PALEOPEDOLOGICAL PERSPECTIVES ON THE DEVELOPMENT OF GRASSLANDS DURING THE TERTIARY

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ABSTRACT--Fossil soils have been little exploited as evidence for understanding the evolution of terrestrial ecosystems. Root traces, profile development, color and mineralogy of fossil soils can be reasonable evidence for the size and structure of vegetation, as well as other features of paleoenvironments. Such independent evidence from fossil soils can be useful in assessing how representative is the preserved fossil record of an ecosystem, and also in assessing the degree to which fossil plants and animals appear to have been adapted to their paleoenvironment.

Causes for the maintenance of modern grasslands appear to be numerous, inter-related and of greatly varying importance. Effects of many of these causal factors may be preserved in fossil soils and associated animal and plant fossils. In what is now Badlands National Park (South Dakota), small tracts of prairie (treeless grassland) appear to have developed primarily in response to semi-arid climate. In the subsequent coevolution of various elements of grassland ecosystems of the Great Plains, the interacting factors of fire, animal activity and plant competition appear to have become more important.

INTRODUCTION

One of the most remarkable transformations of terrestrial ecosystems during the Tertiary was the spread of grasslands on all major continents of the world (Retallack, 1981a). Grasses may have evolved during the Cretaceous, and some sedges were almost certainly present then (Muller, 1981). The oldest securely identified grass pollen are Paleocene in age (Muller, 1981) and the oldest trustworthy megafossil grasses are Eocene (Litke, 1968). It was during the mid and late Tertiary, however, that grasses first formed distinctive and widespread vegetation types. This was a time of dramatic diversification of herbaceous angiosperms in general (Muller, 1981; Tiffney, 1981) and of profound changes in coevolving mammalian faunas (Van Couvering, 1980; Stebbins, 1981). The effects of these changes are known in some detail from studies of living grassland ecosystems and Tertiary fossil mammals. The paleobotanical record is patchy, as grassland habitats are generally unfavorable for preservation of fossil plants (Retallack, 1981a, in press a). In this essay, I explore a little exploited line of evidence for understanding the origin and rise of grasslands, the paleoenvironmental interpretation of fossil soils (paleosols). Grassland soils, like all soils, are products not merely of the organisms which they support, but also of climate, topographic position, parent material and time for formation (Jenny, 1941). Various features of fossil soils may thus be evidence, sometimes of causes and sometimes of effects of biotic changes.

RECONSTRUCTING GRASSLAND ECOSYSTEMS FROM FOSSIL SOILS

Root traces, profile development, color and mineralogy of fossil soils are often reasonable evidence for the size and structure of ancient vegetation and the former degree of waterlogging (Retallack, 1981a). Other aspects of ancient vegetation, for example, whether it was coniferous, sclerophyllous, thorny, broad-leaved or deciduous, as well as the climate in which it formed, are not accurately (if at all) assessed from fossil soils alone. Unfortunately, most classifications of modern vegetation rely on these latter features of vegetation (Beard, 1978), and so are unsuitable for studies of fossil soils in areas in which associated fossil plants are not preserved. I have found the simplified classification of Daubenmire (1968, p. 251) best, and have used it here. Grassland is a generic term for vegetation in which grasses or sedges are prominent, and includes savanna, shrub savanna, parkland, groveland, steppe, meadow steppe, meadow, marsh and salt marsh. Prairie (North America) and pampas (South America) are regional synonyms of steppe.

There are often striking preservational (taphonomic) biases among fossils found in paleosols. In the Late Eocene and Oligocene succession in Badlands National Park, South Dakota (Retallack, in press a,b,c), no fossil leaves, pollen or spores have been found, despite prolonged and deliberate search by numerous investigators. Plants must have grown there at the time, because there are abundant root traces and other features of fossil soils, common fossil hackberry endocarps and abundant fossil herbivores. In addition to many of the usual factors determining the abundance of fossils, such as original population numbers, predation and scavenging (Behrensmeyer and Hill, 1980), fossils in paleosols must also have survived a variety of physically, chemically and biologically destructive processes in soils. From archeological studies (Chaplin, 1971; Evans, 1972), the original Eh and pH of the soils appears to be an important determinant of fossil occurrence in paleosols. None of the fossil soils in Badlands National Park contain siderite nodules or other features of prolonged waterlogging, so all were probably well drained and oxidized (Retallack, in press b). Considering the rapid microbial degradation of modern leaves, pollen and spores in oxidizing conditions (Krumbein and Garrels, 1951; Havinga, 1971; Elsik, 1971), it is not surprising that such plant fossils were not preserved in this sequence of paleosols. Calcareous endocarps of hackberry (*Celtis hatcheri*) and phosphatic bones were only found in moderately calcareous to strongly calcareous paleosols, which were presumably neutral to alkaline in reaction. It is unlikely, however, that mammals did not also live on the other kinds of

fossil soils found in Badlands National Park. Large (2-3 cm diam.) fossil land snails (*Pseudolisinoe leidyi*) were only found in strongly calcareous paleosols which also had large root traces. These latter are evidence of trees, on which snail populations may have been somehow dependent. Snails were not found in non-calcareous paleosols, in which shells would have been dissolved and in which calcium for shell construction was probably in short supply. Nor are they found in strongly calcareous paleosols which lack evidence of trees. Thus each kind of paleosol is a unique taphonomic situation, as well as evidence of a particular paleoenvironment.

Independent evidence of paleoenvironments from fossil soils can be used to assess the evolution of associated plant and animal fossils. Many features of fossil mammals, such as high crowned (hypsodont) teeth and long rigid lower limbs, have been used as evidence for former grassy open vegetation (Van Couvering, 1980). In such work it is necessary to assume that these features were adaptive, an assumption labelled the "Panglossian paradigm" by Gould and Lewontin (1979). Independent evidence from fossil soils can break the round of circular reasoning from which evolution, paleoecology and paleoenvironments have all been interpreted from fossil bones. For example, in Badlands National Park, the appearance of several savanna-adapted mammals during the latest Eocene and Early Oligocene deposition of the Chadron Formation (Clark and others, 1967) is sooner than would have been expected considering the predominance of woodland paleosols at this stratigraphic level (Retallack, in press c). Evidence from paleosols adds credence to the hypothesis that these creatures invaded from savannas elsewhere (Clark and others, 1967; Emry, 1981), rather than evolving locally. Diverse savanna-adapted faunas appear to have been well suited to mid-Oligocene environments of interstream savanna, streamside gallery forest and stream-bank marshes, indicated by paleosols within the Brule Formation. When the overlying Sharps Formation was accumulating during the Late Oligocene, scattered trees appear to have grown beside deeply-entrenched streams, but most of the floodplain supported open grasslands, to judge from fossil soils. Within the Sharps Formation, there are remains of many creatures physically smaller than their presumed ancestors and of more creatures adapted for burrowing than in underlying formations. On the other hand, most endemic lineages persisted, including long-necked camels. Diversity remained high, and there was no acceleration in the acquisition of locomotor or dental adaptations for open grassland (MacDonald, 1963, 1970; Webb, 1977). Despite the changed environment, the fauna changed little and remained basically savanna-adapted. Local and temporary grasslands were probably important selective pressures for the evolution of the whole suite of adaptations characteristic of mammalian faunas of treeless grasslands (as outlined by Gregory, 1971). Open grassland paleosols of the Sharps Formation predate the Miocene appearance and Pliocene diversification of abundant fossil siliceous and calcareous stony bodies (phytoliths) of prairie grasses and forbs (Thomassen, 1979, 1980). Since phytoliths are all that is likely to be preserved of plants growing in oxidizing soils, they may be a very biased representation of original vegetation. The widespread and increased stoniness of propagules and leaves of grasses and herbs during the Tertiary was probably a coevolutionary protection against increasingly rapacious mammalian grazers (Stebbins, 1981). From these examples, it is apparent that the study of fossil soils (paleopedology) can contribute fresh perspectives for understanding the fossil record of ancient ecosystems.

AGE AND DISTRIBUTION OF TERTIARY GRASSLAND PALEOSOLS

There are now numerous published studies on pre-Quaternary paleosols, many of these providing some insights into when and where grasslands developed from earlier woodlands and forests (Retallack, 1981a). Fossil soils in northwest Wyoming provide evidence of Early Eocene valley-bottom woodlands growing in soils identified as aquods, ferrods, ultisols and aquents (Neasham and Vondra, 1972; Bown and Kraus, 1981a,b). Also during the Eocene in nearby Wyoming and Oregon, forested soils appear to have extended to moderate elevations on the flanks of active volcanoes (Dorf, 1964; Fritz, 1980; Retallack, 1981a,b,c). The broad distribution of late Mesozoic and early Tertiary forests throughout the world is especially well seen from the widespread deep weathering zones, laterites and bauxites of that age (Retallack, 1981a, and references therein). Apparently wooded Late Cretaceous and Tertiary paleosols have also been reported in Mexico (McBride, 1974), United States (Fisher, 1964; Johnson and Heron, 1965; Braunagel and Stanley, 1977; Schiebout, 1979; Singer and Nkedi-Kizza, 1980), Ireland (Reffay and Ricq-Debouard, 1970), England (Buurman, 1980) and France (Pomerol, 1964; Freytet, 1971, 1973).

In Eocene and Oligocene volcaniclastic ashy, alluvial and eolian deposits of Argentina, there is an unusually complete record of the transition from savanna or woodland to open grassland, in the form of fossil soils, mammals, phytoliths, burrows of earthworms and insects and the buried larval boli of dung beetles (Frenguelli, 1938, 1939; Andreis, 1972; Spalletti and Mazzoni, 1978; Stebbins, 1981). Few of these paleosols have been described in detail. Some appear to have been savanna or woodland soils with drab-colored eluvial and reddish illuvial horizons (Frenguelli, 1939, p. 384). Others were identified as grassland soils of well-drained (udolls of Soil Survey Staff, 1975) and poorly-drained sites (aquolls) forming in a humid climate (Spalletti and Mazzoni, 1978, p. 278).

A comparable transition from forests, to woodlands, to savanna and open grasslands has been documented in volcaniclastic ashy Late Eocene and Oligocene alluvium of Badlands National Park, South Dakota (Retallack, in press a,b,c). Under initially warm humid climate, a forested kaolinitic ultisol (of Soil Survey Staff, 1975) developed on the unconformity with underlying smectitic Cretaceous marine shales. Drier climates of the Eocene-Oligocene transition are indicated at first by a well-developed paleudalf and then successive paleustalf paleosols, all formed under woodland. During the mid-Oligocene, fluvents of streamside swales supported herbaceous vegetation, petrocalcic paleustalfs of stream margins probably supported gallery woodlands and savanna grew in andic ustochrept soils widespread between streams. Well-drained calciorthid and poorly-drained ustollic eutrandept paleosols of floodplains above deeply entrenched streams, provide the first evidence of open grasslands and semi-arid climate of the Late Oligocene. Other Tertiary paleosols of the Great Plains have not been studied in detail. Fossil vertisols (McBride and others, 1968; Galloway, 1978)

and abundant paleosols with calcic and petrocalcic horizons (Reeves, 1970), are evidence that seasonal, subhumid to semi-arid climates, and probably also savanna and other grassland vegetation, were widespread during the mid and Late Tertiary.

Numerous paleosols in Miocene fluvial outwash of the Himalaya, Karakorum and Hindu Kush Mountains of northern Pakistan and India, appear to have formed in a complex and changing environment of rainforests, woodlands, grovelands and savanna, in a seasonally-dry subtropical climate (Pilgrim, 1913; Johnson, 1977; Visser and Johnson, 1978; Badgley and Behrensmeyer, 1980). The thick volcaniclastic and alluvial sediments of the Rift Valley in Kenya and Tanzania also include many Miocene paleosols. Those at Fort Ternan fossil hominoid site have been identified as "Braunlehm" (Bishop and Whyte, 1962), and presumably formed under open vegetation (Andrews, 1981; Shipman and others, 1981).

FACTORS IN THE DEVELOPMENT OF GRASSLANDS

The numerous proposed causes for the maintenance of modern grasslands (Vogl, 1974; Walker and others, 1981) can be grouped into six major causal factors: climatic seasonality and drying, excessively dry or wet unstable habitats, physiographic flatness, fire, animal activity and plant competition. Dry climates are favored by grasslands, as are physiologically dry habitats such as permafrosted, brackish, saline, bedrock or well-drained locations. Grasslands also develop in excessively waterlogged habitats. Seasonal climates are favored by grasslands as are unstable habitats in general. Grasses are often among the earliest colonizers of new surfaces and can die back to the root stock during unfavorably dry, snowy or windy seasons. Grasslands of the plains produce characteristic soil profiles (mollisols of Soil Survey Staff, 1975), with upper horizons rich in finely-disseminated organic matter and alkaline and alkaline earth cations. As they develop, grassland soils may become attractive for the colonization of trees, provided grass cover is disrupted or shaded out. Physiographic flatness has been cited as a factor, but its role appears to be mainly in facilitating the effect of other factors, such as the spread of fires and the free movement of animals. Grasses recover readily from fires fatal to other plants, especially seedling trees. Grass fires can be caused by lightning, by spontaneous combustion of organic materials or from heated stones. Human use of fire for hunting, clearing, pasture improvement, discouraging predators, repelling insects, communication, warfare or just accidentally spread from camp fires, has greatly increased the importance of fire for grasslands. Within the general factor of animal activity I include a variety of processes which may affect trees, bushes and non-grassy herbs differently than grasses; such as browsing, grazing, girdling, trampling, wallowing, digging, burrowing, overpopulation, lack of predators, mass migration, insect plagues, disease, human land clearing and cultivation. Plant competition includes a number of ways in which grasses can persist over non-grassy plants, for example, by being first to colonize fresh surfaces or by shading out young tree seedlings with their dense low growth. Of course, there are scattered bunch-grasses in marshes of humid mountainous regions which are little burned (Cockayne and Godley, 1967, p. 162). Cases such as this, indicate that these factors vary considerably in importance for different grasslands.

Let us once again consider the Late Eocene and Oligocene sequence in Badlands National Park (Retallack, in press a,b,c) for clues to factors in the origin of the North American prairie. Gradually drying climate is clearly in evidence in this sequence of paleosols in the form of calcic horizons, which first appear during the Early Oligocene during deposition of the upper Chadron Formation, and then become increasingly differentiated and thick in successive paleosols. Open woodlands which presumably vegetated petrocalcic paleustalfs of the upper Chadron Formation may have had some grassy undergrowth, and grasses were probably prominent in savanna vegetation of calcareous andic ustochrept paleosols in the mid-Oligocene Scenic Member of the Brule Formation. The oldest paleosols of open grassland, found in the Late Oligocene upper Poleslide Member of the Brule Formation and in the Sharps Formation, were calciorthids, with well-differentiated, shallow calcareous nodules, and indistinct accreting surface horizons. Judging from the distribution of cracks, clay skins and fine root traces in well preserved examples, these calciorthid paleosols supported scattered bunch grasses or other herbs on dusty well-drained floodplains. A few trees persisted in fluvaquentic eutrochrepts beside deeply-entrenched streams at this stratigraphic level.

Burning of savanna trees commonly leaves charcoal, but grasses may burn leaving only phytoliths and finely-disseminated organic matter, like those ordinarily derived from plant decay, dung and dust. Charcoal is a remarkably decay-resistant organic material (Cope and Chaloner, 1980), found in a great variety of Quaternary paleosols (Vogel and Zagwijn, 1967; Evans, 1972; Fölster and Hetsch, 1978; Csongor and others, 1980). Thus it is surprising that no fossil charcoal was seen in any Badlands paleosols. Fire would not have spread so easily in the presumed bunch grass prairie during the Late Oligocene in the Badlands area, as in sod-forming grasses of the modern North American prairie. It is likely that fires were much less frequent and important to grasslands before the advent of pyromaniac humans.

Since, as already discussed, savanna-adapted mammals appear in the Badlands succession at a time of extensive woodlands, and savanna vegetation appears a few million years later, then it is possible that browsing and other activities of mammals contributed to the development of savanna. The same cannot be said for the initial development of prairie. A savanna-adapted fauna appears to have persisted in the Badlands area at a time of extensive open grasslands. It was only after Miocene desertification (Stanley, 1976) and faunal overturn (Webb, 1977; Emry, 1981) that mammalian faunas show appreciably widespread adaptations to open country grazing.

If the earliest prairie vegetation in the Badlands area consisted of scattered bunch grasses, then competition between adjacent plants is unlikely to have been a factor in its development. Grasses and other prairie herbs do appear, however, to have been more successful than other plants as colonizers of unstable dusty soils in a semi-arid climate. In this sense, plant competition can be seen as a contributing factor, subordinate to climate.

CONCLUSIONS

Prairie in what is now Badlands National Park, South Dakota, appears to have evolved during the Late Oligocene, and savanna somewhat earlier, during the mid-Oligocene, both primarily in response to

increasingly dry climate. In the subsequent development of grasslands on the Great Plains, the interacting factors of fire, animal activity and plant competition may have become more important as various elements of grassland ecosystems became more complexly inter-related.

The degree to which these tentative conclusions can be considered general, needs to be further investigated. The evidence of fossil soils can provide fresh paleoecological perspectives on old problems, but is yet to be fully and rigorously exploited.

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