Mound Building by Pocket Gophers (Geomyidae): Their Impact on Soils and Vegetation in North America

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Mound building by pocket gophers (*Geomyidae*): their impact on soils and vegetation in North America

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SUMMARY. This study assesses the role of fossorial rodents, as exemplified by *Geomyidae,* in the formation of the North American patterned ground feature, the mima mound. Both the literature and original research presented in the paper demonstrate that *Geomyidae* can significantly alter texture, percentage of organic matter, mineral availability, and the soil moisture content of mima mound soils. As a result, plant growth in a semi-arid environment is enhanced, and is accompanied by related changes in the quality and quantity of vegetation in areas of *Geomyidae* activity. Through initiation and sustained development of soils and vegetation, *Geomyidae* provide a dynamic force to direct the biogeochemical attributes of the North American Prairie lands. Evidence that *Geomyidae* can create an open prairie ecosystem in disturbed or badly eroded areas suggests that the activities of fossorial rodents may provide an explanation for the genesis of North American Prairie soils.

Introduction

In the geomorphic literature, 'patterned ground' usually refers to high latitude or high mountain, Pleistocene or recent, symmetrical forms that are characteristic of regions subject to intensive frost action (Washburn, 1956). One such symmetrical form is the circular or mound feature called 'pingo', 'pulsa' or 'polygon' (Washburn, 1973). This paper, in contrast, focuses on the mound-like patterned ground features of middle-latitude and generally semi-arid areas of North America called 'mima mounds' or, alternatively, 'pimple mounds', whose essential characteristics include a regular spatial pattern and bi-convex soil lens (Fig. 1).

Two major groups of theories attempt to explain the origin of mima mounds. The first attributes their origin to physical phenomena such as ice, water, and aeolian forces (Cain, 1974; Péwé, 1948; Ritchie, 1953), while the second traces mound development to animal activity, especially that of fossorial rodents (Dalquest & Scheffer, 1942; Price, 1949, 1950; Scheffer, 1958). A serious problem with the physical hypothesis of mima mound origin in mid-latitudinal regions of medium to low elevation is that such explanations are invariably based on some hypothesized event in the distant past. This paper, however, is based on the assumption that existing well-known and measurable processes, as exemplified by the ecology of one family of fossorial rodents, *Geomyidae,* can provide a comprehensive explanation of mima mound development.

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Geomyidae: general characteristics

Members of the *Geomyidae* family range from 70–350 g in weight and have specialized front claws for digging, with fur-lined cheek pouches which open to either side of the mouth; hence, the name 'pocket gopher'. The distribution of the ten major species of

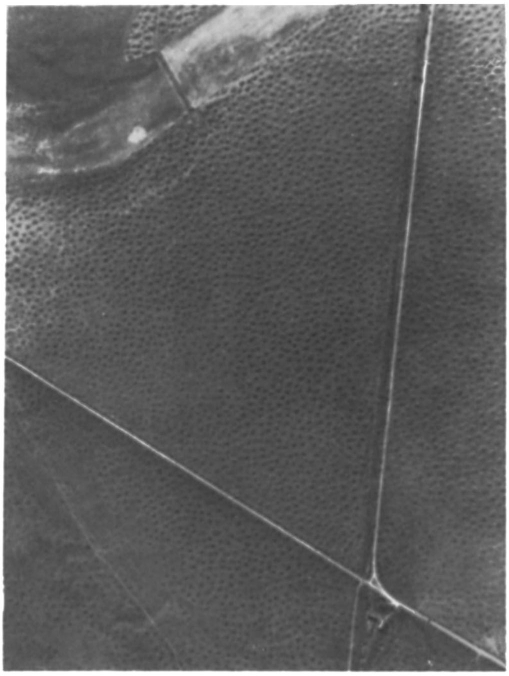

FIG. 1. Mima Prairie, located about 3 km southwest of Tenino, Thurston County, Washington. These mounds have an average diameter of 6 m, an average height of 1.8 m, and contain about 1.42 m^3 of soil. The top of the photograph is west.

the family, including seven subspecies, broadly corresponds to that of the mid-latitudinal grass and shrub lands of North America (Fig. 2).

Gophers are solitary in habit. With the exception of the spring mating season, it is rare to find more than one per burrow (Bailey, 1893). Thus, on each of fifty-three mounds in Black Mesa, Colorado, only one gopher was trapped, and on six other mounds, one adult and one subadult were captured (Scheffer, 1958); and similar findings have been reported by Arkley & Brown (1954), Davis, Ramsey & Arendale (1938), and Hansen (1962). Their preferred diet consists mainly of forbs. Thus at Black Mesa, Colorado, where vegetation in the gopher habitat was estimated to be 50% grasses, 42% forbs, and 8% shrubs, the stomach contents of 397 gophers consisted of 92.6% forbs by volume, 6.0% grasses, and 1.4% shrubs and insects (Ward & Keith, 1962). Although the relative proportion of leaf, stem, and root material of each plant type found in their stomachs varied with the season, the overall percentage of forbs therein remained high at all times, always exceeding 72% by volume.

The effect of forb reduction on gopher populations has been demonstrated: in the case of Grand Mesa herbicide application of 2,4-D resulted in an 83% reduction in forbs, and also gave rise to an 87% reduction in the numbers of pocket gophers (Keith, Hansen & Ward, 1959).

Mima mound characteristics

Mima mounds have been described as ranging in height from less than 610 mm in Texas and Louisiana (Koons, 1948), to between 305 mm and 914 mm in California (Arkley & Brown, 1954), and between 406 mm and 1270 mm in Minnesota (Ross, Tester & Breckenridge, 1968). The locational distribution of the mima mounds which have been examined thus far is shown in Fig. 3. No particular type of geologic formation necessarily comprises the substratum of mima mounds locations: they are present on hardpan near San Diego and Fresno, California (Scheffer, 1947), claypan in northwestern Minnesota (Ross *et al.*, 1968), basaltic rock southeast of Mt Hood, Oregon (Scheffer, 1947), sandy soil underlain by sandstone in the Uncompahgre Plateau, Colorado (McGinnies, 1960), deep clay in Texas and Louisiana (Koons, 1948), tightly compacted gravel pavement at Rocky Flat, Yakima County, Washington (here mounds have been built by the transfer of suitable soil material from beneath to on top of the pavement through a naturally occurring break; Scheffer, 1947); serpentine near Stanford University in California (Proctor & Whitten, 1971), and volcanic ash in Black Mesa, Colorado (Hansen & Morris, 1968). Their presence is unrelated to bedrock units in the gas and coal regions of the lower Mississippi basin (Knechtel, 1949).

Geomyidae and mima mounds

The activity of pocket gophers as a possible explanation for mima mound formation has been carefully studied by Dalquest & Scheffer (1942) on a prairie about 3 km southwest of

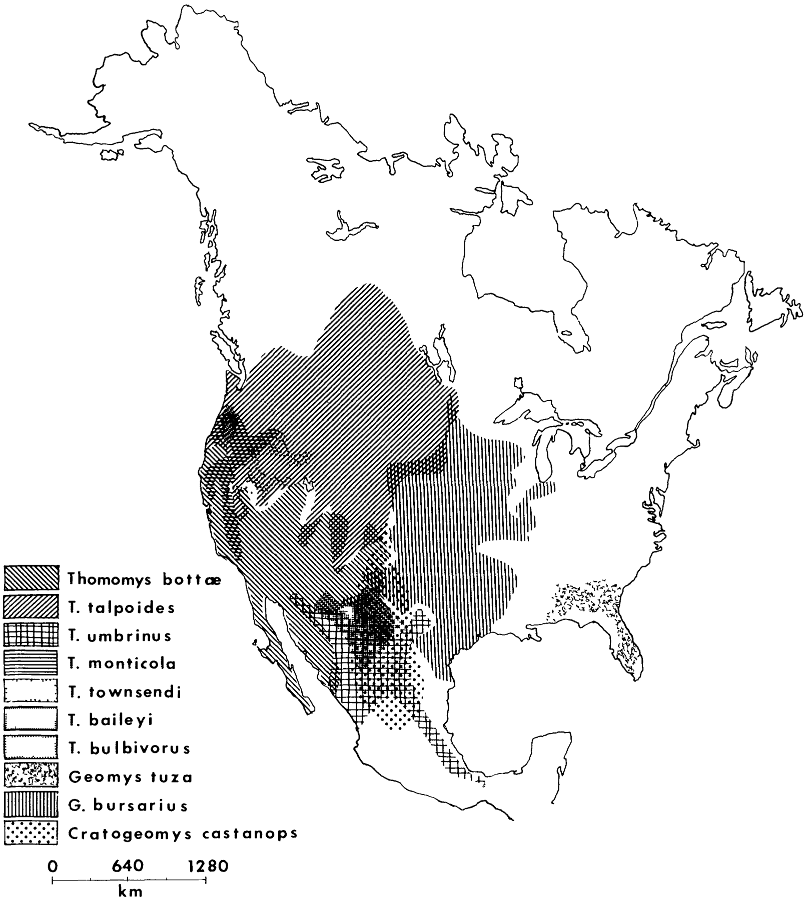

FIG. 2. Generalized distribution of the North American species of *Geomyidae* (from Burt & Grossenheider, 1959). The voids between certain species classes in western North America are probably attributable to the generalized nature of the original maps.

Tenino, Washington (Fig. 1). They suggest that the occurrence of all mima-type mounds of middle-latitude North America can be explained by the digging activities of gophers (this was extended to all fossorial rodents by Scheffer in 1958). Impressed by the amount of soil material that gophers move, they hypothesized the following: (1) gophers move material to the top of the mound from tunnels radiating through the mounds away from the mound entrance; (2) gophers, upon encountering a large stone, dig under it, and eventually the stone settles, forming the cobble bed which characterizes the mounds of Mima Prairie; (3) gophers, upon encountering a small pebble (up to 51 mm in diameter), dig around it and pull it through the mound to the surface; (4) gophers dig 'exploratory' burrows on the edges of mounds, which eventually fill up with worked soil, forming 'mound roots'; (5) gophers dig into the mounds to a depth of several feet to build nests; (6) the constant movement of soil to the top of the mound mixes the mound soil very thoroughly and accounts for the presence of a high organic content throughout the mound.

Further to this, the digging behaviour of the southeastern pocket gopher has been carefully assessed by Hickman & Brown (1973a). An excavating gopher of this group, upon encountering a root, quickly gnaws the plant material away. The gopher pushes loosened soil out of tunnels with its head and forepaws, using its hind legs in a series of jerky movements until the material reaches

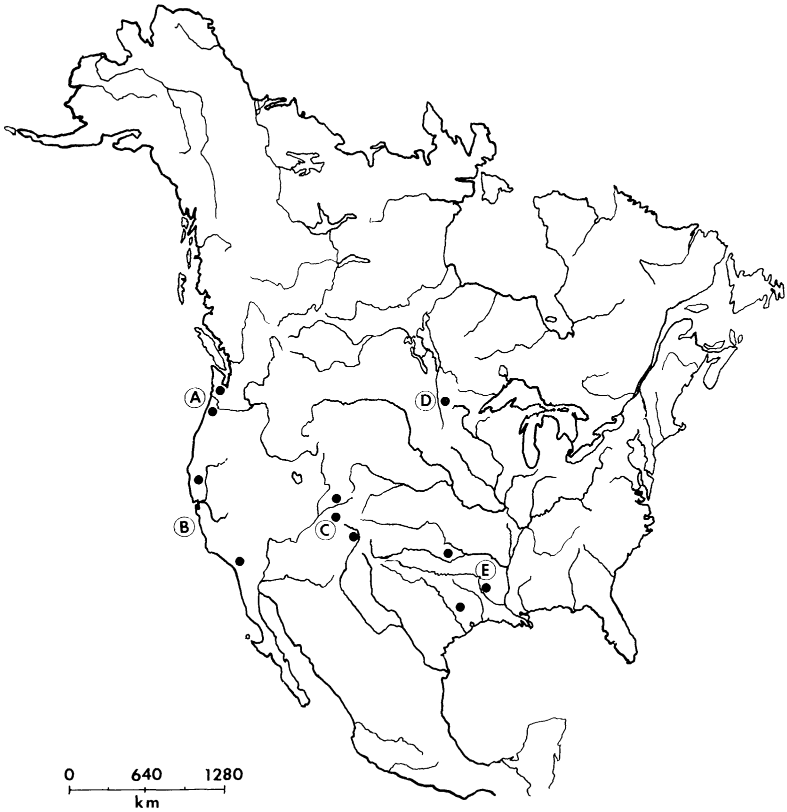

FIG. 3. Distribution of mima mound sites referred to in this paper. A, references by Dalquest & Scheffer, 1942; Péwé, 1948; Price, 1949; Ritchie, 1953; Scheffer, 1947, 1958; B, references by Arkley & Brown, 1954; Scheffer, 1947; C, references by Hansen, 1962; Hansen & Morris, 1968; McGinnies, 1960; D, references by Ross, Tester & Breckenridge, 1968; E, references by Cain, 1974; Knechtel, 1949; Koons, 1948.

the tunnel entrance, where it is thrust out to form the mound.

'Gopher mounds' and 'Mima mounds'

The pile of fresh soil ejecta which marks the activity of a gopher is commonly referred to as a 'gopher mound', 'gopher hill' or 'soil mound'. These small piles or mounds are not to be confused with mima mounds, which are much larger in size. The long-term accumulation of relatively small ejections of soil by gophers and other fossorial rodents leads to the formation of the larger mima mounds.

In northwestern Minnesota, soil ejection activity has been measured on different sizes of mima mounds. It was found there that medium and large mima mounds (6.2 to 13.6 m and more than 13.6 m in diameter, respectively) had proportionately a greater number of soil ejection piles than small mima mounds, of less than 6.2 m in diameter (Ross *et al.*, 1968). Most observations of digging activity have been illustrated in terms of the number of fresh burrow soil ejections, or 'gopher mounds', produced in a given time period, without reference to the soil volume displaced. For example, a 304 g male *Geomys pinetis* (referred to as *G. tuza* by Burt & Grossenheider, 1959) is known to have produced sixty-two 'mounds' a month in one December, while a female (150 g) produced forty-seven over the same period (Hickman & Brown, 1973b). In a fourteen-day period, three Sherburne County, Minnesota, gophers (*Thomomys talpoides*) produced twenty-eight, thirty-five, and forty ejections for an average of 2.86 'mounds'/gopher/day (Bailey, 1929). Twenty *Geomys bursarius* averaged 1.88 'mounds'/gopher/day (Mohr & Mohr, 1936). Other research has provided more precise calculations of the quantities of soil moved by gophers (*G. bursarius*), as for example that near College Station, Texas (Beuchner, 1942) where, in a tall grass area on sandy loam soil, gophers moved an estimated 808 kgs of soil/ha/yr (720 lbs/acre/yr). In a moderately over-grazed area on the same site, which was characterized by more forbs and weedy species, gopher soil ejection activity was found to increase by almost twenty times over that in the tall grass area, and the amount of soil brought to the surface was calculated at 15 903 kg/ha/yr (14 160 lbs/acre/yr).

Vegetation disturbance and mounding activity

Rates of mound building activities of *Geomyidae* tend generally to increase when vegetation has been disturbed, a phenomenon which has been noted by several authors. Thus burrows of *Pappageomys castanops* (referred to as *Cratogeomys castanops* by Burt & Grossenheider, 1959), *Geomys bursarius,* and *Thomomys bottae* have been shown by Best (1973) to be more common in disturbed areas such as roadways and floodplains in New Mexico; and after a logging operation in southwestern Oregon, *Thomomys monticola* subspecies *mazama*) was observed by Hooven (1971) to multiply rapidly in the cleared areas.

Any disturbance of prairie areas, such as that associated with heavy grazing or mowing, tends to favour the growth of forbs over grasses and sedges, because the forbs are then released '. . . from shade and vigorous competition . . .' (Weaver, 1954). Increases in gopher activity observed in disturbed areas may thus be taken to be related to the effects of disturbance on the growth rate and production of forbs, and in turn, the vegetation of areas where gophers are present will reflect the combined effects of their feeding, burrowing, and mound building activities.

This may be exemplified by an eight-year study (1942–1950) conducted on the Wasatch plateau of central Utah (Ellison & Aldous, 1952), in which the air-dry herbage production of two 2-acre plots, designated as 'gopher present' and 'gopher absent' areas, was estimated in order to determine the effects of gophers on vegetation. In the 'gopher present' plot, the total herbage production remained essentially unchanged for the period of the study, although the composition of specific plants changed considerably. Taproot species (especially *Taraxacum officinale*) decreased from 27–4%, while rhizomatous species (all forbs) increased from 55–76% of the total vegetation. In the 'gopher absent' plot, only 88% of the total vegetation present at the beginning of the experiment remained at its conclusion. Taproot species increased from 8–14%, while rhizomatous species decreased from 58–50% of the total vegetation).

Also, in forest land of southwestern Oregon, *Thomomys monticola* (subspecies *mazama*) has been observed to multiply after clear cutting to the point that through feeding and burrowing they can destroy 87–89% of seedlings within 5 years, thus thwarting reforestation efforts (Hooven, 1971). In this particular instance, it is clear that once the forest has been removed and gophers became established, an open prairie habitat could be maintained in a climatic regime which might otherwise be expected to support trees.

In northwestern Minnesota, 83% of the mima mounds studied have been characterized as being colonized by weedy forbs or shrubs with few grasses, as compared to the grass–forb vegetation typical of adjacent upland prairie (Ross *et al.,* 1968). It is suggested that by the activity of ejecting soil during mound-building, gophers themselves create a local disturbance of prairie vegetation which enhances the growth of forbs, the major component of their diet.

In addition to changes in plant species composition, quantities of vegetation also are affected by mounding activity. Thus in a seeding programme on the Uncompahgre Plateau (2438 m) in western Colorado, herbage from mound and intermound areas was sampled with the following results: 'Air-dry herbage yields from the tops of the mounds were greater than the yields from between the mounds, by an average of 94% (intermediate wheatgrass), 180% (crested wheatgrass), 323% (smooth brome), 358% (Russian wild rye), and 542% (big bluegass)

(McGinnies, 1960). McGinnies also noted that even in the droughty spring and early summer of 1959, plants on mounds matured to seed, whereas on intermound areas seed heads were rare, even in favourable years. High quantities of herbage (not specifying vegetation type) have been reported on mima mounds by many other researchers, including Dalquest & Scheffer (1942), Koons (1948) and Hansen (1962).

Biogeochemical significance of mound building

The biogeochemical significance of digging activity by gophers is most easily comprehended by examining and comparing characteristics of mound and intermound soils. An analysis of two sites in western Colorado is presented in the following Tables. Table 1 is a comparison made by McGinnies (1960) of mound and intermound soils found at an elevation of 2438 m on the Uncompahgre Plateau, Colorado; and the soil characteristics presented in Table 2 were collected and prepared by the author. The soils were collected from an open grassland at an elevation of 3048 m near Mesa Creek of Black Mesa, located in the Gunnison National Forest, Colorado.

TABLE 1. Mound and intermound soil characteristics of Uncompahgre Plateau, Colorado.

Soil characteristics	Mound	Intermound
Soil pH	6.4	6.4
Soil salts (%)	0.06	0.06
Phosphorus (kg/ha)	78.6	65.1
Potassium (kg/ha)	290.9	168.5
Organic matter (%)	4.8	2.9
Sand (%)	44.8	42.0
Silt (%)	49.9	47.5
Clay (%)	5.3	10.5

TABLE 2. Mound and intermound soil characteristics of Black Mesa, Colorado.

Soil characteristics	Mound	Intermound
Soil pH	5.2	5.6
Phosphorus (kg/ha)	32.1	22.7
Potassium (kg/ha)	844.5	383.0
Calcium (kg/ha)	3374.5	3774.3
Magnesium (kg/ha)	501.8	429.0
Cation exchange capacity (Meq)	19	17
Organic matter (%)	5.3	3.2
Soil colour (Munsell)	10YR 4/3	10YR 6/3
Sand (%)	44.3	46.0
Silt (%)	39.7	40.0
Clay (%)	16.0	14.0
Soil moisture (%)	7.7	2.6

Several important physical and chemical differences between mound and intermound soils are illustrated in these Tables. Textures of mound and intermound soils differ. The intermound soil in Table 1 is a loam, but the mound soil is a silt-loam. This is a significant factor for vegetation in the Uncompahgre Plateau because the amount of water available for plant growth (i.e. the difference between soil wilting coefficient and field capacity) is greater in a silt-loam than in a loam soil (Brady, 1974). 620 m higher, in the cooler and more humid climate of Black Mesa, water availability is less of a problem for plant growth. Although both mound and intermound soils are technically loams, the mound soils tend to have a higher clay content.

Other researchers have reported on soil mixing and sorting by gophers, and the resulting texture changes. Thus in northwestern Minnesota, gophers have mixed clay hard pan with overlying silt loam (Ross *et al.*, 1968). In west-central Colorado, gopher mounds and mima mounds are composed of a mixture of volcanic ash and topsoil, while the winter burrow casts of gophers and the soils of areas unoccupied by gophers contain no volcanic ash (Hansen & Morris, 1968). The soils of these alpine and grassland areas were further analysed in terms of size categories of particles, ranging from 'fine material' (6.3 mm) to 'medium pebbles and larger' (25.4 mm). It was discovered that fine materials made up 78.3% of the soils uninhabited by gophers in the alpine areas, but constituted 90.0% of soils inhabited by gophers. Medium pebbles and larger material made up 18.0% of the uninhabited alpine soils, but only 5.0% of the soils inhabited by gophers. In the grassland area, fine material accounted for 82.7% of the soils uninhabited by gophers, while it comprised 89.9% of the gopher-inhabited soils. In addition, the soil percentage of medium pebbles dropped from 5.3–1.0% from the unoccupied to the occupied areas respectively (Hansen & Morris, 1968). This study clearly demonstrates that the gopher's role in sorting regolith materials acts to increase soil quality in both alpine and grassland regions.

A second distinguishing feature between mound and intermound soils displayed in Tables 1 and 2 is the disparity in their organic matter content. The mound soils of both sites contain 66% more organic matter than intermound soils. The increase in organic matter content also accounts for the darker colour of the mound soils of Table 2. Increases in organic matter in mound soils have also been measured in northwestern Minnesota. There, the percentage of organic matter in intermound soils decreased from a relatively high value (5.3%) at the soil surface to a relatively low value (3.5%) at a depth of 0.31 m, while the mima mound value remained persistently high (4.9–7.0%) to a depth of 0.76 m (Ross *et al.,* 1968). Soil organic matter is a constituent of major significance because of its influence on soil structure, nutrient availability, and micro-organism activity.

Even small amounts of organic matter aid in the formation of a more granular soil structure and thus increase the friability of a particular soil. The friability of mima mound compared with intermound soils has been noted in many studies (Dalquest & Scheffer, 1942; Ellison & Aldous, 1952; Hansen & Morris, 1968; McGinnies, 1960; Price, 1949; and Ross *et al.,* 1968). Compared with compact soils, friable soils contain more air spaces, which aid root-oxygen metabolism. Roots, being non-green parts of a plant, must undergo respiration, a process which requires a supply of air. Any depletion of soil oxygen would lessen aerobic metabolism and, consequently, the absorption of mineral ions by roots (Epstein, 1972). Granular soil, in addition, facilitates the penetration and extension of roots as they establish new soil contacts for absorbing moisture and nutrients (Brady, 1974). Finally, the results obtained by the author illustrate the principle that a friable soil absorbs more water and has a higher water holding capacity than does a more compact soil of lower organic matter. The mound soils of Black Mesa contained 196% more soil moisture than the intermound soils.

Greater quantities of organic matter also foster cation exchange capacity and mineral availability. Tables 1 and 2 indicate that the Uncompahgre mounds have 20.7% and 72.7% more phosphorus and potassium than intermound soils, and the Black Mesa mounds have 41%, 120% and 17% more phosphorus, potassium and magnesium than the intermound soils. Even though the level of calcium of Black Mesa mound soil is 11.8% lower than the intermound soil, the overall cation exchange capacity is still more favourable in the mound soils. These results indicate that mound soils have a relatively high level of fertility, so that plants would require less soil moisture to produce a given amount of herbage (Brady, 1974).

Moreover, soil mixing by gophers also influences mineral availability. In a Russian study, burrowing mammals, including gophers, were found to be major agents of transport of enriched chemical substances from deeper to upper soil layers in steppe, semi-desert, and desert environments (Abaturov, 1972). Some evidence of gopher-mixing of a specific mineral has been found in northwestern Minnesota, where mound soils lack the calcium-enriched lower horizon which is characteristic of prairie soils (Ross *et al.,* 1968).

Other soil characteristics of the mima mound are related to its external morphology. Its dome-shaped surface has a degree of slope which increases the intensity of solar radiation income in periods when the angle of incidence is low, a feature which is especially important in increasing the heating of the mound soil during the winter season. Indeed the existence of higher winter temperatures on mima mounds, as compared to neighbouring non-mounded soils, has been reported in northwestern Minnesota. Another feature is that near-surface wind speeds have been shown to greatly increase on the lee side of mounds (Ross *et al.,* 1968), thus encouraging the deposition of aeolian (dust) materials and snow, and so leading to an increase in the quantities of fine materials and moisture present, as opposed to flat, unmounded regions.

Compared with well-drained soils, wet soils are generally colder because they require more available energy to be heated to a given temperature than do drier soils. The top of the bi-convex lens of soil of the mima mound is well drained, yet the mound retains a moisture reserve at its dish-shaped bottom, similar to that which has been observed in impervious geological strata such as clay (Price, 1949; Scheffer, 1947; McGinnies, 1960; Koons, 1948; Ross *et al.,* 1968). The good drainage at the top of the mound increases the rate of soil-warming during spring, thereby increasing the length of the growing season and accelerating the rate of plant growth.

Hence, soil mixing, sorting, and mounding by gophers have a positive influence on vegetation development by altering soil texture, humus content, mineral availability, friability, and even topography. These changes are especially important in an arid environment, because each of them contributes either to an increased availability of water or to an increased efficiency of water use. Furthermore, the local enhancement of vegetation growth in itself plays an additional role in soil development by providing food material for gophers which, on passing through the intestinal tract of the animal, goes to increase the amount of humus in the soil. This enclave of enriched soil and vegetation also furnishes sustenance for migrating herbivores, whose activities in turn increase the biogeochemical complexity of the mounds.

Conclusions

The impact of gophers on the North American prairie environment

Several events have significantly altered the extent of gopher activity in North America within the last century. One of the key areas in which such events may be studied in detail is that originally occupied by prairie grasslands. In the early nineteenth century, the gopher was part of the American bison-prairie system. Although no precise computations were made at the time that the wild herds existed, Ernest Thompson Seton's estimate of 40 000 000 bison (weighing as much as 910 kg for bulls and 545 kg for cows) is considered 'well-reasoned' for the early 1800's (Roe, 1951). Pronghorn, weighing 45–57 kg each, also roamed the prairie at the same time in numbers equal to those of the bison (Skinner, 1922). These herbivores exercised a considerable impact on prairie vegetation, for the bison were known to graze heavily certain areas of the prairies, so much so, in fact, that both detachments of the United States Army and early settlers commonly complained of huge herds which left so little grass that it was difficult to find sufficient fodder for their horses and other domesticated animals (Roe, 1951).

The activities of the bison and the gopher complemented each other. The bison grazed and trampled the dense prairie vegetation, accelerating forb growth, on which the gophers thrived. The gopher, in turn, worked the soil, thus increasing soil fertility and stimulating vegetation growth, to provide food for the bison.

The completion of the first transcontinental railroad in 1869, coupled with a deliberate programme of bison slaughter by the federal government, led to a rapid decrease in the number of bison thereafter. The extension of the northern route of the railroad to Bismarck, North Dakota, and further (1876–1882), quickened the pace of extermination. By 1883, the American bison was virtually extinct as a free-roaming animal in North America. Domesticated cattle and sheep then replaced it as the principal grazing animals on the prairie (Clark, 1956). The settlement of the prairies was hastened as a result of laws which provided for the division of the land through the use of the rectangular survey (Land Ordinances of 1785–1832), and the distribution of the land under the Homestead Act of 1862. The combined effect of the grid pattern of land partitioning and the late nineteenth century development of steam-powered tractors for ploughing, followed by kerosene- and gasoline-powered tractors, placed a great strain on prairie soils, leading to their precipitous deterioration (Johnson, 1974; Bennett, 1955).

At the same time, mima mounds were destroyed by ploughing (Ross *et al.*, 1968); furthermore, the consequence of soil movement by gophers was viewed increasingly in a negative term. The 1892 *Yearbook of Agriculture* noted that gophers '. . . injure almost every farm crop that can be raised, but are especially destructive in alfalfa patches, meadows, and fields of small grain, where every hill thrown up covers and kills the plants on the spot where it lies'. In gardens, gophers were reported to '. . . feed eagerly upon potatoes, carrots, turnips, and the like, and also on the roots of vines and fruit trees' (Bailey, 1893). Indeed in 1892, the United States Department of Agriculture took the position that the injury to crops caused by pocket gophers '. . . is an evil of such magnitude over more than two-thirds of the total area of the United States that there is a general demand for some economic means of destroying them' (Bailey, 1893). Traps and poisons of various kinds were advanced as the most economical means of gopher destruction. The public response to the 'evils' of the pocket gopher is illustrated in the creation, by the early settlers and residents of Viola, Minnesota, of a festival called the Viola Gopher Count, '. . . dedicated to the extinction of gophers,' which has been held since 1874 (Molda & Smith, 1974), with bounties paid by both state and federal governments. Present scientific inquiry into the prairie environment must take into account activities such as these, and also the influence of animal life forms living therein if the development of prairie soils and vegetation is to be placed in its proper perspective.

With many prairie soils now being badly eroded, it is difficult to appreciate the forces that once made them unequalled in depth, and quality. Weaver, in a summary discussion of a fifty-year study of the American prairies, remained skeptical about the prospects for recovery of vegetation in areas in which soils had deteriorated due to plowing, drought, and erosion, and noted that '. . . where there is a good cover of grass there is no serious problem of erosion. But where the cover of grass is broken or removed, erosion is the inevitable consequence' (Weaver, 1968). Weaver found it difficult to explain how, with an absence of topsoil, prairie vegetation would ever regenerate in such regions.

Results from this study of *Geomyidae* suggest that these animals may form the necessary link which might give rise to the recovery of prairie ecosystems, about whose existence Weaver was perplexed. The underground digging and mixing activities of fossorial rodents, as exemplified by the gopher, have been shown to enrich prairie soils to the point at which prairie vegetation growth may be initiated once again in disturbed areas, or enhanced in mounded areas. The mima mound is a site of intensive biogeochemical activity, stimulated by an organism which can exert a substantial influence upon the pedological and botanical characteristics of the treeless, semi-arid regions of North America.

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