (mollic, near mollic, or nonmollic) and (2) the depth to calcic horizon (in centimeters) in the same paleosol. These variables can be plotted against geological time to show their distribution in the past (fig. 2). Converting depth to calcic horizon to paleoprecipitation, using published transfer functions (Retallack 1994, 2000), gives an interpretation of the distribution of these different kinds of soils and vegetation in the past on a paleoprecipitation gradient (fig. 3). Expansion of grassland paleosols on paleoprecipitation gradients implies substantial geographic expansion. Similar patterns in the origin and expansion of mollic paleosols are found on three continents (fig. 4).

A remarkable observation arising from the consideration of these 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 (Retallack 1995, 1997*b*). Furthermore, paleosols provide evidence of sod-forming short grasslands in dry regions (<400-mm mean annual precipitation) well back into the Miocene. Desert rangelands lacking sod-forming grasses may be as old as the Oligocene in South Dakota (Retallack 1997*a*) and Argentina (Marshall and Cifelli 1990; MacFadden 2000). Sod-forming grasslands thus replaced preexisting dry woodlands during Miocene time, dramatically expanding their climatic and geographic range.

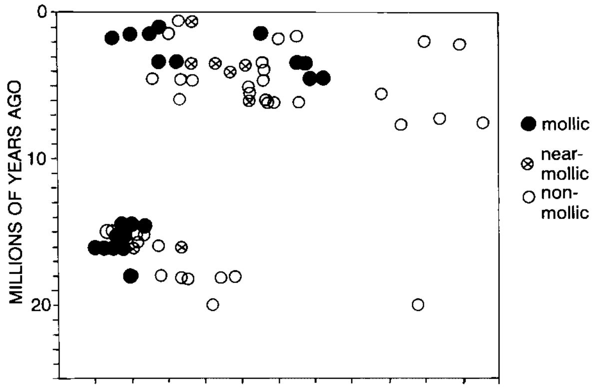

Figure 2. Variation in depth to calcic horizon for different kinds of paleosols of Cenozoic age in East Africa (table 1). Mollic paleosols have abundant fine root traces, fine crumb structure, dark color, chemical fertility, and thickness of grassland soils (fig. 1). Near-mollic paleosols show only some grassland soil features, and nonmollic paleosols are mainly blocky structured, red claystones.

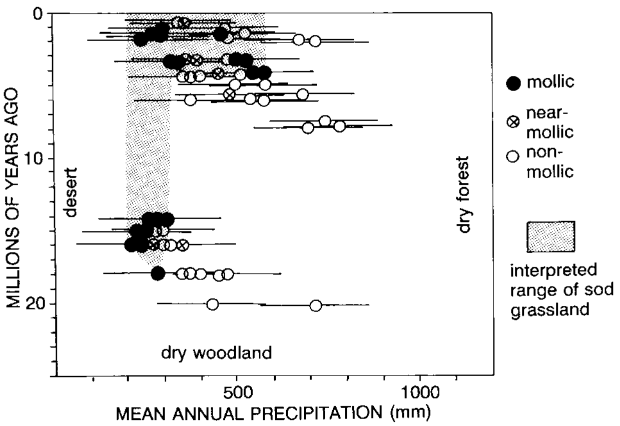

Figure 3. Expanding climatic range of grasslands through time (*stippled polygon*) in East Africa, inferred from paleosol mollic epipedons (indicating grasslands from criteria of Retallack 1997*b*) and calcic horizons (indicating paleoprecipitation using a transfer function of Retallack 1994).

This evidence from paleosols shows that grasslands did not necessarily appear because of climatic drying. Paleosols of arid to humid climates are known for the entire 40-m.yr. record, and there were dramatic fluctuations in aridity, with dry, dustbowl conditions in North America at 29, 24, 19, 14, 10, and 5 Ma (Retallack 1994, 1997*b*). Against this background of varied and fluctuating climate, grasslands spread to increasingly humid climates and, in doing so, must also have expanded geographically. By 7 Ma, grasslands had already expanded to near the current tallgrass prairie woodland ecotone. Subsequent human grassland-based agroecosystems have spread grasslands throughout the world, even into perhumid rain forests of Amazonia (Fisher et al. 1994; Nepstad et al. 1994).

Fossils. Post-Eocene expansion of grasslands can also be inferred from paleontological data (Jacobs et al. 1999). The past 40 m.yr. was a time of evolutionary radiations for a variety of grassland flora, including grasses, daisies, and legumes, and fauna, including dung beetles, bees, colubrid snakes, passerine birds, murid rodents, and ungulate mammals (Retallack 1997*b*). Both pollen and charred cuticle fragments of grasses increase dramatically in abundance through the Cenozoic (fig. 5*A*; Hoorn et al. 2000). The grass phytolith record also indicates increases in diversity and abundance of grasses since the Late Eocene (Meehan 1994; Stromberg 2000).

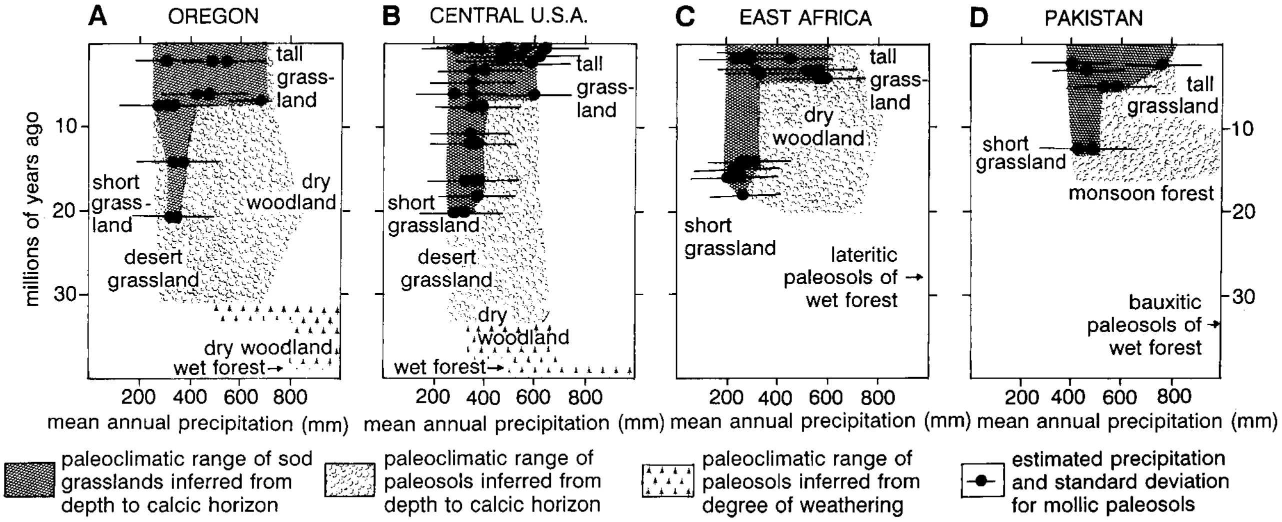

Figure 4. Climatic expansion of sod grasslands through Miocene time in (*A*) Oregon (Retallack 1997*b*), (*B*) North American Great Plains (Retallack 1997*b*), (*C*) East Africa (table 1), and (*D*) Pakistan (Quade et al. 1994, 1995; Retallack 1995; Tanaka 1997*a*, 1997*b*), based on mollic epipedons and depth to calcic horizon of paleosols. A Late Miocene advent of tall grasslands is inferred for each area from mollic paleosols with deep calcic horizons. Earlier Miocene short sod-forming grasslands are represented by mollic paleosols with shallow calcic horizons, and Oligocene desert grasslands are indicated by near-mollic paleosols (Retallack 1997*b*). These newly evolved grasslands replaced preexisting dry woodlands represented by nonmollic paleosols in each area (as interpreted from paleosols by Retallack [1983, 1991*a*, 1995] and Retallack et al. [2000]).

The coarse gritty fodder of grasses provided significant selection pressure for the evolution of high-crowned (hypsodont) teeth in ungulates (fig. 5*B*). Several groups of ungulates, notoungulates, and marsupials showed evolutionary elongation of the outer digits to increase running stride (cursoriality) (fig. 5*C*), reduction in the number of digits, development of hard, narrow hooves, and increase in body size (fig. 5*D*). Large, hypsodont, hard-hooved ungulates coevolved with a variety of defenses among grasses: abrasive coatings of opal phytoliths, sod-forming underground systems of roots and rhizomes, telescoped terminal meristems, and intercalary meristems (Retallack 1990). There has also been a steady decline in the abundance and diversity of browsing mammals since the Early Miocene (Janis and Damuth 1990; MacFadden 2000).

The Middle Miocene (14 Ma) site of Fort Ternan, Kenya, is particularly impressive for its evidence of grass-grazer coevolution. The fossil grasses there have the high phytolith abundance and low stomatal density of heavily grazed grasses (Retallack 1992*a*; Dugas and Retallack 1993), and the abundant antelope show both the striated microwear on their teeth and broad muzzle of mixed grazer-browsers (Cerling et al. 1997*a*). Another informative site is Late Miocene (10 Ma), Ash Hollow, Nebraska, where a herd of rhinoceros with the high-crowned teeth of grazers have been found with strongly silicified grass husks in their teeth (Voorhies and Thomasson 1979). There is little evidence of such grass-grazer interaction during Oligocene time, but it was extensive during the Pliocene. The Neogene can be viewed as a time of protracted evolutionary arms race between grasses and grazers, during which grassland ecosystems displaced preexisting dry woodlands of subhumid regions (fig. 6).

The fossil record of grassland mammals reveals thresholds of increased ungulate cursoriality and size at 25 and 15 Ma and in hypsodonty at 17 and 5 Ma (fig. 5). There was thus not a single origin of grassland fauna but a series of adaptations building on those that went before in a coevolutionary process, uncoordinated with physical forcings such as volcanic eruptions, bolide impact, CH_4 clathrate release, mountain uplift, or ocean current change (Prothero 1998).

Stable Isotopes. Tropical lowland grasses now use the Hatch-Slack or C_4 photosynthetic pathway, rather than the Calvin-Benson or C_3 pathway of trees, shrubs, and cool-climate to montane grasses. Because the C_4 pathway is less discriminating than is the C_3 pathway between the stable isotopes of C (^{13}C and ^{12}C), C_4 grasses are isotopically heavier (en-

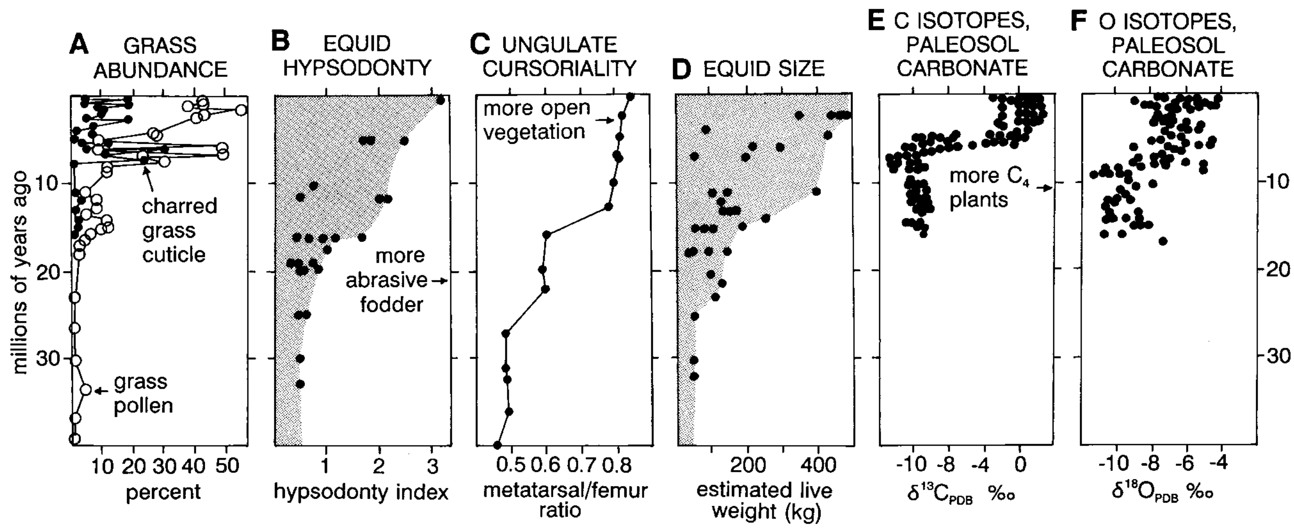

Figure 5. Paleontological and geochemical indicators of the Neogene expansion of grasslands. *A*, Abundance of fossil grass pollen and charred cuticle in Nigeria, Africa (Germeraad et al. 1967; Morley and Richards 1993). *B*, Increased hypsodonty in molars of North American horses (MacFadden 1992). *C*, Increased cursoriality of North American ungulates revealed by the length ratios of metatarsal/femur (Bakker 1983). *D*, Increased size estimated by body weight of North American horses (MacFadden 1992). *E*, Changing C isotopic composition ($\delta^{13}C_{PDB}$) of pedogenic carbonate in paleosols of Pakistan (Quade et al. 1995). *F*, Changing oxygen isotopic composition ($\delta^{13}C_{PDB}$) of pedogenic carbonate in paleosols of Pakistan (Quade et al. 1995).

riched in ^{13}C) than are C_3 grasses (Koch 1998). This isotopic difference can be seen in calcareous nodules of paleosols supporting these grasses (fig. 5*E*) and in apatite of teeth of fossil mammals that ate the grasses (Quade et al. 1995; Cerling et al. 1997*b*; MacFadden 1998, 2000). Along with $\delta^{13}C$ enrichment of pedogenic nodules and mammalian teeth, there is commonly also enrichment in $\delta^{18}O$ (fig. 5*F*), which may also reflect diminished discrimination of C_4 plants for heavy CO_2 ($^{13}C^{16}O_2$ or $^{12}C^{18}O^{16}O$) (Farquhar et al. 1993), although this isotopic shift has conventionally been attributed to a change in source or amount of precipitation (Quade et al. 1994; Stern et al. 1997, 1999).

A limitation of this approach is that the heavy isotopic composition is not unique to grasses (Koch 1998). There are abundant C_3 grasses in cool, humid regions today, and C_3 fossil grasses also are known from the Miocene of Nebraska (Smith 1996) and Kenya (Retallack 1992*a*; Cerling et al. 1997*a*). There is another physiological pathway of crassulacean acid metabolism (CAM) found in desert plants, such as sage and cacti, and aquatic plants, such as quillworts, that also creates organic matter with an isotopically heavy composition. Such plants are presumably responsible for isotopically heavy C from the Carboniferous (Jones 1994) and Cretaceous (Bocherens et al. 1994).

Isotopic evidence for C_4 grasses has been found as ancient as Miocene: 15 Ma in pedogenic nodules from Kenya (Kingston et al. 1994) and 12.5 Ma in permineralized fossil grasses with Kranz anatomy from California (Tidwell and Nambudiri 1989; Whistler and Burbank 1992). Nevertheless, such heavy isotopic compositions are uncommon in fossil plants and soils during the Middle Miocene. By the Late Miocene (6–7 Ma), heavy isotopic C values are widespread in pedogenic nodules and mammalian teeth in the United States, Bolivia, Argentina, Kenya, Pakistan, and China (Quade et al. 1994, 1995; Cerling et al. 1997*b*; Ding and Yang 2000). This isotopic evidence of geographic expansion of C_4 grasses in tropical lowlands during the Late Miocene supports paleosol evidence for grassland expansion at this time (fig. 4).

Isotopic evidence casts doubt on hypotheses that grasslands evolved because of increased monsoonal seasonality or declining atmospheric CO_2 levels. Monsoonal seasonality increases were a plausible explanation for the advent of C_4 grasslands inferred from isotopically heavy C in Late Miocene (6–7 Ma) mammal teeth and pedogenic carbonate from Pakistan, but this explanation fails to explain comparable isotopic excursions at the same time in nonmonsoonal North and South America (Cerling et al. 1997*b*). Furthermore, there is evidence from the

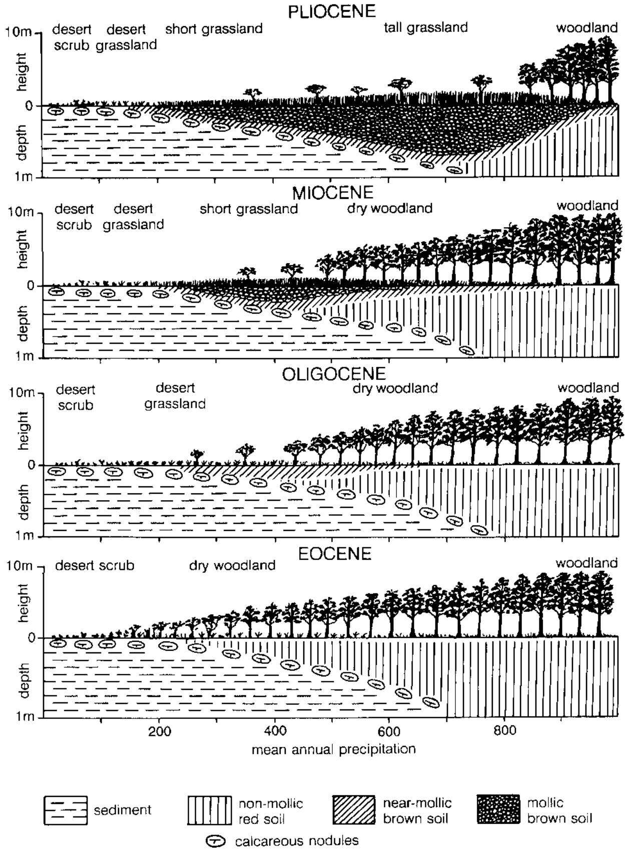

Figure 6. A scenario for the stepwise evolution of grassland ecosystems in arid to subhumid climatic regions during the past 50 m.yr. (Retallack 1997*b*).

isotopic composition of growth bands in Pakistani mammal teeth for monsoonal seasonality back at least 9.5 m.yr. (Kohn et al. 1999), and interlayered carbonate-hematite concretions in Pakistani paleosols are evidence of monsoonal climate back to 16 Ma (Retallack 1991*a*). Because C_4 plants outcompete C_3 plants at low atmospheric CO_2 levels (<500 ppm by volume), it has also been proposed that declining CO_2 at 7 Ma caused geographic spread of C_4 grasses at that time (Cerling et al. 1997*b*). A Late Miocene decline in CO_2 is indicated by the rising stomatal index of fossil oak leaves (van der Burgh et al. 1993) and rising oceanic pH interpreted from the boron isotopic composition of foraminifera (Pearson and Palmer 2000), although this second proxy could have been compromised by variable riverine inputs (Lemarchand et al. 2000). Curiously, a paleobarometer of CO_2 using the difference between open ocean organic and carbonate isotopic composition indicates a Miocene rise (not fall) from only 180 to 300 ppm by volume, which is comparable to historic values (Cowling 1999; Pagani et al. 1999). Perhaps isotopic shifts in the atmosphere were not profound enough to be recorded in the open ocean or were compromised there by other influences, such as isotopically light methanogenic C.

Roles for Grasslands in Neogene Global Change

Isotopic, paleontological, and paleopedological evidence for grasslands is now in agreement that grasslands have expanded their geographic and climatic distribution substantially. There is no evidence of grasslands during the Eocene, but now they are widespread in subhumid to semiarid regions where they displaced preexisting woody vegetation broadly comparable to modern desert scrub, shrublands, and dry woodland. In displacing this earlier vegetation, grasslands would have had significant effects as C sinks, fertilizers, dehumidifiers, fire starters, and animal farms. These are fundamental roles of grasses in grasslands, but animals of grasslands in some cases hinder and in other cases help these roles of grasses.

C Sink. CO_2 and CH_4 (which rapidly oxidizes to CO_2) are important greenhouse gases, and mechanisms for burial of their C may result in climatic cooling (Berner 1999). The most important long-term C sink from grasslands is their supply by erosion to sedimentary basins of crumb peds, which are unusually rich in organic matter intimately admixed with clay (Pawluk and Bal 1985). Tropical forests, in contrast, yield highly oxidized spherical micropeds with virtually no organic content (Retallack 1991*a*). Organic C in sediment derived from forested lands is typically 0.1–0.3 g m^{-2} yr^{-1}, whereas nearby pasturelands yield 1–3 g m^{-2} yr^{-1} and mostly graminaceous croplands yield 100–300 g m^{-2} yr^{-1}. These figures tabulated by Stallard (1998) suggested to him that erosion of croplands and grasslands and sequestration of their C in agricultural dams and rice paddies is an important balance to current C oxidation by fossil-fuel consumption and deforestation. Once added to the huge C reservoirs of the deep ocean and sediments, this C is removed from actively recycling biota and soils for geologically significant times of millions of years. As the premier colonizing plants of streamsides, lake shores, and sea shores (Grime 1979), grasses also suppress oxidation and erosion of recently buried carbonaceous sediments.

Other C sinks of grasslands are significant because they respond to short-term climatic change (Knapp and Smith 2001) but are probably not as important in the long term as the burial of carbonaceous soil peds. Grasses themselves are C sinks, especially considering their mass of roots and rhizomes underground. Nevertheless, grasslands are not as impressive in biomass as tropical rain forests, nor in soil C content as high-latitude peats (Hall et al. 2000). Biomass and productivity increase steadily with mean annual rainfall, culminating in tropical rain forests (Franzemeier et al. 1985; McGuire et al. 1992; Mellilo et al. 1993). C storage in soils also increases with inhibition of decomposition by stagnation or low temperature, culminating in high-latitude swamps and tundra (Sellers et al. 1997). There is evidence from paleosols and paleobotany for rain forest (Retallack and Germán-Heins 1994) and high-latitude swamps and tundra (Retallack 1999; Retallack and Krull 1999) as far back as the Carboniferous, and these ecosystems have been important players in global change since that time. Grasslands were the new ecosystems of the Cenozoic.

The C perturbation created by newly evolved grasslands is best considered in comparison with the dry woodlands that they replaced (figs. 4, 6). An appropriate modern comparison is between grassland and woodland vegetation of similar climatic belts. Grasslands have only about one-sixth the biomass of woodlands, but the biomass is dwarfed by an order of magnitude more C in grassland soils (table 2). Globally averaged, tall grasslands store 16.0 kg C m^{-2} organic matter underground and 0.7 kg C m^{-2} aboveground, compared with 11.1 kg C m^{-2} underground and 4.5 kg C m^{-2} aboveground for dry woodlands (McGuire et al. 1992), for a net C storage of 16.7 kg C m^{-2} for tall grasslands compared with 15.6 kg C m^{-2} for woodlands (McGuire et al. 1992). Studies of agricultural replacement of woody savanna by deep-rooted tropical pasture grasses in Brazil showed increased subterranean organic C storage from 19–20 kg C m^{-2} for savanna woodland to 22–27 kg C m^{-2} for pasture (Fisher et al. 1994). These and other results (Deshpande et al. 1971; de Wit 1978; Jager 1982; Murthy et al. 1982) indicate that past estimates of organic C in tropical grassland soils have been low, in part because soils were not analyzed to sufficient depths (Fisher et al. 1994). Grassland and woodland soils may have comparable amounts of organic C in the surface 15 cm. Beyond that depth, organic C 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 C reservoir.

One might expect burial of grassland paleosols themselves to be a C sink, but it is unlikely to be an important one. Grassland paleosols, unlike grassland soils, do not commonly have high amounts of organic C (Retallack 1991*a*, 1997*b*). While some of the fossil Mollisols examined were marsh grasslands with much organic matter, most were well drained when formed and lost much of their organic matter to overlying ecosystems soon after burial above the dry-season water table (Retallack 1991*a*, 1991*b*).

Hydrolysis is a relentless C sink but a minor sink. On coastal terraces in humid northern California, some 2%–8% of C sequestered by grassland soils was consumed by hydrolysis, with the remainder stored as organic C. This small amount declined further over hundreds of thousands of years as weatherable minerals were depleted from the soil (Chadwick et al. 1994). Comparison of these Californian soils with others in arid Wyoming and humid New York shows that an increasing fraction of C 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). Hydrolytic weathering in grassland soils is also promoted by an order-of-magnitude-larger internal surface area and moisture retention of deep

Table 2. Mean, Range, and Standard Deviation (SD) of C Content in Soils under Modern Grasslands and Adjacent Woodlands

Country/region	Vegetation	Soils	Source	Mean annual temp. (°C)	Mean annual precipitation (mm)	No. of soils	Min. C (kg m^{-2})	Max. C (kg m^{-2})	SD C (kg m^{-2})	Mean C (kg m^{-2})
Tanzania:										
Serengeti	Tall grassland	Haplustolls	1	23	750	8	23.2	79.0	16.3	51.4
Serengeti	Dry woodland	Argiustolls	2	21	900	30	5.6	19.7	3.2	12.8
India:										
Uttar Pradesh	Terai grassland	Mollisols	3	23	1400	6	16.3	30.4	5.7	23.5
Uttar Pradesh	Monsoon forest	Inceptisols	4	26	1200	2	3.3	4.5	.6	3.9
U.S.A.:										
Iowa	Tall prairie	Udolls	5	10	800	27	7.4	19.3	3.2	14.9
Illinois	Oak forest	Udalfs	5	10	900	30	2.3	15.6	2.6	8.2

Sources. 1, de Wit 1978; 2, Jager 1982; 3, Deshpande et al. 1971; 4, Murthy et al. 1982; 5, Franzmeier et al. 1985.

mollic epipedons compared with the coarse blocky texture of subsurface horizons of woodland soils (Retallack 1997*b*). Simple geometric constraints of the face-centered cubic arrangement (Conway and Sloane 1999) give an internal surface area of 2221 $m^2\ m^{-3}$ for balls 3 mm in diameter, compared with 150 $m^2\ m^{-3}$ for cubes 4 cm across. This internal volume effect and the export of bicarbonate to the ocean in ground water may be important C sinks in grasslands of humid regions such as coastal northern California, but most of the Cenozoic paleosols surveyed here (figs. 2–4) are similar to calcareous soils of Wyoming rangelands and formed in regions with an excess of evaporation over precipitation in which most bicarbonate was stored as pedogenic carbonate (Chadwick et al. 1994).

Fertilizer. Grasslands can be considered fertilizer ecosystems because of their capacity to rapidly fix P and N in plant tissue that is entirely herbaceous and more easily decayed than woody plant tissues (Knapp and Smith 2001). P and N are the most important limiting nutrients on land and in the sea (Tyrell and Law 1997; Chadwick et al. 1999). A metered supply of P, along with other essential nutrients (Ca, Mg, K, Na), comes mainly from weathering of minerals in soils. N is fixed primarily by leguminaceous forbs and bushes of grasslands. In most landscapes with grassland and woodland, grasslands occupy soils on the freshest, nutrient-rich parent materials (St. Arnaud and Sudom 1981; Harden et al. 1992; Chadwick et al. 1994; Quideau and Bockheim 1996). Grasses mobilize nutrients more quickly than other plants, in part because they are usually the first to colonize newly disturbed ground because of a variety of adaptations including copious wind-dispersed pollen and seeds, nodal growth, and herbaceous stature (Grime 1979). Nutrient procurement declines with time as ecosystems develop into old-growth forest (Chadwick et al. 1994, 1999).

Grasses are not only well placed for nutrient procurement temporally as early successional communities, but as permanent communities, they occupy the prime fertile real estate of the planet in some 24.1×10^6 km^2, or about 16% of total land area (Mellilo et al. 1993). The modal global mean annual precipitation of 746 mm for land areas (Baumgartner and Reichel 1975) is about the same as for grasslands (300–1000 mm). Grasslands are not limited by cold climate, short growing season, and water withholding by ice, as in tundra and taiga regions. Nor is grassland production limited by high temperatures and lack of moisture in deserts. Nor is grassland production limited by infertile, deeply leached soils of tropical humid regions. Grasslands currently account for 11%–19% of global net primary productivity on land and 10%–30% of soil C storage (Hall et al. 2000). Studies of the isotopic composition and abundance of atmospheric CO_2 have repeatedly indicated large C sinks in the midlatitudes of the northern hemisphere (Ciais et al. 1995; Keeling et al. 1996; Fan et al. 1998), which is the location of the world's most productive grasslands. As a plant biome that commandeered the most fertile substrates temporally and geographically, grassland expansion though the Cenozoic would have had a significant global effect.

Enhancement of nutrient mobilization by grasses could have affected lacustrine and oceanic productivity, extending further offshore the zone of waters rich in C, N, and P. Fertile waters stimulate productivity, especially in upwelling zones, and actively recycle CO_2 in such a way as to suppress deep oceanic release of CO_2 (Martin 1996). Over Cenozoic time, ocean sediments record increased terrestrial weathering as an increased rate of accumulation of alumina in the ocean (Donelly 1982) and an increased Sr isotopic ratio of carbonates (fig. 7*B*).

Dehumidifier. Water vapor is another important greenhouse gas (Chaline 1992), and grasslands promote very different water balance and albedo than woodlands. Grasslands are lighter colored (albedo 19%–25%) than woodlands and forests (albedo 14%–16%) (Wilson and Henderson-Sellers 1985) and so reflect about 5% more solar radiation back into space. Grasslands also are less active in evapotranspiration than trees. Grassland sod keeps soil moist but the air above dry, whereas forests and woodlands actively transpire water drawn from deep in the soil to create a humid atmosphere and soil some 20%–30% drier than that of adjacent grassland (Nepstad et al. 1994). The effect of rain forest clearance in Amazonia has been markedly reduced evapotranspiration, cloudiness, and precipitation (Sellers et al. 1997). The differences between open woodland or shrubland and grasslands are unlikely to have been so profound but are likely to have resulted in a significantly drier atmosphere.

Fire Starter. Seasonally dry grasslands are prone to wildfire. Grasses with their underground rhizomes and weedy reproduction recover readily from wildfires that are catastrophic for trees. This has been an important mechanism for maintaining grassland ecosystems, until historic fire suppression of rangelands (Wells 1970). Grass fires are transient CO_2 sources to the atmosphere, but in promoting soil erosion and burial of C-rich soil crumbs from grassland soils, grass fires can be important

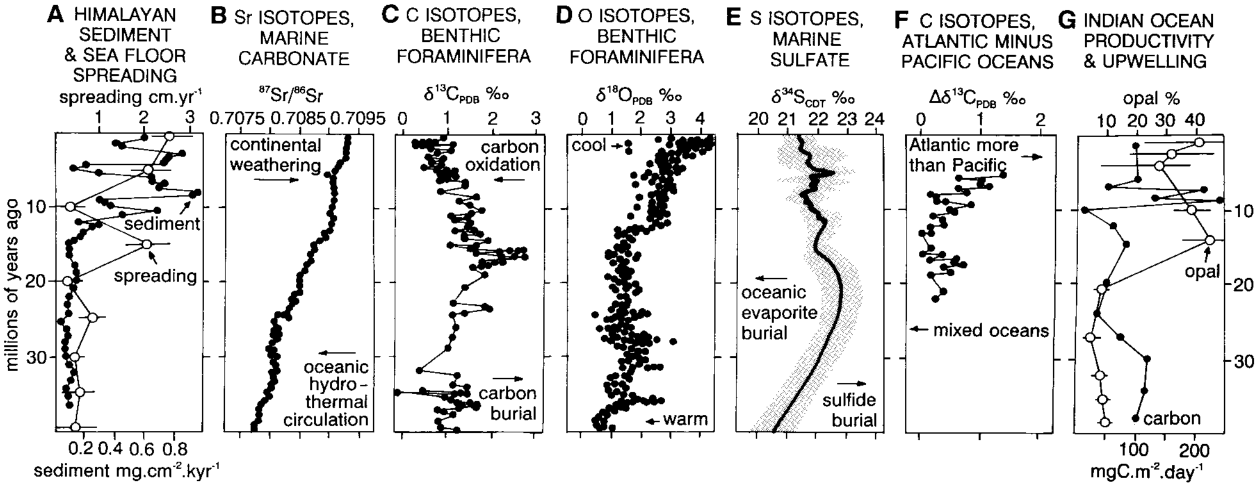

Figure 7. Indicators of Neogene global change from oceanographic records. *A*, Mean normalized mass accumulation rate of sediments in the Bengal Fan, Indian Ocean (Rea 1993) and global seafloor spreading rate (Kominz 1984). *B*, Value of $^{87}Sr/^{86}Sr$ of marine carbonates (Compton and Mallinson 1996). *C*, C isotopic composition ($\delta^{13}C_{PDB}$) of benthic foraminifera from the Atlantic Ocean (Shackleton et al. 1984). *D*, Oxygen isotopic composition ($\delta^{18}O_{PDB}$) of benthic foraminifera from the Atlantic Ocean (Flower and Kennett 1994). *E*, Sulfur isotopic composition ($\delta^{34}S_{CDT}$) of sulfate evaporites (Paytan et al. 1998). *F*, Amount by which the C isotopic composition ($\delta^{13}C_{PDB}$) of Atlantic Ocean benthic foraminifera is greater than the C isotopic composition of Pacific Ocean benthic foraminifera of the same geological age (Flower and Kennett 1994). *G*, C accumulation rate and biogenic opal percent in Indian Ocean sediments (Siesser 1995).

long-term C sinks (Stallard 1998). Grass fires are also transient albedo reducers but have little effect on deep soil water balance because they mostly occur during the dry season, when soils are near permanent wilting point. Fires also redistribute nutrients across the landscape. Their longer-term effects on promoting moist soil, high albedo, and organic sediment yield from grasslands are more important climatically.

Animal Farm. In many cases, herbivores negate the effects of grasses. By thinning the sward with their high-crowned teeth and biting grip, and by trampling the sod with their hard hooves, they consume and damage grasses, leaving them prone to decay. This causes an oxidation of C that would otherwise be stored in the grasses and soil, exposing darker soil to lower overall landscape albedo and opening the soil to evaporative drying and crusting. Buffalo wallows and dustbowls are two especially dramatic consequences of overgrazing rangelands. Nevertheless, such soil erosion delivers sediment of higher organic content than that formed in woodland soils to dams, lakes, and the ocean (Stallard 1998), and this is an important long-term C sink (Berner 1999).

In other cases, the destruction of trees by megaherbivores, such as elephants and rhinos, encourages the spread of grasslands (Owen-Smith 1988). Herbaceous legumes, willow seedlings, and other nongrassy fodder are often preferred by grazers, so that grazing lawns are preferentially enriched in less palatable grasses that promote soil organic matter accumulation. Large body size and herding in mammals can be a factor promoting grasslands over woodlands.

A New Model—Grasslands as a Biological Force

A new explanation for Neogene climatic cooling is now apparent from an old explanation for grasslands as a product of the coevolution of grasses and grazers (Kovalevsky 1873). Simply put, grasses proved best suited to increasingly large, hard-hooved, durable-toothed herds of large grazers, and grazers proved best suited to extensive open grassy terrane (Retallack 1990; Jacobs et al. 1999). By this view, grasslands and their soils were a "mollic machine": a biologically evolved system commandeering fertility, fire, and erosion to produce an unprecedented long-term C and water vapor sink that mitigated the earlier Tertiary greenhouse atmosphere.

This model does not rely on physical forcing by mountain uplift or ocean current pathways but does postulate biologically induced global change during thresholds in the accelerating coevolution of grasses and grazers. Evolutionary advances that allowed grasses to proliferate, such as telescoped internodes, basal tillering, dense adventitious roots, and small pollen and seeds, generally resulted in a greater C, nutrient, and water vapor sink in grassland soils and sediments. Evolutionary advances of mammals, such as hypsodonty, cursoriality, and greater size resulted in dispersal of C, nutrients, and water vapor but not to the extent that it completely destroyed their graze. While grasses and grazers have different effects, they both effectively exclude trees, which are eaten by megaherbivores, prevented from germination by a dense sward, and burned by ignition of dry-season grassy tinder. Grass-grazer interactions are complex, but their net effect, like that of many successful biological systems, is natural selection of grasslands in preference to woodland and desert vegetation. The special demands of successful and newly evolved ecosystems can have widespread environmental effects, as we have seen with human domination of the landscape and pasture improvement (Vitousek et al. 1997).

Earliest Oligocene Appearance of Desert Grasslands. The Eocene-Oligocene boundary is the most profound paleoclimatic change of the Cenozoic. In the sequence of fossil soils and plants of central Oregon, there was a geologically abrupt (<200 ka) decline in mean annual precipitation of 500 mm, in mean annual temperature of 5°C, and in mean annual range of temperature of 7°C (Retallack et al. 2000). Comparable paleosols in South Dakota and Nebraska were drier climatically at all times than in central Oregon but show similar appearance of open rangeland paleosols and loessial sedimentation at the Eocene-Oligocene boundary (Retallack 1983, 1986, 1994), though with less temporal resolution than in Oregon (Retallack 1998; Terry 1998). Surprisingly, these dramatic climatic changes had limited effect on both fossil mammals (Prothero 1998) and fossil grasses (Stromberg 2000), with most kinds of mammals and plant phytoliths continuing through the boundary. Biotic changes associated with the appearance of rangelands include increased abundance in paleosols of burrows and burrowing mammals (Retallack 1983; Prothero 1998), dung beetle boli (Retallack 1990), and earthworm pellets (Meehan 1994; Retallack et al. 2000). Root distributions in Oligocene paleosols are compatible with bunchgrasses and small shrubs in settings prone to frequent disturbance. None of these paleosols contain charcoal in abundances anything like those later in the Cenozoic (Retallack 1983, 1991*a*). Comparable changes in paleosols can be seen in many parts of the world at the Eocene-Oligocene boundary (Retallack 1992*b*).

These earliest rangeland paleosols were near-mollic, with a coarse soil structure. They were also drab-colored and little-oxidized chemically, and probably had only a modest organic content, even before burial mobilization of soil organic matter (Retallack 1997*b*). They were also both physically and chemically immature (Retallack 1983; Bestland 2000). This colonizing phase of soil development is one of unusually high weathering rates and biological productivity (Chadwick et al. 1994, 1999), and mass balance analysis of geochemical data on Early Oligocene paleosols indicates a significant intensification of net weathering and C flux through soils at this time (Bestland 2000). These early bunch grasslands may have accelerated weathering during colonization of fresh sediments in disturbed habitats, such as stream margins and alluvial fans, where there is high potential for erosion and burial of organic upper-soil horizon clods.

In the oceans at the Eocene-Oligocene boundary (33 Ma), there were decreases in C burial from C isotopic data (fig. 7*C*) and in sulfide burial from evaporite isotopic data (fig. 7*E*), followed by later Oligocene increases in burial of both. This major perturbation of weathering may also be reflected in hafnium isotopic composition of ferromanganese crusts in the deep sea (Lee et al. 1999). A marked oceanic cooling with growth of polar ice is indicated by marine O_2 isotopic data (fig. 7*D*) and also by marked global marine regression (Wilgus et al. 1988). Extinctions of molluscs and foraminifera at this time may be related to cooling and marine eutrophication (Martin 1996).

These observations on land and sea could be explained by the key biological innovation of ephemeral bunchgrass ecosystems replacing arid shrublands and woodlands in dry regions of the world. Grassy ground cover would have built greater reserves of soil organic matter and increased regional albedo in arid lands. Herbivorous mammals still had relatively low-crowned teeth and would have been much more devastating on woody shrubs than gritty bunchgrasses, which consequently flourished as ground cover. Arid land environments maintained a flashy hydrology, but this also favored grasses with a more ephemeral lifestyle than stress-tolerant, slow-growing desert shrubs. Flash floods and sheet wash in arid lands now buried more organic soil particles in lakes and floodplains as a long-term C sink. Dissolved and detrital organic C, together with P, N, and other nutrients from enhanced weathering, may also have fertilized oceanic productivity, as indicated by a slight increase in oceanic Sr isotopic ratios (fig. 7*B*), but this would have been limited as long as grasslands were confined to arid and inland regions. With productivity, C storage, and albedo up in arid lands, atmospheric water vapor and CO_2 were reduced, resulting in cooling, expansion of alpine and polar ice caps, and sealevel drop.

Early Miocene Appearance of Short Sod Grasslands. The Early Miocene (20 Ma) was a time of paleoclimatic change to wetter climate in both the midwestern and northwestern United States. Desert loessites of the Marsland and upper John Day Formations were replaced with abundant paleosols of short grasslands in the Harrison and uppermost John Day Formation (Retallack 1997*b*). Declining sedimentation rates and a more stable landscape are indicated by sequences with moderately developed paleosols, in contrast to very weakly developed desert paleosols beforehand. The most striking feature of these short grassland paleosols is the abundance of small crumb peds and fine root traces, indicating that these grasslands formed a sod, or natural carpet on the landscape. Such dense herbaceous ground cover would have limited the distribution of woody desert shrubs by choking out their seedlings and by the spread of fire. By Middle Miocene time (17 Ma), charcoal became a more conspicuous part of the rock record (fig. 5*A*). Another consequence was initiation of a steady decline in the number of browsing mammals through time (Janis and Damuth 1990; MacFadden 2000). Also at this time (17 Ma), there was an explosive adaptive radiation of horses and antelope, as well as acquisition in many independent mammal lineages of hypsodonty (fig. 5*B*), cursoriality (fig. 5*C*), and large body size (fig. 5*D*). With larger size, harder hooves, and more effective teeth, grazers served to promote grasses at the expense of trees and also weakened the sod for erosion and burial of organic-rich soil crumbs.

In the ocean during the Early Miocene (20 Ma), C and sulfide burial rates were initially low, but by the Middle Miocene (17 Ma), both increased dramatically (fig. 7*C*, 7*E*). By Middle Miocene time, enhanced oceanic productivity is also indicated by large increases in biogenic opal abundance in marine sediments (fig. 7*G*). A sustained increase in degree of continental weathering is indicated by Early to Middle Miocene Sr isotopic data (fig. 7*B*). An Early Miocene decrease in oceanic pH, inferred from B isotopic composition of foraminifera, probably reflects declining atmospheric CO_2 levels (Pearson and Palmer 2000) and is mirrored in a decline and stabilization in Hf isotopic composition of ferromanganese crusts in the deep sea (Lee et al. 1999).

These observations on land and sea could be explained by the key biological innovation of sod-forming grassland ecosystems replacing mixed-grass shrublands in dry regions of the world and then being exploited by increasingly destructive large mammals. The evolution of sod-forming grasslands at first would increase local albedo, water retention, and C storage. These gains were then partly undone by the evolution of increasingly hard-hooved, hypsodont mammalian herbivores, which eventually promoted soil erosion, burial of eroded organic soil, and oceanic fertilization.

Late Miocene Appearance of Tall Sod Grasslands. The Late Miocene was a time of climatic and geographic expansion of tall sod grasslands (fig. 4). Such a dramatic expansion in depth and breadth of the mollic epipedon revealed by paleosols constituted an unprecedented C and water vapor sink. There is evidence of increased weathering in tall grassland paleosols from increased $^{87}Sr/^{86}Sr$ in pedogenic clays of sub-Himalayan floodplains (Quade et al. 1997), with the locus of most intense weathering moving eastward across the Indo-Gangetic lowlands as tall grasslands migrated away from increasing aridity of the Potwar Plateau and Thar Desert (Retallack 1991*a*; Tanaka 1997*a*). Such lateral shifts through time make it unlikely that Sr isotopic composition of paleosols reflects that of rocks in local drainage basins, which is variable and complex (Jacobson and Blum 2000). Tall grasslands expanded into more humid regions with less calcareous soils and more permanent streams than found in regions with short grasslands (fig. 6). Charcoal in paleosols and sediments and rising abundance of grass pollen worldwide (fig. 5*A*; Hoorn et al. 2000) indicate that fire played a role in the expansion of grasslands at this time. Also by Late Miocene (5–7 Ma), hypergrazers such as large, monodactyl horses and alcephaline antelope were widespread in Africa, Europe, and North America (Jacobs et al. 1999), increasing grazing pressure on vegetation.

C isotopic studies of pedogenic carbonate, mammalian tooth enamel, and mollusc shells in many parts of the world indicate a dramatic Late Miocene (5–7 Ma) expansion of tropical grasses using the C_4 photosynthetic pathway (Cerling et al. 1997*b*; Ding and Yang 2000). This expansion may have been encouraged by declining levels of atmospheric CO_2, which is indicated by a rising stomatal index of plant cuticles (van der Burgh et al. 1993) and by a rise in oceanic pH interpreted from the boron isotopic composition of foraminifera (Spivack et al. 1993; Pearson and Palmer 2000; opposing view given by Lemarchand et al. 2000). Why this CO_2 decline is not recorded in the isotopic composition of open oceanic plankton remains a puzzle (Cowling 1999; Pagani et al. 1999). Although C_4 grasses can do more with less CO_2 than C_3 grasses, C_4 grasses also have a lower productivity, which allows them to exploit sites of high evapotranspiration and low mineral fertility.

In the marine realm, the Late Miocene is famous for the Messinian (5.33–7.24 Ma) episode of Mediterranean desiccation and salt deposition as a result of extensive ice-sheet expansion and marine regression (Krijgsman et al. 1999). The high internal surface area and fertility of subhumid grassland soils also would have accelerated chemical weathering, which is indicated for 5–7 Ma by increased marine carbonate $^{87}Sr/^{86}Sr$ ratios (fig. 7*B*) and P and other nutrient elements in marine rocks (Filipelli and Delaney 1994). Oceanic fertilization was particularly noticeable in upwelling zones of the Indian and southern oceans (fig. 7*G*; Dickens and Owen 1994, 1999). Diversion of isotopically heavy C of C_4 plants into soil carbonates may have contributed to the shift at 5–7 Ma to isotopically lighter C in marine carbonate (fig. 7*C*). Oxidation of shallow-marine C at a time of general marine regression may also have played a role in this isotopic shift (Flower and Kennett 1994). Overall decline in burial of C at sea has been inferred from C isotopic data, as well as from the generally declining isotopic values of S ($\delta^{34}S_{CDT}$) in marine sulfates (fig. 7*E*). However, Derry and France-Lanord (1996*a*) and France-Lanord and Derry (1997) argue that C sequestration increased, and the apparently contrary isotopic changes in the ocean reflect diminished C isotopic fractionation by marine algae and terrestrial plants. Not only do C_4 plants discriminate less than C_3 plants do against C-heavy CO_2 ($^{13}C^{16}O_2$) but also against O_2-heavy CO_2 ($^{12}C^{18}O^{16}O$), so that plants exert a significant control in the O_2 isotopic composition of CO_2 (Farquhar et al. 1993), though the dehumidifying effects of grasslands would also have altered regional O_2 isotopic composition (Stern et al. 1999). These terrestrial changes may have affected the O_2 isotopic composition of marine foraminifera at 5–7 Ma (fig. 7*D*), adding to the even more pronounced effects of increased ice volume and cooling (Flower and Kennett 1994).

These observations on land and sea could be explained by the key biological innovation of C_4, sod-forming, tall-grassland ecosystems replacing dry woodlands in warm subhumid regions of the world and substantially augmenting the geographic spread of grasslands into less-productive and more-humid sites. In such well-watered regions, the effects of hydrolytic consumption and storage of C and water-vapor retention in grassland soils would have been more profound, and the leakage into the ocean of nutrients in solution and particulate C and clay from soil erosion would have increased.

Tectonic Forcing or Feedback?

The new model presented here challenges conventional wisdom because it is widely assumed that grasslands evolved as climate became drier or more seasonal (Cerling et al. 1997*b*; Stern et al. 1997; Pagani et al. 1999; MacFadden 2000) and that the prime driver of these climate changes was physical forcing such as mountain uplift (Raymo and Ruddiman 1992) or dwindling ocean currents (Broecker 1997). Mountains and oceans have undeniable effects on climate, but environmental systems include complex feedbacks that undermine their role as simple and direct physical forcings of paleoclimate.

Stagnation of Oceanic Circulation. A common explanation for Neogene global change is the dwindling importance through time of a conveyor of thermohaline circulation that distributes heat throughout the oceans (Flower and Kennett 1994). By this model, warm salty water from Indonesia flows past South Africa into the tropical Atlantic and then north with the Gulf Stream to cool and sink off the coast of Greenland. This cool water mass is then recycled through the deeps of the Atlantic to circum-Antarctic and then Pacific Oceans (Broecker 1997). Declining interconnection between the Atlantic and Pacific Oceans through geological time can be seen from the increasingly different C isotopic composition of their benthic foraminifera (fig. 7*F*). Thermal isolation of Antarctica and tortuosity of global thermohaline circulation would be expected to have increased though Neogene time if it were to explain global cooling. In contrast, plate-tectonic reconstructions show that ocean basin tortuosity decreased with the northward drift of the southern continents and closure of the ancient Tethys Ocean (Scotese and Sager 1986).

Although Tethys and Carribean ocean currents are small compared with those of the southern ocean, tropical tectonic reorganization has also been regarded as forcing climatic change (Driscoll and Haug 1998). Archaic circulation involving remnants of the Tethys Ocean was minimal after 50 Ma and completely gone by 10 Ma (Ramstein et al. 1997). Panamanian isthmus closure was well advanced during this time and completed during the marine regression at 3.5 Ma, but Carribean islands had long deflected Atlantic-Pacific exchange of water from the main oceanic thermohaline conveyer (Iturralde-Vinent and MacPhee 1999).

This leaves, as the major source of tortuosity and Antarctic isolation, the Miocene and Pliocene growth of sea ice around Greenland and Antarctica, revealed in deep ocean cores by increased abundance of ice-rafted debris (Flower and Kennett 1994) and enriched oxygen isotopic values ($\delta^{18}O_{PDB}$) of foraminifera (fig. 7*D*). Also contributing to diminution of thermohaline circulation and closure of the Panamanian land bridge was marine regression accompanying sea ice and ice cap growth (Wilgus et al. 1988). Declining influence of thermohaline global warming, which has had an important long-term flywheel effect in stabilizing global climate, could be a consequence rather than cause of ice growth and marine regression.

Thus it is now unclear whether declining thermohaline circulation allowed the spread of sea ice (as is widely assumed) or whether sea ice curtailed oceanic thermohaline circulation (as proposed here). This problem has some similarity to the classic paradox of whether the chicken or the egg came first because oceans and climate are linked in a mutually interdependent system of iterative feedback that makes changes in either system synchronous within the limits of temporal resolution of the rock record. Sea-ice curtailment of thermohaline circulation now becomes plausible because grasslands as a biological force provide an independent explanation for climatic cooling.

Mountain Uplift. Another popular explanation of Neogene global change is uplift of Himalayan and American Cordilleran ranges and their extensive ice caps, which are thought to have disrupted the jet stream and intensified monsoonal circulation. By itself this mechanism would merely redistribute heat and not result in global cooling (Barron 1985). Central to this hypothesis is the glacial debris and outwash of mountains envisaged to have consumed CO_2 by weathering, thus mitigating a preexisting greenhouse (Raymo and Ruddiman 1992). However, chemical-biological, not merely physical, weathering is needed, and chemical-biological weathering is accelerated by warmth, water, and plants (Retallack 1997*a*). Uplift of the sparsely vegetated and glaciated Tibetan Plateau and Himalaya and extraordinarily rapid deposition of alluvial outwash of the Indo-Gangetic Plains decreased, rather than increased, chemical weathering (Retallack 1991*a*; Derry and France-Lanord 1996*b*). Although current-dissolved nutrients in water from the Himalaya into the ocean is impressive, this comes mainly from weathering under terai grassland, monsoon forest, and jungle in the Indo-Gangetic lowlands rather than from the glaciated highlands.

Pulses of Himalayan uplift are now well documented at 9 and 2 Ma from dating of igneous rocks (Turner et al. 1993) and from sediment influx in sub-Himalayan basins, including the Indus and Bengal submarine fans (fig. 7*A*). Despite the intervening lull in mountain building in the Himalaya at 5–7 Ma, this was a time of markedly greater weathering revealed by increased $^{87}Sr/^{86}Sr$ in pedogenic clays of the Bengal Fan and their source rivers (Derry and France-Lanord 1996*a*; Quade et al. 1997). An eastward spread of C_4 tall sod grasslands across the Indo-Gangetic Plains at the same time (Retallack 1991*a*; Cerling et al. 1997*b*; Tanaka 1997*a*, 1997*b*; Hoorn et al. 2000) may explain this pulsed increase in chemical weathering at the same time as a decrease in physical erosion and sedimentation (Derry and France-Lanord 1996*b*). The Late Miocene (5–7 Ma) was also a time of increased delivery of P and other nutrients to the ocean (Filipelli and Delaney 1994).

Another orogenic explanation for paleoclimatic change is a decrease in tectonic degassing of CO_2 due to metamorphism within the Alpine-Himalayan ranges and American Cordillera or rates of seafloor spreading declining through time. Both mountain building (Beck et al. 1995) and seafloor spreading (Kominz 1984) declined precipitously after Cretaceous to Early Eocene (90–50 Ma) heightened activity, but they have shown modest increases that should have liberated more, not less, CO_2 through the past 40 m.yr. (fig. 7*A*).

Molnar and England (1990) have presented an intriguing alternative to the orographic cooling hypothesis: expansion of glaciers that scoured out Himalayan valleys allowed subsequent isostatic uplift of the highest peaks. By their view, apparent Neogene mountain uplift was largely an artifact and consequence, rather than a cause, of climatic cooling. While significant climatically induced topography is plausible, some tectonic component to mountain building is undeniable (Whipple et al. 1999), though acting over longer time scales than many Cenozoic paleoclimatic shifts. Thus it is now unclear whether mountain uplift induced climatic cooling or whether mountainous topography was exacerbated by climatic cooling and glacial erosion. Here is another chicken-and-egg paradox of complex iterative environmental feedbacks, reflected in the apparent global synchrony of paleoclimatically sensitive evidence taken as evidence for mountain uplift. A role for climate in creating mountainous topography now becomes plausible because grassland expansion is a potential biological forcing for climatic cooling.

Conclusions

As grasslands joined the global C pool, ripples spread widely. Their soils can be considered engines of global change: new weathering regimes initiated by grasslands may have altered the mass distribution and isotopic composition of C, O_2, and Sr at the earth's surface in predictable ways that are unexplained by physical forcings of mountain uplift, monsoon intensification, or disrupted oceanic circulation. Coevolution of grasses and grazers created grasslands as a biological force that was to be exceeded only by later evolution of grass-based human agroecosystems.

The new model of grassland soils as a mollic machine that manufactured much Neogene global change has three elements, each of which is amenable to testing by modern experiment and reexamination of the rock and fossil record. First, grasses and grazers evolved primarily because of coadaptations such as phytoliths in grasses and hypsodonty in grazers, which selected for them but not other creatures. Second, grass-grazer ecosystems expanded their climatic and geographic range during the Cenozoic, from a negligible extent during the latest Eocene to a substantial fraction of the current land area. Third, grassland expansion initiated increased organic C storage in soils, soil water retention, speed of nutrient exploitation, surface albedo, and C burial in sediments eroded from their soils. These changes had many consequences, including long-term global cooling.

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