

Neogene Expansion of the North American Prairie

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Neogene paleosols of the Great Plains and central Oregon provide abundant evidence of grasslands of the past. The characteristic surface horizon (mollic epipedon) of grassland soils (Mollisols) can be recognized in paleosols from granular ped structure, abundant fine root traces, dark color, and common carbonate or other easily weatherable minerals. The fossil record of such soils indicates a three-stage evolution of grasslands. Eocene to Oligocene rangelands are represented by paleosols with near-mollic soil structure and fine root traces similar to soils of modern desert grasslands with scattered bunch grasses and shrubs. Paleosols with mollic epipedon and shallow (less than 40 cm down into the profile) calcic horizons are evidence for the appearance of sod-forming short grasslands during the early to middle Miocene. Mollic paleosols with deeper (some 1 m or more) calcic horizons represent tall grasslands and have not been found older than late Miocene. Early stages in the evolution of grassland soils correspond to climatic coolings near the end of the Eocene and middle Miocene. The best understood climatic cooling and drying during the late Miocene (Messinian or 5–7 Ma) is synchronous with the expansion of tall C₄ grasslands.

INTRODUCTION

The origin of grasslands has long been a fundamental question in natural history (Darwin, 1872). Answers have remained elusive because of shortcomings in evidence for grasslands from fossil plants, mammals, and stable isotopes. The fossil record of grasses and their pollen in well drained soils is poor (Thomasson, 1987; Retallack, 1991a, 1992a; Leopold et al., 1992). With few exceptions (Retallack, 1992b; Dugas and Retallack, 1993), fossil plants are best preserved in swampy low-lying areas with vegetation unlike that of dry grasslands (Retallack, 1984). The silicified anthoecia of grasses in late Cenozoic paleosols represent several clades that independently evolved this mineral defense against increasing grazing pressure (Thomasson, 1985). There is no fossil record of their less-siliceous ancestors. The high-crowned teeth and elongate limbs of fossil mammals have been interpreted as adaptations to the open spaces and gritty fodder provided by grasslands (Bakker, 1983; MacFadden, 1992; Janis, 1995). The amount of time needed for such evolutionary adaptation, and the kind and extent of grasslands needed to induce it, are uncertain. More recently, the carbon isotopic composition of mammalian teeth and of paleosol carbonate has been used to infer the advent of plants using the C₄ photosynthetic pathway (Wang et al., 1994; Kingston et al., 1994; Morgan et al., 1994). Desert succulents and shrubs using the CAM photosynthetic pathway have a

heavy carbon isotopic composition overlapping that of C₄ grasses, and those grasses using the C₃ photosynthetic pathway cannot be distinguished from woody C₃ plants using the isotopic approach (Quade et al., 1989a; Smith, 1996; MacFadden et al., 1996).

Fortunately, there is also evidence of ancient grasslands from the nature of fossil soils. Paleosols can be considered trace fossils of terrestrial ecosystems, and have the additional advantage of being in the place where they formed, unlike some fossils and materials analyzed for stable isotopic composition. The study of paleosols is not without problems, but they are different problems than those for fossil plants, mammals, and stable isotopes. Much has been learned in recent years about such basic problems as paleosol recognition (Retallack, 1988), identification (Retallack, 1993), and burial alteration (Retallack, 1991b).

The aim of this field-based research was to identify grassland ecosystems, indicated by root traces and soil structure of paleosols, within a paleoclimatic context. This was accomplished by assessing soil structure and measuring the depth to calcic horizon in as many paleosols as possible of Tertiary geological age in Oregon and in South Dakota-Nebraska-Kansas (Fig. 1).

MOLLIC EPIPEDONS

A characteristic feature of soils supporting grassy vegetation is a surface horizon of small (2–5 mm) rounded clods of clayey soil, dark with organic matter intimately mixed with clay. This distinctive tilth is called a mollic epipedon (Buol et al., 1980) and is produced by the deep net of fine roots and abundant earthworms and other invertebrates of grassland ecosystems. Mollic epipedons are occasionally found under grassy woodland. Such anomalies are woodlands that invaded former grasslands following historic fire suppression (Johannessen et al., 1971) or late Holocene climatic change (Ruhe, 1970). These exceptions thus serve to prove the rule that mollic epipedons form under grasslands, not forests.

Mollic epipedons were recognized in the paleosols from common (10–20% by volume) thin, dark, clayey rinds to abundant, small (2–5 mm), rounded soil peds, in addition to abundant fine (1–2 mm diameter) root traces (Fig. 2). Mollic epipedons of surface soils are dark brown to black (Munsell hues 7.5YR-10YR and values 2–5) with organic matter, and this dark color is sometimes preserved in paleosols (Retallack, 1991a). More often paleosols are lighter colored than soils because of burial decomposition of organic matter (Retallack, 1991b). Dark color is thus a useful but not definitive character of a buried mollic epipedon. Mollic epipedons also are clayey enough to take the impression of fingerprints when moistened, even when partially lithified as paleosols. Mollic epipedons are rich in nutrients, indicated for paleosols by common carbonate or eas-

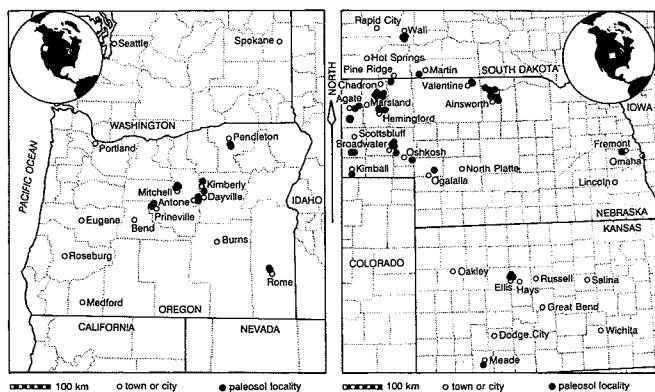


FIGURE 1—Localities for Neogene paleosols examined in Oregon and the Great Plains, U.S.A.

ily weathered minerals such as plagioclase. Other kinds of soil and soil horizons are clayey and nutrient rich (Buol et al., 1980), so these criteria are necessary but not sufficient indicators of a mollic epipedon. In summary, mollic epipedons were characterized for this study by granular peds and carbonate, and they commonly also were dark and clayey.

A category of near-mollic was used in this study for surface horizons with a structure of subangular to rounded peds some 5–10 mm in size, along with abundant fine root traces and darker color than associated horizons (Retallack, 1983; Bestland and Retallack, 1994). Near-mollic epipedons are presently found in desert grasslands and grassy woodlands with scattered bunch grasses, rather than under sod-forming grasses (Buol et al., 1980). Also used was a category of non-mollic to include all other kinds of paleosols. Among the Neogene paleosols examined for this study, these were primarily red, with platy to blocky ped structure, large root traces, and subsurface horizons of clay (Bt) and carbonate (Bk) accumulation (Retallack, 1991a). These were similar to soils of deserts and woodlands.

All the paleosols found with calcareous nodules were

classified into one of the three categories (mollic, near-mollic and non-mollic) using a reference collection of rocks (Fig. 2) to maintain consistency. Comparison also was made to the mollic and near-mollic epipedons in surface soils exposed in road cuts and creek banks in both Oregon and the Great Plains.

RAINFALL AND DEPTH TO CALCIC HORIZON

The depth to the subsurface horizon of calcareous nodules was measured in numerous Neogene paleosols, because depth to calcic horizon shows a clear relationship to mean annual rainfall (Munn et al., 1978; Retallack, 1994) and both primary (Cannon and Nielsen, 1984; Sala et al., 1988) and secondary productivity (East, 1984). In the Great Plains of North America, for example, soils of the short-grass prairie of semi-arid Colorado Springs, Colorado, have calcic horizons within 30 cm of the surface. In contrast, the calcic horizon is a meter or more down in the productive tall-grass prairie of subhumid Lincoln, Nebraska. A global compilation of 307 soils (by Retallack, 1994) yielded the following relationship between depth to the calcic horizon (d in cm) and mean annual precipitation (P in mm) with reasonable accuracy ($r=0.79$; $2\sigma = \pm 282$ mm).

$$P = 139.6 - 6.388d - 0.01303d^2$$

Calcic horizons of soils also vary in their degree of development from films and wisps of carbonate, formed in tens to hundreds of years, to nodular and solid layers, formed over several tens of thousands of years (Gile et al., 1966, 1980). Soils in the nodular stage of development are the most reliable indicators of former rainfall and productivity of paleosols (Retallack, 1994). Only these were considered in this study.

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 CO₂ in the past. Severe erosion would leave an horizon that would not qualify as mollic, nor a soil with a deep calcic horizon, so such paleosols are not significant to the first geological appearance of

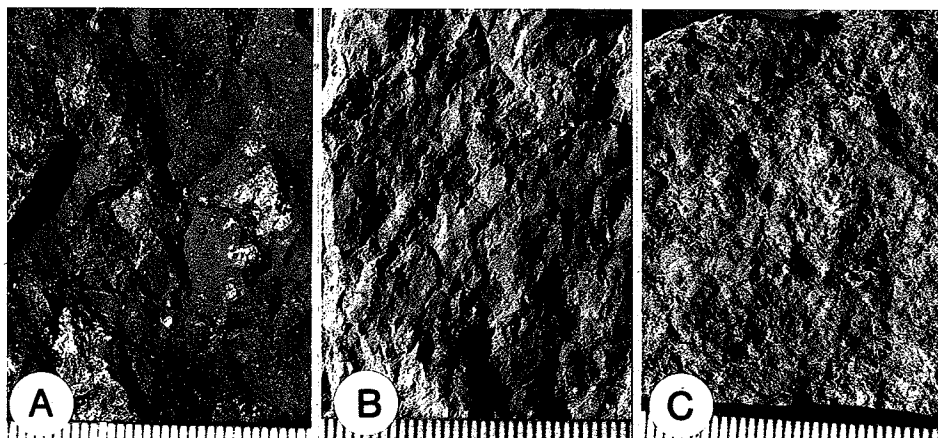


FIGURE 2—Increasingly fine and rounded units of soil structure (peds) defined by clay skins in paleosol hand specimens, here classed as (A) non-mollic (blocky angular), (B) near-mollic (fine subangular) and (C) mollic (granular). Specimens are from (A) Tuksay paleosol in late Eocene lower John Day Formation of Painted Hills Oregon (John Day Fossil Beds National Monument specimen JODA5164), (B) Ticam paleosol in early Oligocene lower John Day Formation of Painted Hills, Oregon (JODA5520), (C) “Yarmouth-Sangamon” paleosol in bluffs south of Fremont, Nebraska (Retallack specimen R1588A).

these features. Many eroded and overgrazed soils are incorporated within the modern data (Retallack, 1994), thus accounting for the substantial standard error of the equation given above. Nor are Oligocene or later changes in atmospheric CO₂ thought to have been significant enough to have altered the relationship between rainfall and carbonate depth (Cerling, 1991).

A more significant problem is compaction of paleosols after burial. Geological estimates of overburden (*D*, in km) were used to calculate compaction (*C*, as a fraction) using an equation of Sclater and Christie (1980).

$$C = -0.5/[(0.49/e^{(D/3.7)})-1]$$

A final problem is semantic confusion of the unrelated concepts of "depth to calcic horizon" and "depth of carbonate leaching". Quade and Cerling (1995) cited research by several soil scientists including me (Retallack, 1994) on the depth to the calcic horizon as if it were research on depth of carbonate leaching. The soil matrix around carbonate nodules sometimes is, and sometimes is not leached of carbonate (Retallack, 1983, 1991a), so that the depth of leaching of carbonate and the top of the zone of carbonate nodules are at different levels in soils and paleosols. The depth of carbonate leaching is known to increase with time for formation of soils (Ruhe, 1965), and shows no known relationship with rainfall. Quade and Cerling (1995) have estimated the depth of carbonate leaching for Miocene paleosols using a novel mass-balance geochemical approach that factors out bulk density. I am uncomfortable with their disregard for bulk density, because small differences in bulk density measured from paleosols can make substantial differences in molar mass transfer (Bestland et al., 1996). Nevertheless, I agree with them that depth of carbonate leaching has little paleoclimatic significance.

RESULTS FROM THE GREAT PLAINS

The scenic badlands of western Nebraska, South Dakota and Kansas are famous for fossil mammals that have been used to construct a detailed sequence of North American Land Mammal "Ages". These sequences have been radiometrically dated by a variety of means (Bayne, 1976; Thomasson, 1979; J.E. Martin, 1985; L.D. Martin, 1985; Hunt, 1985; Tedford et al., 1985; Swinehart and Diffendal, 1987; Wayne and Aber, 1991; Gardner et al., 1992; Retallack, 1992a; Woodburne and Swisher, 1995) so that numerical ages can be interpolated for most stratigraphic levels. Many of the Cenozoic paleosols of this region have been studied in detail (Singler and Picard, 1981; Retallack, 1983; Gardner et al., 1992; Lander and Hay, 1993; Terry and Evans, 1994), but for this study many additional paleosols were examined in outcrops well dated by mammal fossils and radiometry (Fig. 2, Table 1).

Remarkably, no paleosols with mollic epipedons stratigraphically lower than the Ash Hollow Formation, or older than 6 Ma (Late Miocene), had deep (more than 40 cm) calcic horizons (Fig. 3). This pattern remains equally striking upon conversion of depth of the calcic horizon, adjusted for compaction, to former mean annual rainfall (Fig. 4A). These data can be interpreted to infer that grasslands before the Pliocene were in regions receiving less than 400 mm mean annual rainfall, and that grasslands expanded

during late Miocene to early Pliocene time to fill in the area between the 500–750 mm isohyets. This area is currently occupied by tall grass prairie (Sims, 1988).

Also of interest from these data are the oldest known paleosols with mollic epipedons, in the Harrison Formation of Nebraska, perhaps as old as 22 Ma or early Miocene (Hunt, 1985). The oldest paleosols with near-mollic epipedons are known from the Scenic Member of the Brule Formation probably as old as 33 Ma or early Oligocene (Retallack, 1983, 1992a). Thus, from 7–22 Ma sod-forming short-grass prairie was present in North America. Before 22 Ma back to 33 Ma, grasslands were not sod-forming, but included bunch grasses and probably also shrubs in areas receiving some 300–400 mm mean annual rainfall.

RESULTS FROM CENTRAL OREGON

In addition to published paleosols in Cenozoic rocks of central Oregon (Retallack, 1981, 1991c,d; Getahun and Retallack, 1991; Bestland and Retallack, 1994; Bestland et al., 1994), additional profiles were examined at many well-known localities for fossil mammals (Table 2). These can be correlated using North American Land Mammal "Ages" to coeval sequences of the Great Plains (L.D. Martin, 1985; Prothero and Swisher, 1992; Woodburne and Swisher, 1995). Many Oregon localities also have been dated radiometrically (Manchester and Meyer, 1987; Bestland et al., 1994).

Paleosols with both mollic epipedons and deep calcic horizons first appear about 7 Ma (Late Miocene), in sediments associated with the Rattlesnake Tuff, a widespread ash-flow tuff (Walker, 1979). The advent of tall grassland with the range extension of grasslands to near the 750 mm isohyet was during the late Miocene to early Pliocene in Oregon, perhaps a little earlier than in the Great Plains. The first appearance of paleosols with mollic epipedon and shallow calcic horizons about 20 Ma in the Haystack Valley Member of the John Day Formation is a little later (Hemingfordian rather than late Arikareean) than in the Great Plains. The first appearance of near-mollic calcareous paleosols in Oregon, at about 30 Ma within the lower Turtle Cove Member of the John Day Formation (Bestland et al., 1994), also is a little later (lower Arikareean rather than Orellan) than in the Great Plains. These differences in timing may be due to local migration of rain shadows created by Cascade volcanoes and the Rocky Mountains, an effect already documented for Eocene and Oligocene paleosols of Wyoming compared with coeval paleosols to the east in South Dakota (Retallack, 1992a). Nevertheless, there is a similar schedule of each evolutionary advance in grassland ecosystems in Oregon and the Great Plains.

CLIMATIC EXPANSION OF GRASSLANDS

A remarkable observation arising from consideration of paleosols of Neogene age in two separate parts of North America is that mollic epipedons first appear during the early Miocene in paleosols with calcic horizons at depths of 40 cm or less, but mollic paleosols with calcic horizons as deep as 1 m appear in both areas during the late Miocene, about 6–7 Ma. This simple observation could be falsified by discovery of paleosols older than 7 Ma with a calcic ho-

TABLE 1—Neogene calcareous paleosols of South Dakota, Nebraska and Kansas.

County	Locality	Level	Ma	A horizon	Cm-Bk	Meters burial	Ref.
Morrill	SW NW S21 T19N R47W	soil	0	mollic	25	0	4, 5
Morrill	SE NE S20 T19N R47W	soil	0	mollic	36	0	4, 5
Morrill	SW NW S21 T19N R47W	Farmdale	0.05	mollic	32	1	4, 5
Morrill	SW NW S21 T19N R47W	Sangamon	0.1	mollic	76	2	4, 5
Brown	NE NW S13 T32N R21W	Sangamon	0.1	mollic	61	18	4, 6
Saunders	NW SE S34 T17N R8E	Yarmouth	0.3	mollic	62	6	7
Saunders	NW SE S34 T17N R8E	Yarmouth	0.3	mollic	73	7	7
Meade	NW NE S21 T33S R28W	Crooked Ck	1.6	mollic	88	6	16
Meade	NW NE S21 T33S R28W	Crooked Ck	1.7	mollic	92	7	16
Meade	NW NE S21 T33S R28W	Crooked Ck	2.0	mollic	59	14	16
Morrill	SE NE S20 T19N R47W	Broadwater	2.5	non-mollic	28	54	4, 5
Morrill	SE NE S20 T19N R47W	Broadwater	2.5	near-mollic	32	66	4, 5
Morrill	SE NE S20 T19N R47W	Broadwater	2.5	mollic	58	70	4, 5
Morrill	SE NW S20 T19N R47W	Broadwater	2.5	mollic	37	77	4, 5
Morrill	SE NW S20 T19N R47W	Broadwater	2.5	mollic	33	76	4, 5
Meade	NW NE S21 T33S R28W	Ballard	2.7	near-mollic	54	16	16
Meade	NW NE S21 T33S R28W	Ballard	2.8	near-mollic	42	17	16
Morrill	SW NE S20 T19N R47W	Broadwater	3.5	mollic	49	79	4, 5
Meade	NW NE S21 T33S R28W	Ballard	3.5	non-mollic	44	18	16
Brown	SW SE S24 T30N R21W	Keim	4	near-mollic	32	48	4, 6
Brown	SW SW S24 T31N R22W	Keim	4	near-mollic	43	50	4, 6
Brown	SW SW S24 T31N R22W	Keim	4	near-mollic	52	51	4, 6
Brown	SW NW S25 T31N R22W	Keim	4	mollic	38	51	4, 6
Brown	NE SE S11 T31N R23W	Keim	4	near-mollic	52	51	4, 6
Brown	NE SE S11 T31N R23W	Keim	4	mollic	29	52	4, 6
Morrill	SW NW S21 T19N R47W	"Kimball"	5	near-mollic	23	81	4, 5
Morrill	SE NE S21 T19N R47W	"Kimball"	5	non-mollic	48	81	4, 5
Morrill	SW NE S20 T19N R47W	"Kimball"	5	non-mollic	22	81	4, 5
Morrill	SE NE S21 T19N R47W	"Kimball"	5	non-mollic	52	82	4, 5
Keith	NW NW S10 T14N R38W	"Kimball"	5	non-mollic	35	82	4
Banner	NW SW S25 T18N R56W	"Kimball"	5	near-mollic	48	82	4, 8
Kimball	NW NW S8 T14N R55W	"Kimball"	5	near-mollic	24	82	4, 8
Morrill	NW SW S20 T18N R46W	"Kimball"	5	mollic	29	82	4
Ellis	NW NW S3 T12S R20W	"Kimball"	5	non-mollic	52	18	15
Ellis	NW NW S3 T12S R20W	"Kimball"	5	non-mollic	48	20	15
Ellis	SE SE S32 T11S R20W	"Kimball"	5	non-mollic	36	18	15
Ellis	SE SE S32 T11S R20W	"Kimball"	5	near-mollic	31	20	15
Ellis	SW SW S17 T12S R20W	"Kimball"	5	non-mollic	28	20	15
Keith	NW NW S10 T14N R38W	"Kimball"	5.5	near-mollic	21	84	4
Banner	NW SW S25 T18N R56W	"Kimball"	5.5	non-mollic	29	85	4, 8
Morrill	SE NE S20 T19N R47W	"Kimball"	5.5	non-mollic	67	86	4, 5
Garden	NE NE S10 T15N R42W	"Kimball"	5.5	mollic	21	87	9
Morrill	NW SW S20 T18N R46W	"Kimball"	5.5	mollic	28	88	4
Ellis	NW NW S3 T12S R20W	"Kimball"	5.5	non-mollic	48	20	15
Ellis	NW NW S3 T12S R20W	"Kimball"	5.5	non-mollic	66	22	15
Ellis	NW SW S3 T12S R20W	"Kimball"	5.5	non-mollic	36	20	15
Ellis	NW SW S3 T12S R20W	"Kimball"	5.5	non-mollic	55	22	15
Ellis	SE SE S32 T11S R20W	"Kimball"	5.5	non-mollic	35	22	15
Ellis	SE SE S4 T12S R20W	"Kimball"	5.5	non-mollic	24	20	15
Ellis	SE SE S4 T12S R20W	"Kimball"	5.5	non-mollic	42	22	15
Ellis	SW SW S17 T12S R20W	"Kimball"	5.5	non-mollic	20	22	15
Ellis	SW SW S17 T12S R20W	"Kimball"	5.5	non-mollic	19	22	15
Banner	NW SW S25 T18N R56W	Ash Hollow	6	non-mollic	22	90	4, 8
Morrill	SW NE S20 T19N R47W	Ash Hollow	6	non-mollic	22	90	4, 5
Keith	NW NW S10 T14N R38W	Ash Hollow	6	near-mollic	22	88	4
Morrill	SW NW S21 T19N R47W	Ash Hollow	6	near-mollic	25	88	4, 5
Keith	NW NW S10 T14N R38W	Ash Hollow	6	near-mollic	23	89	4
Morrill	SW NW S21 T19N R47W	Ash Hollow	6	near-mollic	32	89	4, 5
Ellis	NW NW S3 T12S R20W	Ash Hollow	6	mollic	36	24	15
Ellis	NE NE S4 T12S R20W	Ash Hollow	6	mollic	79	31	15
Ellis	NE NE S4 T12S R20W	Ash Hollow	6	near-mollic	37	32	15
Ellis	SW SW S17 T12S R20W	Ash Hollow	6	near-mollic	63	24	15
Morrill	SE NE S20 T19N R47W	Ash Hollow	6.5	near-mollic	44	93	4, 5
Kimball	SW SW S5 T14N R55W	Ash Hollow	6.5	mollic	33	93	4, 8
Banner	NW SW S25 T18N R56W	Ash Hollow	6.5	near-mollic	39	95	4, 8
Morrill	NW SW S20 T18N R46W	Ash Hollow	6.5	non-mollic	24	98	4
Garden	NE NE S10 T15N R42W	Ash Hollow	6.5	non-mollic	47	102	4, 9

TABLE 1—Continued.

County	Locality	Level	Ma	A horizon	Cm-Bk	Meters burial	Ref.
Morrill	NW SW S20 T18N R46W	Ash Hollow	7	near-mollic	37	106	4
Garden	NE NE S10 T15N R42W	Ash Hollow	7	non-mollic	33	106	4, 9
Cherry	NW NE S22 T34N R27W	Cap Rock	10	near-mollic	44	69	4, 10
Cherry	NW NE S22 T34N R27W	Cap Rock	10	mollic	36	70	4, 10
Cherry	NW NE S22 T34N R27W	Cap Rock	10	non-mollic	71	71	4, 10
Bennett	SW NE S8 T36N R39W	Cap Rock	11	near-mollic	20	183	11
Morrill	NE NW S10 T18N R47W	Duer Ranch	12	non-mollic	73	151	5
Morrill	NE NW S10 T18N R47W	Duer Ranch	12	non-mollic	41	152	5
Brown	SE SW S33 T33N R23E	Cornell Dam	15	near-mollic	44	135	4, 10
Brown	SE SW S33 T33N R23E	Cornell Dam	15	near-mollic	39	136	4, 10
Cherry	NW SE S22 T34N R27W	Cornell Dam	15	mollic	32	137	4, 10
Brown	SE SW S33 T33N R23E	Cornell Dam	15	near-mollic	66	138	4, 10
Cherry	NW SE S22 T34N R27W	Cornell Dam	15	mollic	29	138	4, 10
Cherry	NW SE S22 T34N R27W	Cornell Dam	15	mollic	36	139	4, 10
Cherry	NW SE S22 T34N R27W	Cornell Dam	15	mollic	32	140	1, 7, 8
Cherry	NW SE S22 T34N R27W	Cornell Dam	15	mollic	31	141	1, 7, 8
Sioux	SE NE S30 T26N R55W	Sheep Creek	16	mollic	33	308	1, 7, 8
Sioux	SE NE S30 T26N R55W	Sheep Creek	16	near-mollic	29	310	1, 10
Sioux	SE NE S30 T26N R55W	Sheep Creek	16	non-mollic	42	316	1, 10
Sioux	SE NE S30 T26N R55W	Sheep Creek	16	non-mollic	39	328	1, 10
Dawes	NW NW S14 T30N R49W	Dawes	17	near-mollic	69	276	11
Box Butte	NW NW S29 T28N R51W	Dawes	17	near-mollic	53	286	11
Dawes	NW NW S14 T30N R49W	Dawes	17	near-mollic	32	287	11
Box Butte	NW NW S29 T28N R51W	Dawes	17	near-mollic	69	289	11
Box Butte	NW NW S29 T28N R51W	Dawes	17	near-mollic	46	292	11
Box Butte	NW NW S29 T28N R51W	Dawes	17	near-mollic	66	295	11
Box Butte	NW NW S29 T28N R51W	Dawes	17	near-mollic	44	300	11
Dawes	NW SE S29 T30N R47W	Red Valley	17	non-mollic	64	303	11
Dawes	NW SE S29 T30N R47W	Red Valley	17	non-mollic	52	303	11
Dawes	NE NE S15 T30N R49W	Runningwater	18	mollic	33	308	11
Dawes	NE NE S15 T30N R49W	Runningwater	18	near-mollic	29	311	11
Box Butte	SW NW S8 T28N R49W	Runningwater	18	near-mollic	31	311	11
Box Butte	SW NW S8 T28N R49W	Runningwater	18	non-mollic	41	313	11
Box Butte	SW NW S8 T28N R49W	Runningwater	18	near-mollic	29	315	11
Dawes	NE NE S15 T30N R49W	Runningwater	18	non-mollic	28	316	11
Dawes	NW SE S29 T30N R47W	Runningwater	18	non-mollic	26	316	11
Dawes	NW SE S29 T30N R47W	Runningwater	18	non-mollic	71	319	11
Dawes	NE NE S15 T30N R49W	Runningwater	18	non-mollic	33	323	11
Bennett	NE NE S36 T37N R39W	Batesland	18	non-mollic	15	369	9
Sioux	SW NE S10 T28N R55W	"Harrison"	20	mollic	30	156	12
Sioux	SW NE S10 T28N R55W	"Harrison"	20	mollic	25	156	12
Sioux	NE SE S27 T32N R56W	Harrison	21	non-mollic	30	157	12
Sioux	SE SE S36 T29N R54W	Monroe Ck	22	near-mollic	43	578	13
Sioux	SE SE S36 T29N R54W	Monroe Ck	22	near-mollic	78	581	13
Sioux	SE SE S36 T29N R54W	Monroe Ck	22	near-mollic	59	584	13
Sioux	SE SE S36 T29N R54W	Monroe Ck	22	near-mollic	61	628	13
Box Butte	NE NW S27 T28N R49W	Marsland	23	non-mollic	41	331	11
Box Butte	NE NW S27 T28N R49W	Marsland	23	non-mollic	52	332	11
Cherry	NW SE S22 T34N R27W	Rosebud	24	near-mollic	43	142	7, 8
Brown	NE SW S33 T33N R23W	Rosebud	24	non-mollic	45	144	7, 8
Brown	NE SW S33 T33N R23W	Rosebud	24	non-mollic	47	145	7, 8
Brown	NE SW S33 T33N R23W	Rosebud	24	non-mollic	51	146	7, 8
Brown	NE SW S33 T33N R23W	Rosebud	24	near-mollic	51	148	7, 8
Sheridan	NE NE S11 T34N R46W	brown silst.	30	non-mollic	60	244	14

References: 1, Shultz and Stout (1980); 2, Swinehart and Diffendal (1987); 3, Skinner and Hibbard (1972); 4, Wayne (1987), Wayne and Aber (1991); 5, Gardner et al. (1992); 6, Diffendal (1987); 7, Skinner and Johnson (1984); 8, Voorhies (1987); 9, Martin (1985); 10, Skinner et al. (1977); 11, Galusha (1975); 12, Hunt (1985); 13, Yatkola (1978); 14, Tedford et al. (1985); 15, Thomasson (1979); 16, Bayne (1976).

rizons at more than a reconstructed depth of 1 m and a mollic epipedon.

These observations of fossil mollic epipedons (Fig. 4) can be interpreted as evidence for expansion of grasslands at 6–7 Ma into wetter climatic regions. The ecotone between grassland and woodland shifted from the 400 mm isohyet to near the 750 mm isohyet, closer to where it is today near

1000 mm (Sims, 1988). This was a time of dramatic geographic, as well as climatic, expansion of grasslands and of the origin of tall grasslands in subhumid to humid regions. Short grasslands on the other hand evolved well back in the Miocene. Rangelands lacking sod-forming grasses may be as ancient as Oligocene in South Dakota (Retallack, 1983), and Eocene in Argentina (Retallack, 1990a; Mac-

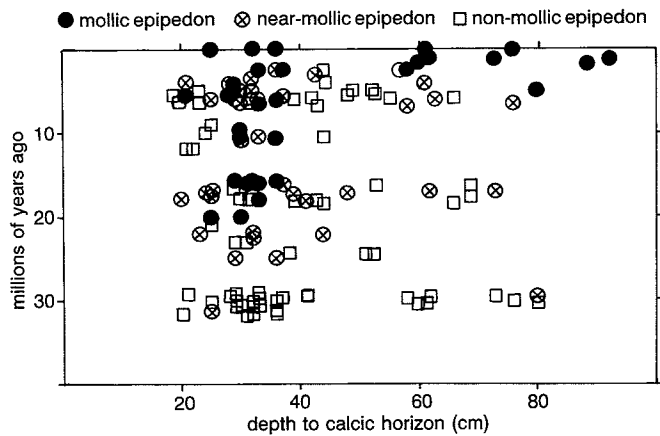


FIGURE 3—Nature of surface horizon (mollic, near mollic or non-mollic) and depth to calcic horizon of Neogene calcareous paleosols of South Dakota, Nebraska and Kansas, showing an early Messinian (6–7 Ma) expansion of mollic horizons to paleosols with calcic horizons deeper than 40 cm.

Fadden et al., 1996). There was thus no single origin of grassland ecosystems, but several discernable thresholds of modernization corresponding to the sequential appearance and spread of early rangelands, short grasslands, and tall grasslands (Fig. 5).

This new view from paleosols may aid in reconciling past debate concerning the evolution of grasslands. Oligocene rangeland paleosols are evidence for an ecosystem most like modern desert grasslands and shrublands of the intermontane western U.S.A. Few Oligocene grass fossils are known (Galbreath, 1974; Bestland and Retallack, 1994), but sediments of Oligocene mesic bottomlands and lake deposits include mainly woody plants (Wolfe, 1987; Manchester and Meyer, 1987; Leopold et al., 1992). Oligocene mammals are only slightly more hypsodont and cursorial than those of the late Eocene (Bakker, 1983; MacFadden, 1992), and their overall level of adaptation is more like that of creatures now living in woodlands than grasslands (Janis, 1995). The early Oligocene advent of open country was simultaneous with a variety of indica-

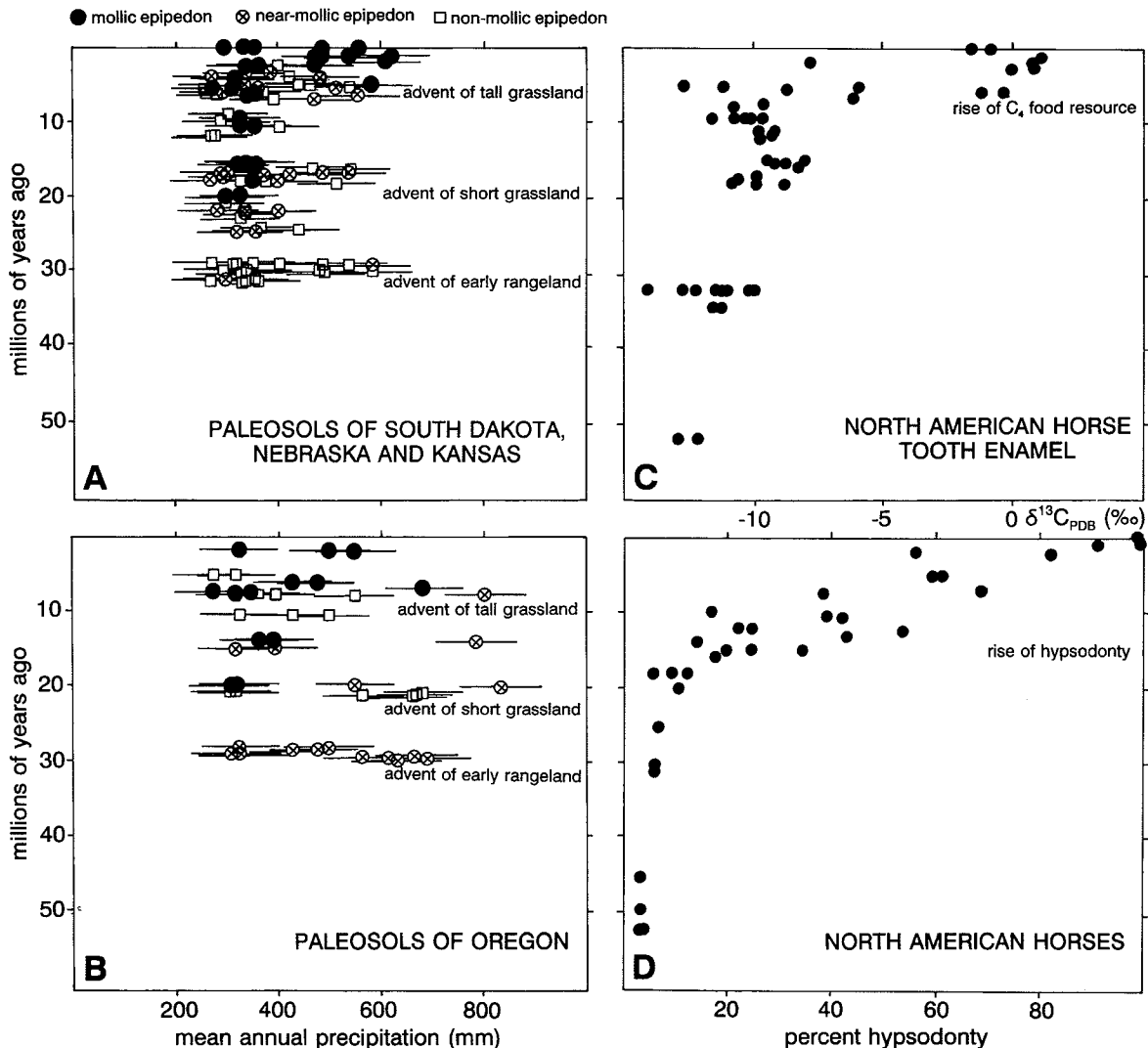


FIGURE 4—Early Messinian expansion of grasslands (mollic epipedons) into paleosols of more humid climate in South Dakota-Nebraska-Kansas (A) and Oregon (B), compared with other indications of grassland evolution, from the carbon isotopic composition of horse tooth enamel (C; from Wang and others, 1994) and the increased hypsodontology of fossil horses (D; from MacFadden, 1992).

TABLE 2—Neogene calcareous paleosols of Oregon.

County	Locality	Level	Ma	A horizon	Cm-Bk	Meters burial	Ref.
Wheeler	NE SW S3 T11S R21E	terrace gravel	2	mollic	31	1	1
Wheeler	NE SW S3 T11S R21E	terrace gravel	2	mollic	65	2	1
Wheeler	NE SW S3 T11S R21E	terrace gravel	2	mollic	76	2	1
Crook	NW SE S1 T15S R15E	Deschutes	5	non-mollic	28	20	2
Crook	NW NE S1 T15S R15E	Deschutes	5	non-mollic	34	20	2
Umatilla	SW NE S3 T1N R32E	"McKay"	6	mollic	50	20	3
Umatilla	SW NE S3 T1N R32E	"McKay"	6	mollic	60	21	3
Wheeler	SE SE S24 T12S R25E	"Rattlesnake"	7	near-mollic	68	211	4
Wheeler	NW SE S16 T13S R25E	"Rattlesnake"	7	mollic	21	227	4
Wheeler	NW SE S16 T13S R25E	"Rattlesnake"	7	mollic	33	228	4
Grant	NE NW S31 T12S R26E	"Rattlesnake"	7	non-mollic	48	230	4
Wheeler	SE SE S24 T12S R25E	"Rattlesnake"	7	near-mollic	48	230	4
Wheeler	NW SE S16 T13S R25E	"Rattlesnake"	7	mollic	28	231	4
Wheeler	NW SE S16 T13S R25E	"Rattlesnake"	7	non-mollic	24	235	4
Wheeler	NW SE S16 T13S R25E	"Rattlesnake"	7	near-mollic	31	236	4
Wheeler	SE SE S24 T12S R25E	"Rattlesnake"	7	non-mollic	39	240	4
Wheeler	SE SE S24 T12S R25E	"Rattlesnake"	7	non-mollic	37	241	4
Wheeler	SW NE S36 T12S R25E	"Rattlesnake"	7	mollic	103	244	4
Malheur	SW NE S6 T32S R41E	"Rome"	10	non-mollic	35	20	5
Malheur	SW NE S6 T32S R41E	"Rome"	10	non-mollic	25	21	5
Malheur	SW NE S6 T32S R41E	"Rome"	10	non-mollic	33	22	5
Wheeler	NW SE S31 T12S R25E	Mascall	14	mollic	36	248	6
Wheeler	NE SW S16 T12S R25E	Mascall	14	mollic	41	248	6
Wheeler	NE SW S16 T12S R25E	Mascall	14	near-mollic	58	249	6
Wheeler	SE NW S24 T12S R25E	Mascall	15	near-mollic	120	820	6
Wheeler	SE NW S24 T12S R25E	Mascall	15	near-mollic	125	832	6
Wheeler	SE NW S24 T12S R25E	Mascall	15	near-mollic	136	833	6
Grant	NW NW S20 T10S R26E	Haystack Vall.	20	mollic	24	1165	7
Grant	NW NW S20 T10S R26E	Haystack Vall.	20	mollic	22	1172	7
Grant	NW NW S20 T10S R26E	Haystack Vall.	20	near-mollic	39	1174	7
Wheeler	NE SW S34 T10S R21E	Haystack Vall.	20	near-mollic	76	1209	1
Grant	NW NW S20 T10S R26E	Kimberly	21	non-mollic	26	1217	7
Grant	NW NW S20 T10S R26E	Kimberly	21	non-mollic	25	1218	7
Grant	NW NW S20 T10S R26E	Kimberly	21	non-mollic	32	1219	7
Grant	NW NW S20 T10S R26E	Kimberly	21	non-mollic	33	1220	7
Grant	NW NW S20 T10S R26E	Kimberly	21	non-mollic	21	1221	7
Grant	NW SW S20 T9S R26E	Kimberly	21	non-mollic	20	1259	7
Grant	NW SW S20 T9S R26E	Kimberly	21	non-mollic	20	1259	7
Wheeler	NW SE S36 T10S R20E	Turtle Cove	28	near-mollic	67	1753	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	28	near-mollic	82	1755	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	28	near-mollic	58	1764	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	28	near-mollic	76	1780	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	28	non-mollic	98	1793	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	29	near-mollic	106	1812	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	29	near-mollic	83	1815	
Wheeler	NW SE S36 T10S R20E	Turtle Cove	29	near-mollic	96	1816	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	29	near-mollic	110	1821	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	29	near-mollic	83	1825	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	30	near-mollic	82	1854	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	30	near-mollic	86	1855	1
Wheeler	NW SE S36 T10S R20E	Turtle Cove	30	near-mollic	72	1856	1
Grant	SW SE S31 T10S R26E	Turtle Cove	30	near-mollic	76	1853	7

References: 1, Bestland et al. (1994); 2, Swanson (1969); 3, Shotwell (1956); 4, Merriam et al. (1925); 5, Wilson (1937); 6, Downs (1956); 7, Fisher and Rensberger (1972).

tions of climatic drying, including fossil soils, plants, snails, turtles, alligators and mammals (Retallack, 1992a, 1994; Bestland et al., 1994).

Grassland paleosols with sod-like structure are clearly recognizable by early to middle Miocene time, which was a time of dramatic evolutionary adaptive radiation for a variety of grassland creatures, including grasses (Thomason, 1987), daisies (Singh, 1988), legumes (Axelrod, 1992; Wheeler and Landon, 1992), dung beetles (Retallack, 1990b), bees (Burnham, 1978; Thackray, 1994), colubrid

snakes (Rage, 1984), passerine birds (Feduccia, 1980; Unwin, 1988), and ungulate mammals (Bakker, 1983; MacFadden, 1992; Janis, 1995). The coarse gritty fodder and open spaces of grasslands provided significant selection pressure for the evolution of hypsodonty and cursoriality in fossil ungulates, which can be dated at 18 Ma and 23 Ma, respectively (Fig. 3D). Middle Miocene moderately hypsodont and cursorial ungulates coexisted with grasses richly invested with defensive silica. Wide subrectangular snouts and striated tooth microwear are additional evi-

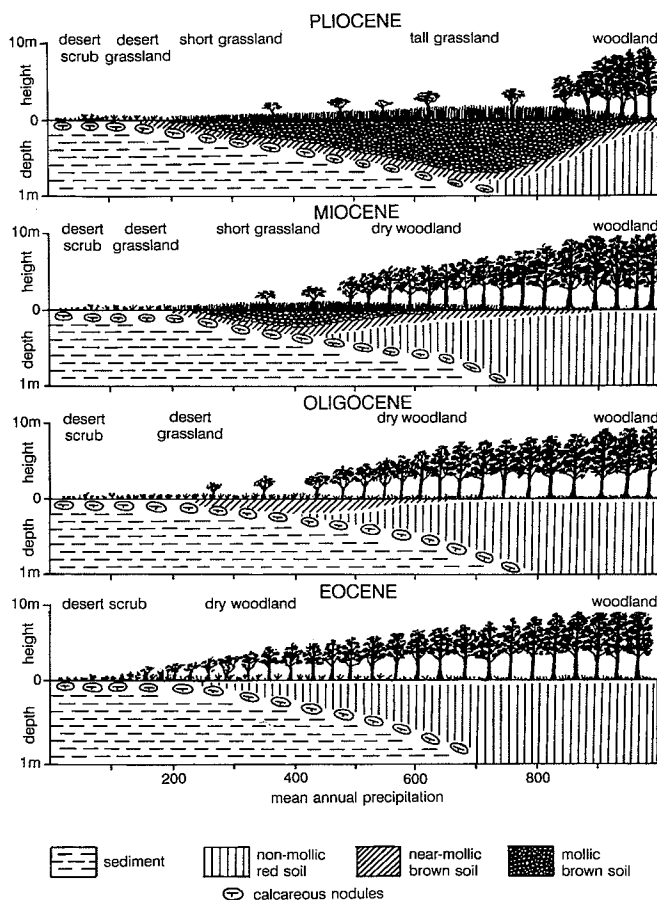


FIGURE 5—A scenario for the stepwise evolution of grassland ecosystems in arid to subhumid climatic regions during the past 50 million years.

dence that some mammals were grazing by middle Miocene time (Hayek et al., 1992). The middle Miocene was another prominent episode of climatic cooling and drying, judging from fossil soils, plants and mammals (Schultz and Stout, 1980; Retallack, 1991a; Axelrod, 1992). This time of global change was coincident with the Monterey isotopic excursion in the ocean (Vincent and Berger, 1985). Coevolution of grasses, grazers, and other rangeland creatures was well underway by middle Miocene, when the pressure of climatic drying may have selected for new levels of coadaptation.

This is not to say that middle Miocene grassland ecosystems were identical to modern North American prairies. Modern levels of ungulate size, hypsodonty, and cursoriality were not achieved until late Miocene and Pliocene time (Bakker, 1983; MacFadden, 1992; Harris, 1993; Janis, 1995). This was a time when protection of grass anthocia by biological silicification appeared in several evolutionary clades of grasses and an increased number of species (Thomasson, 1987). Thus the 6–7 Ma climatic expansion of grasslands to include tall-grass prairie (proposed here) was another significant step toward modernization in a protracted coevolution of grasses and grazers.

Such a schedule of grassland evolution also has become apparent from isotopic approaches. Isotopic studies aim to detect grasslands from the distinctive heavy ratio of $\delta^{13}\text{C}$

found in tropical to warm temperate grasses using the Hatch-Slack or C_4 photosynthetic pathway, compared with light $\delta^{13}\text{C}$ of the Calvin or C_3 pathway used by trees, shrubs, and cool-climate to montane grasses. The isotopic signature of C_4 grasses is reflected in the carbon isotopic composition of carbonate in paleosols and apatite in teeth and bones of herbivores (Wang et al., 1994). The dramatic shift to isotopically heavier values at 5–7 Ma has proven robust and widespread in both pedogenic carbonate and mammalian tooth enamel from Nebraska and South Dakota (Fig. 3C), as well as other parts of the world (Cerling, 1992; Kingston et al., 1994; MacFadden et al., 1994, 1996).

When this prominent isotopic shift was first discovered in paleosol carbonate from Pakistan and Kenya, Quade et al. (1989b) and Cerling (1992) argued that it meant that grasslands first appeared no earlier than late Miocene. This is unlikely because middle Miocene isotopic signatures of C_4 grasslands have been found in Kenya (Kingston et al., 1994; Morgan et al., 1994), complementing evidence from fossil grasses, mammals, and soils for middle Miocene grasslands there (Retallack, 1991a, 1992b, Dugas and Retallack, 1993; Retallack et al., 1990; Solounias and Moelleken, 1993). Similarly a drift toward heavier values after 20 Ma in North America (Fig. 4C) may indicate initial infiltration of C_4 grasses into C_3 grasslands and woodlands (Smith, 1996; MacFadden et al., 1996).

In another early explanation for the isotopic shift in Pakistan, Quade et al. (1989b) argued that it reflected the origin or a marked intensification of monsoonal circulation in the northeastern Indian Ocean. This is also unlikely because a similar isotopic shift has been found in North and South America which are remote from the Indian Ocean (Wang et al., 1994; MacFadden et al., 1994, 1996). Strong monsoonal circulation can be inferred from Pakistani paleosols as old as 16 Ma, but is not apparent from Miocene paleosols in Kenya (Retallack, 1991a) or the North American profiles examined for this study.

What the isotopic evidence does demonstrate is that expansion of tall grasslands from 6–7 Ma involved dramatically increased abundance of C_4 grasses. The rise of the C_4 photosynthetic pathway in such widely dispersed localities has more recently been attributed to a global lowering of atmospheric CO_2 at this time (Cerling et al., 1993). The C_4 grasses have a competitive advantage over C_3 plants when CO_2 becomes limiting (Ehleringer et al., 1991). Independent confirmation of CO_2 drawdown comes from the rise in oceanic pH from 7.4 to 8.2 at 6 Ma inferred from boron isotopes (^{11}B) in marine foraminifera (Spivack et al., 1993). Studies of the stomatal distribution of fossil oak leaves indicate reduction at about 6 Ma from some 350 to 280 ppmV (parts per million by volume: van der Burgh et al., 1993), which is comparable to the change from preindustrial levels of about 280 ppmV to 1990 levels of 353 ppmV (Su, 1994).

The 6–7 Ma spread of grasslands was synchronous with the Messinian stage of the Late Miocene, currently dated at 5.32 to 7.12 Ma (Berggren et al., 1995). This was a time of marked changes in the world ocean. There was a particularly marked excursion of $\delta^{13}\text{C}$ in benthic foraminifera at 5.75 Ma (Zhang and Scott, 1996), which was to isotopically lighter values (Flower and Kennett, 1994), due in part to storage of isotopically heavier carbon in C_4 vegetation and soil organic matter. Such negative excursions also would

reflect diminution of organic carbon burial in the sea (Schidlowski and Aharon, 1992), if isotopic composition and quantity of carbon delivered to the ocean remained constant, which is unlikely (Cerling et al., 1993). Marine regression began with the Messinian (7.12 Ma) and culminated in a series of low stands at 6.59, 6.01, 5.89, 5.75, 5.7, 5.65 and 5.55 Ma (Zhang and Scott, 1996). The Lower Evaporite representing extreme dessication of the Mediterranean Sea probably correlates with the very profound low stand at 5.75 Ma, and the Upper Evaporite with the low stand at 5.55 Ma (Hsü et al., 1973; 1977; Hodell et al., 1986; Berggren et al., 1995). The geographic and climatic expansion of C₄ tall grasslands was an additional component of these global changes during the Late Miocene.

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