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Causation and plant succession in disturbed areas of southwestern Montana

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CAUSATION AND PLANT SUCCESSION
IN DISTURBED AREAS OF SOUTHWESTERN MONTANA

by

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INTRODUCTION

Patternization resulting from soil disturbance has been of reported interest in recent years. Most attention has centered on surface land form patterns exemplified by so-called Mima mounds (Dalquest and Sheffer, 1942), i.e., repeated humps on the landscape. Both speculation and investigations have chiefly been concerned with possible causes of various disturbance patterns (Arkley and Brown, 1954; Kaatz 1959, Kelly 1948, Scheffer 1960, Washburn 1956). Relatively little attention has been directed toward aggregated colonies of plants which are so spaced and repeated as to form definite patterns or toward succesional changes resulting from patterned soil disturbance (Larrison 1942, Tevis 1956, Thomas 1962).

Preliminary examination in 1960 and early 1961 of more or less circular, regularly-spaced aggregations of *Artemisia tridentata* as well as disturbed spots of similar size and distribution supporting forbs and grasses led to the discovery of a somewhat unique patterned area of soil disturbance in southwestern Montana. Aerial photographs showed extensive development of a spotted pattern of disturbance. While initial observations strongly suggested a biological origin of soil disturbance, the nature of the causal agent was not then determined.

Even though the pattern found in southwestern Montana bears superficial similarity to some of those reported in the literature, mound development is not always a characteristic and the term "spot" is used for the individual disturbance rather than "mound" or "Mima mound." Two peculiar aspects of the Montana situation also are that it lies in a tension zone between grassland and sagebrush (*Artemisia tridentata*) vegetation and the causal agent of the disturbance is not currently active on a wide scale.

Under the direction of Professor Melvin S. Morris of Montana State University, I undertook detailed study of the described pattern in April, 1961. Field work was carried out through September, 1961 and intermittently during 1962 and 1963.

The subject investigation deals with landscape patternization of biological origin and the related vegetational changes involved. The pattern is formed by spots of soil disturbance usually twenty to thirty feet in diameter regularly repeated and spaced. Spacing distance varies by locations but is usually from fifty to two hundred and fifty feet. The spots are level in some cases, humped in others, stair-stepped on slopes, and subcircular in shape with the long axis of the somewhat elliptical form approximately parallel to the contour. The vegetative changes involved are successional in nature with features of migration, invasion, and aggregation prominent. The place of *Artemisia tridentata* is of particular interest in considering the successional changes evident.

Research objectives deemed most important were the determination of:

1. The geographical extent of the patterned soil disturbance in southwestern Montana characterized by spotting of the landscape.

2. The agent or agents causing the patterned soil disturbance.

3. The successional stages of vegetation involved in the disturbance with particular attention to the place of *Artemisia tridentata* in these changes.

REVIEW OF LITERATURE

Patterns and Agents of Disturbance

Washburn's (1956) analysis indicates that land patternization may be defined as an area having more or less symmetrical forms including circles, polygons, nets, stripes, and steps characteristic of but not confined to intensive frost action areas. According to Washburn, the term "patterned ground" should be restricted to patternization developed mainly as a result of frost action. However, it is used here in his broader definition since frost action does not seem to be involved in the disturbance. Comprehensive consideration of frost action phenomena resulting in patterns is made by Washburn (1956) and Johnson and Billings (1962). Important diagnostic points of reference in this connection are the downslope orientation of many of the patterns, the sorting of rock material which brings the large pieces to the surface, the troughing related to the sorted rock deposits, the terracing of solifluction material (6 to 10 feet high and 60 to 75 feet apart), the presence of permafrost either now or in the past as periglacially existent (Kaatz,1959), and the absence of indications of biological activity on any major scale.

Since these diagnostic features are not characteristic of the pattern in Montana, literature concerning biological agents of disturbance was also reviewed. Reported studies of patterns similar to the one considered here indicate ants, ground squirrels, and pocket gophers as possible agents. Ants (*Pogonomyrmex occidentalis*) have been described as causative agents by Hull and Killough (1951), Killough and LeSueur (1953), and Sharp and Barr (1960). Ground squirrels (*Citellus* spp.) have been reported by Burnett (1931), Day (1937), Edwards (1946), and pocket gophers (*Thomomys* spp.) by Arkley and Brown (1954) and Dalquest and Sheffer (1942) as agents of soil disturbance.

Descriptive data on ant activity given by Sharp and Barr (1960) in their review of literature show wide variation in size of the denuded areas around anthills. Although active ant heaps in southwestern Montana may be as much as three feet in diameter, the clearings do not exceed eight and one-half feet. Killough and LeSueur (1953) report ant clearings in Wyoming as much as twenty-one to twenty-six feet in diameter and show a pattern similar to the disturbance reported here. Thomas (1962), in England, found anthill and clearing sizes comparable to those in Montana.

Seton (1928) and Storer (1958) describe diagnostic features and illustrate tunnel systems of ground squirrels. Edwards (1946) also presents a drawing of such a tunnel system. Arkley and Brown (1954) in their eight-year study in California on patterns similar to the ones described here ruled out ground squirrels because of the indiscriminate shape of the ground squirrel mounds, the colonizing habit which localizes any possible extensive pattern development, and lack of any tendency to form dome-like mounds on the scale which they found. However, since the biological agent in southwestern Montana is not now active over most of the study area, need for considering ground squirrels is also suggested by the history of a heavy outbreak of sylvatic plague (*Pasteurella pestis*) which occurred in the general vicinity of the study area in 1935-36 (Day 1937; Jellison, Parker, and Davis 1937; Jellison 1939). Jellison (1960) indicates that, prior to the epizootic, ground squirrels were very abundant in the vicinity in 1932.

Tryon (1947) in Montana presents a clay model of a pocket gopher tunnel system revealing several diagnostic features. Descriptions and drawings of burrows of various species of *Thomomys* (Crouch 1933, Gabrielson 1938, Grinnell 1923, Hixson and Stiles undated, Moore and Reid 1951, Seton 1904-1928, Storer 1958, Technical Committee 1960) and of the eastern pocket gopher (*Geomys* sp.) and pocket gophers as a whole (Scheffer 1931), all show common characteristics in that tunnels are separable as shallow feeding systems with drop tunnels to lower nesting areas. These authors also describe nest chambers, food storage and fecal chambers as part of the lower system together with the habit of the pocket gophers sometimes putting excavated dirt in unused parts of the tunnels. Most of these descriptions give data on tunnel and chamber sizes and some report feeding tunnels up to five hundred or six hundred or even nine hundred feet long (Gabrielson 1938, Moore and Reid 1951, Technical Committee 1960).

Pattern Extent and Description

Following Dalquest and Sheffer's (1942) description of Mima mounds in Washington, Arkley and Brown (1954) state that such mounds occur from Missouri to southern Texas, on the Colorado plateaus, in the northwestern states, and California. These authors quote Price (1949) on the occurrence of these mounds in eighteen western states on twenty different types of geomorphic units and say the mounds have been found on a wide variety of soils, with concentrations up to ten thousand mounds per square mile, on slopes of five to twenty percent.

Soils present with this kind of patternization are found to be almost invariably shallow to cemented hardpans, claypans, bedrock, gravel beds, or may contain water tables all of which limit both root growth and rodent activity (Arkley and Brown 1954, McGinnies 1960).

Mound microrelief, as indicated by Arkley and Brown (1954) consists of circular or oval domes one to three feet high, fifteen to one hundred feet in diameter, with interveining basin shaped depressions, and often no external drainage. Measurements given by Hansen (1962) for mounds on Black Mesa in Colorado fall within these limits as do those given by Formosov (1928) who quotes Mushketov's study on the Kalmouk steppe in Russia. Nikiforoff (1941) in California and Larrison (1942) in Washington found mounds up to four and five feet high but with other measurements within the above limits. Distance between mounds may be from thirty-five to sixty feet (Hansen 1962).

Biological Population Densities

Since the individual disturbance elements forming the pattern studied and the patterns reviewed are regularly spaced, it seemed that available information on frequency of biological workings should also be examined. Hull and Killough (1951) found that the ant activity in the Bighorn Basin averaged thirty-two hills per acre. These quthors also quote Costello's (1944) study in abandoned fields in northern Colorado where fifteen to fifty-seven anthills per acre were found.

Howard and Childs' (1959) report showed male pocket gopher territories to be about twenty-two hundred square feet and female territories about thirteen hundred square feet. Hansen (1962) found twleve to fifteen snow nests of pocket gophers per acre on poorly drained flat parks and meadows of Black Mesa in Colorado. For comparison, gopher densities reported by other authors are indicated in the following table:

Table 1. Gopher densities per acre from various studies.

Location	Gophers/acre	Authority
Mountain meadows (Oregon)	7 or 8	Gabrielson (1938)
Subalpine grassland (Central Utah)	33 (sampling) 16.3 (trapping)	Ellison and Aldous (1952)
Foothills (Calif.) Alfalfa fields	0 - 10 up to 50	Howard and Childs (1959)
Montana	2 - 28	Tryon (1947)
High Mountain Watershed (Utah)	4 - 16	Ellison (1946)
Colorado	22 average	Technical Committee (1960)

Invasion and Plant Succession

A number of workers have studied plant invasions on disturbed areas caused by rodents or ants and on areas similar to those here considered. Tevis (1956) in California reports establishment of Red Fir (*Abies magnifica*) in gopher-cleared areas in what was formerly a turf of *Festuca idahoensis*. The miniature transects run by Thomas (1962) in England showed a distinctly different vegetation on the ant mounds studied as compared to the surrounding matrix plant types. He also quotes instances of plant damage by harvester ants in tropical Africa.

Ellison and Aldous (1952) mention the presence of small patches of spruce and fir at intervals in a herbaceous type forming a parkland. They do not indicate any connection with the gopher activity under study but describe an increase in Artemisia discolor and other changes in plant composition where the pocket gopher was present. Vegetational changes ascribed to the work of various fossorial rodents in Russia are described by Formosov (1928) and Formosov and Kodachova (1960) and those differences brought about by pocket gopher activity are shown by Branson and Payne (1958) in Montana and Marston and Julander (1961) in Utah.

Larrison (1942) in Washington states that the gopher activity there results in succession from grass to small herbs to balsamroot to sagebrush and Ribes and ultimately to Pinus ponderosa and Pseudotsuga menziesii. Studies by Laycock (1958), Bond (1945), and the Technical Committee (1960) all indicate the significance of pocket gophers and other small mammals in bringing about invasion by annual plants. Other than Larrison's (1942) work, little information is available on successions along a tension zone between plant communities. In addition, most of the reports reviewed deal with active populations of rodents or ants whenever the disturbances studied are attributed to biological agents.

DESCRIPTION OF AREA AND METHODS OF STUDY

The study area lies chiefly in Beaverhead and adjoining Madison Counties of southwestern Montana. Figure 8 shows the general and specific location of the study area. Typically the topography is composed of broad open valleys with rugged, sometimes timbered, mountains surrounding them. Above the usually irrigated river bottoms, wide gently-sloping benchlands merge into steeper foothills subtending the high mountains. Primary drainages included are the Red Rock, Beaverhead, and Bighole Rivers with Sheep Creek, Sage Creek, the Horse Prairie, Blacktail, Grasshopper, and Rattlesnake Creeks as main tributaries. Average monthly temperature in the valleys is sixty to sixty-four degrees Fahrenheit in July and twelve to eighteen degrees Fahrenheit in January. Precipitation averages ten to fifteen inches annually in the valleys and occurs largely as srping-fall rain (Shearer 1958, USDC 1960, USDC no date).

Most of the study area lies between five thousand and seven thousand feet elevation, Dillon being 5228 feet m.s.l., Wisdom 6058 feet, Lima 6265 feet, and Monida, the most southwesterly town, 6790 feet. Detailed study was confined to the benchlands lying in this elevational range since the most extensive patternization is located on them. Soils here are gravelly or sandy with considerable silt content. They are generally derived from alluvial valley fill, tertiary sediments, and terrace deposits. Tertiary volcanics form much of the mountain mass and higher slopes. Occasional outcrops of lacolith structure occur on the benchlands (Ross, Andrews, and Witkind 1955). Detail of soil mapping classification is on file at the Soil Conservation Service office in Dillon. As examples of the sort of soils present in the study area, information on two sites is given here. On the bench above the Briggs Ranch, north of Dell, the SCS records show Riechle fine sandy loam formed from outwash. Standard SCS soil mapping symbols designate its character as $\frac{2\ S\ 5\ T}{35\ C\ 1}$. In the Stone Creek vicinity, the soil is described as Riechle sandy loam from weakly developed outwash alluvium, strongly calcareous from seven to eleven inches with a calcium carbonate zone at ten to fifteen inches depth. The map designation given is $\frac{\quad\quad}{35\ B\ 1}$. Immediately adjacent to the south the soil is Avalanche loam, light-colored, brown, from reworked tertiary sediments. It is designated $\frac{\quad\quad}{36\ B\ 1}$.

The study area is mainly on the grassland and adjacent sagebrush types present on the benchlands. Timber occurs above the study area at times and the valley bottoms are usually irrigated. Although Table 2 was compiled as part of the results of this study, it is included here to furnish more detail describing the study area. Vegetational, physical, and geological conditions are summarized in the table.

Methods used to investigate the subject situation may be divided into the three categories listed as research objectives in the introduction, i.e. determination of geographic extent of the patterned disturbance, determination of the causal agent, and identification of vegetation changes and plant succession resulting from the soil disturbance.

1942 aerial photographs furnish the first complete photographic coverage of southwestern Montana. These were used to make a map defining boundaries of the spot pattern. The mapped extent of patternization was checked by ground reconnaissance. Presence of plant aggregations and contagious distribution of plant species were considered in this ground survey (Brown 1954).

Following boundary determination, study locations were chosen where the least amount of secondary distrubance appeared to have occurred.

TABLE 2.--ASSOCIATION OF DISTURBANCE PATTERN WITH VEGETATIONAL, PHYSICAL AND GEOLOGICAL CONDITIONS

VEGETATION					SOIL			
ZONE	SUBTYPE	TYPICAL SPECIES	ELEV.	PCPT.	SOIL GROUP	DEPTH TO HARDPAN	GEOLOGIC DERIVATION	TYPE OF SPOT IN PATTERN
I. NEEDLE-GRASS	A. NEEDLE-GRASS-BLUE GRAMA	STIPA COMATA BOUTELOUA GRACILIS SPOROBOLUS CRYPTANDRUS	BELOW 6000'	9"	SIEROZEM	10"	TERTIARY SEDIMENTS SOME ALLUVIAL VALLEY FILL	DARK AND LIGHT
	B. NEEDLE-GRASS-RICEGRASS	STIPA COMATA ORYZOPSIS HYMENOIDES EUROTIA LANATA	6-7000	9"	SIEROZEM	10"	TERTIARY SEDIMENTS SOME ALLUVIAL VALLEY FILL	DARK AND LIGHT
	C. NEEDLE-GRASS-WHEATGRASS	STIPA COMATA AGROPYRON SPICATUM KOELERIA CRISTATA	6-7000	11"	SIEROZEM TO BROWN	16"	TERTIARY SEDIMENTS PRE-BELT GNEISS-SCHISTS TERRACE DEPOSITS VALLEY FILL	CHIEFLY LIGHT SPOTS SOME DARK
II. WHEAT-GRASS	A. WHEATGRASS-SAGEBRUSH	AGROPYRON SPICATUM ARTEMISIA TRIDEN-TATA GUTIERREZIA SAROTHRAE	6-7000	11"	BROWN	19"	TERTIARY SEDIMENTS TERTIARY VOLCANICS	CHIEFLY DARK SPOTS VERY FEW LIGHT
	B. WHEATGRASS-NEEDLE-GRASS	AGROPYRON SPICATUM STIPA COMATA AGROPYRON SMITHII	6-7000 7-8000	11" 12"	BROWN	16"	TERTIARY SEDIMENTS	DARK AND LIGHT
III. IDAHO FESCUE	A. IDAHO FES-CUE-SAGEBRUSH	FESTUCA IDAHOENSIS ARTEMISIA TRIDEN-TATA-CAREX SPP.	6-7000	11"	BROWN TO CHESTNUT	18"	TERTIARY SEDIMENTS VALLEY FILL TERRACE DEPOSITS SOME QUARTZITES	DARK SPOTS
	B. IDAHO FES-CUE	FESTUCA IDAHOENSIS AGROPYRON SPICATUM POTENTILLA FRUTI-COSA	7-8000	13"	CHESTNUT	19"	ALLUVIAL VALLEY FILL TERTIARY SEDIMENTS	DARK SPOTS

Both grass-covered and sagebrush-covered spots are included. For comparison, locations of active disturbance were also investigated.

Identification of the causal agent of the spots and mounds was determined by excavation of stabilized (non-active) spots to examine residual internal evidence. Diagnostic criteria were set up on the basis of the literature review pertaining to the various possible agents and by comparison with existing known workings, burrow systems, or soil particle groupings. All skeletal remains were collected and identified and samples were taken of crotovinal material including fecal, nesting, or other debris. Inactive spots excavated were mapped in cross-section for vertical and horizontal components. Some trapping of small mammals was carried out when opportunity occurred. This included trapping of pocket grophers when they were present in a location. Stomach contents of the pocket gophers trapped were examined and compared to the vegetation present at the trap site but no major effort was made toward a complete food habit study.

Vegetation was measured by line intercept (Canfield 1941) and one foot wide belt transects. Point quadrat (Grieg-Smith 1957, Oosting 1956) and Parker (1951) loop transect methods were tried but did not furnish sufficient data. Intercept or transect lines were run across the spots of disturbance and plants were recorded by species inside the spot and outside. Usually two parallel lines were laid out, each five feet from the spot center and either with the contour or at right angles to it. In some cases, in order to include more spots, only one line was used and this was laid through the spot center.

When belt transects were used, only species presence in each square foot was recorded with separation inside and outside the spot noted.

1942 aerial photographs were compared to those taken in 1955 and where vegetation changes were apparent, the species involved were identified on the ground.

Since shrubs were usually present, one hundred and two hundred square foot plots were laid out inside and outside the spots examined in detail. All shrubs within these plots were counted by species. All spots with intercept or transect lines had these shrub count plots overlying the lines and, in addition, plots were taken on a number of spots without the intercept or transect measurements.

Sagebrush plants were aged by ring counts (Ferguson ___) and plant heights measured. These data were taken either along transect lines when sagebrush was present, or in belts of variable width across the spots and adjacent ground, or by selecting both the largest and oldest appearing plants inside and outside spots examined. Supplemental aging of younger age classes and of plants seemingly not related to spots was done (Brown 1954, Grieg-Smith 1957, Oosting 1956).

Other data measured were spacing, diameter, and frequency of spots along straight lines and along random lines going from one spot to the next nearest spot or by going from one anthill to the next nearest anthill (recording all spots enroute) and by mapping within one acre belts sixty-six feet wide by six hundred and sixty feet long. Mound counts were made in locations of present pocket gopher activity to estimate population density as described by

Howard (1961). Soil pits were dug for subsurface examination of anthills, ant clearings, and interspot sites. Spot and mound surface profiles were surveyed, active gopher workings were mapped for surface disturbance, plants present were collected in all locations except the Wisdom vicinity, pictures in color and black and white were taken, and daily notes of observations kept.

RESULTS

Nature and Extent of Patterned Soil Disturbance

The type of patterned ground under study in southwestern Montana is composed of spots of soil disturbance more or less regularly spaced. Aerial photographs show the pattern in some locations as light spots as in Figure 1 and in other places as dark spots as in Figure 2. My examination of the difference in spot color on the ground showed that the light spots are often vegetationally similar to the surrounding grass matrix but appear lighter on the photographs due to much calcium-coated gravel and small rock at the surface of the spots. I found the dark color in other locations to be due to woody vegetation or shrubs, usually *Artemisia tridentata* and *Chrysothamnus viscidiflorus* covering the ground surface. The dark spots are either in locations of nearly closed sagebrush communities or occur as isolated islands in a grassland matrix. The last column of Table 2 shows the color pattern related to general vegetation types.

Careful study of the aerial photographs reveals some of the light spots with slightly darker centers. My field observations of such spots indicate that the darker center may be due to a time

Figure 1. 1942 aerial photograph showing an area of light spots. Approximate width of picture is five-eighths mile. Date of flight, August 21, 1942.

Figure 2. 1942 aerial photograph showing an area of dark spots. Approximate width of picture within the closed border is five-eighths mile. Date of flight, September 1, 1942.

These figures compare differences in spot appearance in different locations in the same year. Light spots are due to soil conditions within the spots. Dark spots are due to Big Sagebrush plants on the spots which obscure the soil surface.

differential in disturbance with the peripheral edge of the spot being the most recently disturbed and therefore with more calcium-coated gravel evident, or, it may be due to plants such as Eurotia lanata occupying the center but not yet filling the more recently disturbed edge of the spot.

These spots appear on the ground as level topped stairsteps on moderate slopes, humped spots on hillsides, or humped spots on level ground. Forms are usually consistent in any one location except for secondary disturbance activity of various kinds. To illustrate the different appearances of these spots, several pictures are included here. Figure 3 shows a general view of a slope with light-colored grass spots present, Figure 4 shows the stairstep effect often present, Figure 5 indicates a sagebrush spot appearance, and Figure 6 shows well developed humps with virtually no internal drainage.

Table 3 further characterizes the spots which form the pattern studied. This table summarizes the descriptive data and quantitative averages I found in the various study locations. Examples of surveyed spot profiles in four study locations are illustrated in Figures 7 and 7a. The vertical scale in these profile diagrams is greatly exaggerated to emphasize detail of the profiles.

In applying the procedure described in the Methods section to determine the geographic extent of the pattern found in southwestern Montana, I examined aerial photographs for Beaverhead, Madison, Silver Bow, Jefferson, Broadwater, and Deer Lodge Counties. Most of the available 1942 photographs were on a four or eight inch scale,

Figure 3. General view of slope near Wagner Creek in the Blacktail Creek vicinity. White appearance of individual spots indicates a greater density of Stipa comata on the spots than in the area between spots.

Figure 4. Stairstep profile development of spots on a slope in the Blacktail Creek drainage. Road indicates relative size and flat-topped profile of these spots.

Figure 5. Aggregated Sagebrush growth on a stairstep spot. Matrix vegetation is grassland located on the bench above the Briggs Ranch, 35 miles south of Dillon.

Figure 6. Humped development of spots on nearly level subirrigated bench meadow lands 6 miles west of Wisdom. Note lack of internal drainage. Humps are one to two or more feet high.

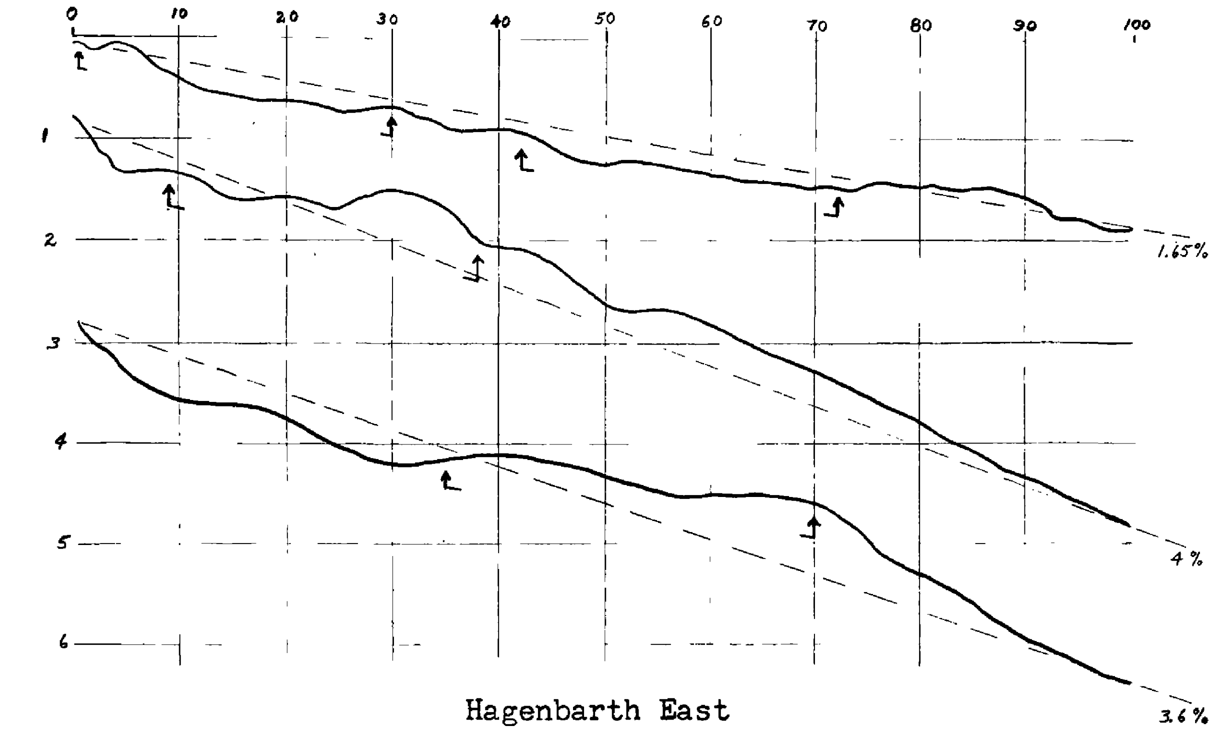
TABLE 3.--CHARACTER OF SPOTS SHOWN BY TRANSECTS, PACED LINES, AND INDIVIDUAL MEASUREMENTS

ZONE	VEGETATION SUBTYPE	DOMINANT SPP. SPOT	GENERAL SURFACE	SPOT FORM	STABILITY[A]	DIAMETER	ORIENTATION	INTERVAL
1.	A. NEEDLEGRASS-BLUE GRAMA	EUROTIA LANATA STIPA COMATA CHRYSOTHAMNUS VISCIDIFLORUS OPUNTIA POLYCANTHA	ROLLING UPLAND WITH OCCASIONAL OUTCROPS. SPOTS NEARLY LEVEL WITH ONLY SLIGHT STEP DEVELOPMENT.	INACTIVE: SUBCIRCULAR ON SLOPES - SLIGHT STEP. ACTIVE: CIRCULAR TO INDISCRIMINATE - HUMPED AROUND CACTUS.	INACTIVE TO REACTIVATED TO ACTIVE. (MOST ACTIVITY IN SWALES.)	15 TO 35 FT. MOST UNDER 30 FT.	ON CONTOUR EXCEPT IN FLATTEST PART OF SWALES - THEN NEARLY CIRCULAR.	30 TO 100 FT. EDGE TO EDGE. INDETERMINATE IN SWALES.
		SWALES ACTIVE TO RECENTLY INACTIVE. DIGGING REVEALED SPOTS HIDDEN UNDER VEGETATION. PROBABLY PREDATE BLUE GRAMA.						
	B. NEEDLEGRASS-RICEGRASS	STIPA COMATA ORYZOPSIS HYMENOIDES EUROTIA LANATA CHRYSOTHAMNUS VISCIDIFLORUS ARTEMISIA NOVA	LEVEL TO SLOPING BENCHLAND AND ROLLING OR BROKEN FOOTHILLS.	SLIGHT STEP-HUMPING MOSTLY AROUND THE FEW CACTUS	INACTIVE TO RECENT TO ACTIVE. ACTIVE SPOTS: INDISCRIMINATE IN FORM.	20 TO 35 FT.	ON CONTOUR. ACTIVE: INDISCRIMINATE, ON CONTOUR, OR AT RIGHT ANGLES - TRAVELING.	12 TO 90 FT. EDGE TO EDGE.
	C. NEEDLEGRASS-WHEATGRASS LOCATION GROUP 1.	INACTIVE: STIPA COMATA AGROPYRON SPICATUM AGROPYRON SMITHII POA SECUNDA OR ARTEMISIA TRIDENTATA CAREX ELEOCHARIS AGROPYRON SMITHII	SLOPING BENCHLAND AND ROLLING FOOTHILLS. OCCASIONAL AREAS NEARLY LEVEL.	STAIR STEP.	STABILIZED. SLIGHT REACTIVATION.	16 TO 40 FT.	ON CONTOUR INCLUDING ACTIVE EXCEPT TRAVEL TUNNELS AT RT. ANGLES	30 TO 65 FEET. SOME ONLY 12 FT.
	LOCATION GROUP 2.	ACTIVE: SALSOLA PESTIFER ARTEMISIA FRIGIDA EUROTIA LANATA CHRYSOTHAMNUS VISCIDIFLORUS		LITTLE HUMPING UNLESS CACTUS PRESENT IRREGULAR BOUNDARY.	RECENT TO ACTIVE	15 TO 30 FT.		8 TO 60 FT. MOST 12 TO 35 FT.

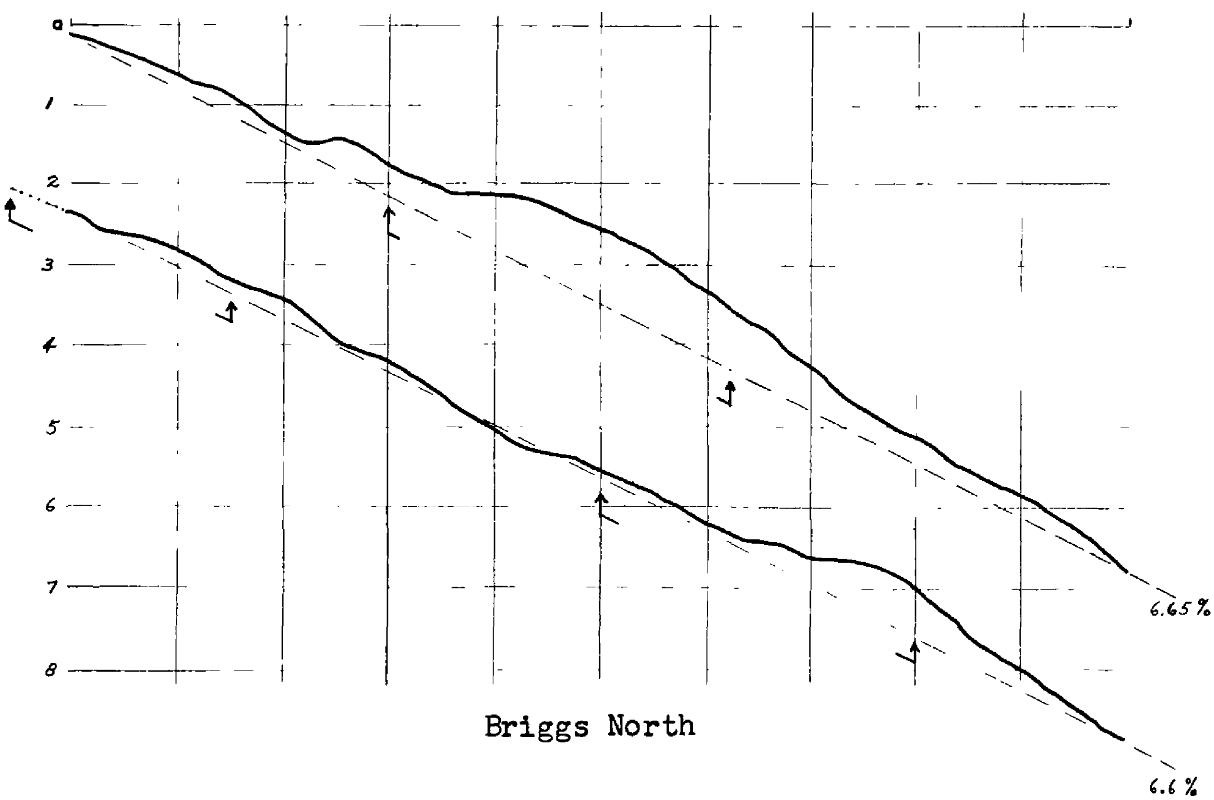
TABLE 3. (CONTINUED)

ZONE	SUBTYPE	DOMINANT SPP. SPOT	GENERAL SURFACE	SPOT FORM	STABILITY[A]	DIAMETER	ORIENTATION	INTERVAL
II.	A. WHEATGRASS-SAGEBRUSH	ARTEMISIA TRIDENTATA CAREX ELEOCHARIS AGROPYRON SPICATUM POA SECUNDA	ROLLING FOOT-HILLS OR LONG ROLLING FOOT-HILLS AND DRAWS.	SLIGHT HUMP TO STAIRSTEP SECONDARY ACTIVITY CAUSING IRREG-ULAR HUMPING IN SOME.	STABILIZED.	20 TO 40 FT.	ON CONTOUR	20 TO 60 FT. (TO 100 ON UPPER SLOPES)
	B. WHEATGRASS-NEEDLEGRASS	STIPA COMATA AGROPYRON SMITHII AGROPYRON SPICATUM CALAMAGROSTIS MONTANENSIS	NEARLY LEVEL BENCHLAND JUST ABOVE CREEK BOTTOM.	SLIGHT STEP TO LOW HUMP. SOME IRREGU-LAR HUMPING FROM SECOND-ARY ACTIVITY.	STABILIZED.	20 TO 31 FT.	ON CONTOUR WHERE ANY SLOPE PRES-ENT. INDIS-CRIMINATE WHERE LEVEL.	40 TO 125 FT.
III.	A. IDAHO FESCUE - SAGEBRUSH	FESTUCA IDAHOENSIS MUHLENBERGIA RICHARDSONIS (LUPINUS SP.-CHRYSOTHAMNUS VISCIDIFLORUS VAR. LANCEOLATUS) OR ARTEMISIA TRIDENTATA	BENCH MEADOWS AND GRASSLAND-NEARLY LEVEL TO GENTLY SLOPING.	IRREGULAR HUMPS TO WELL DEVEL-OPED HUMPS.	STABILIZED BUT MUCH BADGER AND GROUND SQUIRREL AC-TIVITY NOW. BENCH MEADOWS DRY AND DETERIORATED.	45 TO 55 FT. WITH SOME ONLY 15 TO 25	ON CONTOUR WHERE ANY SLOPE PRES-ENT. INDIS-CRIMINATE WHERE LEVEL.	10 TO 60 FT.
	B. IDAHO FESCUE	AGROPYRON TRACHYCAULUM FESTUCA IDAHOENSIS MUHLENBERGIA RICHARDSONIS (LUPINUS SP.-CHRYSOTHAMNUS VISCIDIFLORUS VAR. LANCEOLATUS)	BENCH MEADOW-LEVEL TO SLIGHT SLOPE.	WELL DEVEL-OPED MIMA TYPE HUMPS. FLAT TOPPED.	STABILIZED. SOME FEW GOPHERS PRES-ENT (SHALLOW WORK). NO DRAINAGE PATTERN.	6 TO 52 FT. 30 TO 40 FT. COMMON. SOME COALEXED.	INDISCRIMIN-ATE. VIRTUALLY LEVEL TERRAIN.	12 TO 66 FT. 15 TO 30 COMMON.

[A]ACTIVITY REFERS TO THAT OF THE POCKET GOPHER (THOMOMYS TALPOIDES) WHICH IS THE ONLY CONSISTENT ACTIVITY PRESENT OR EVIDENCED.



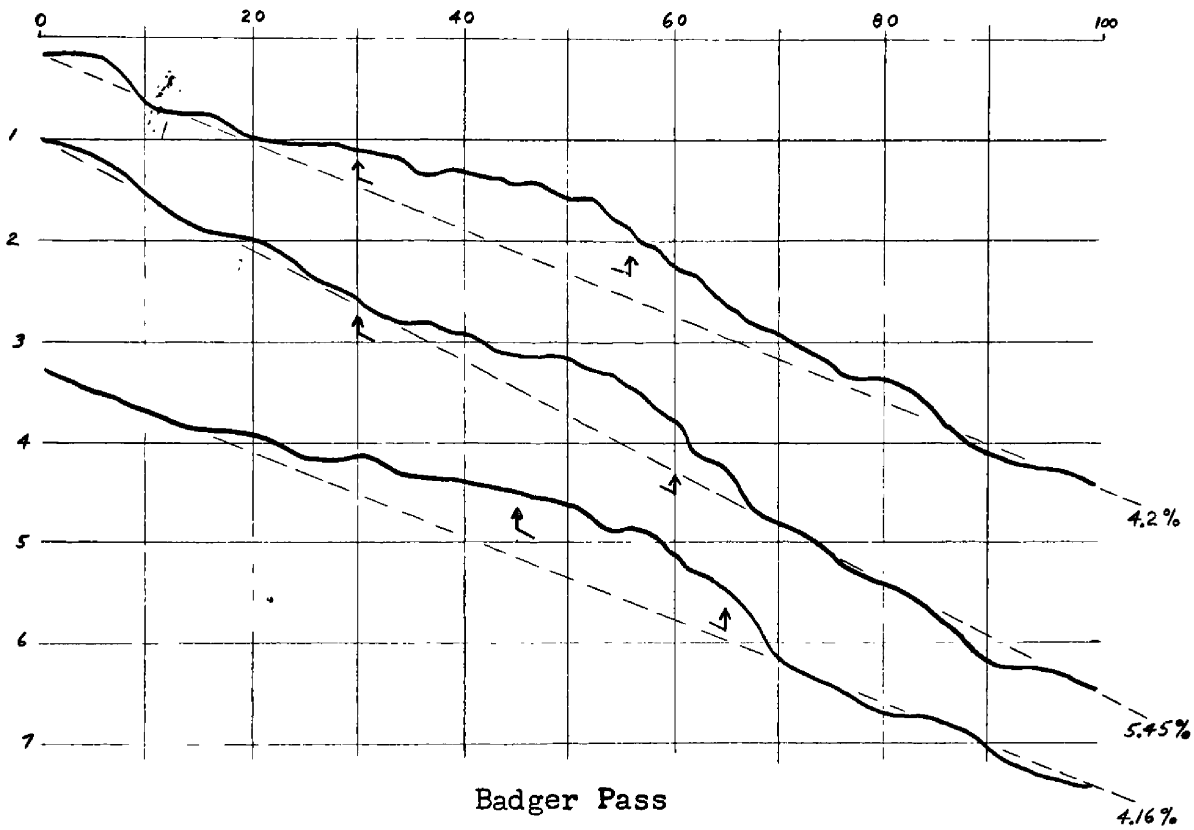
Hagenbarth East



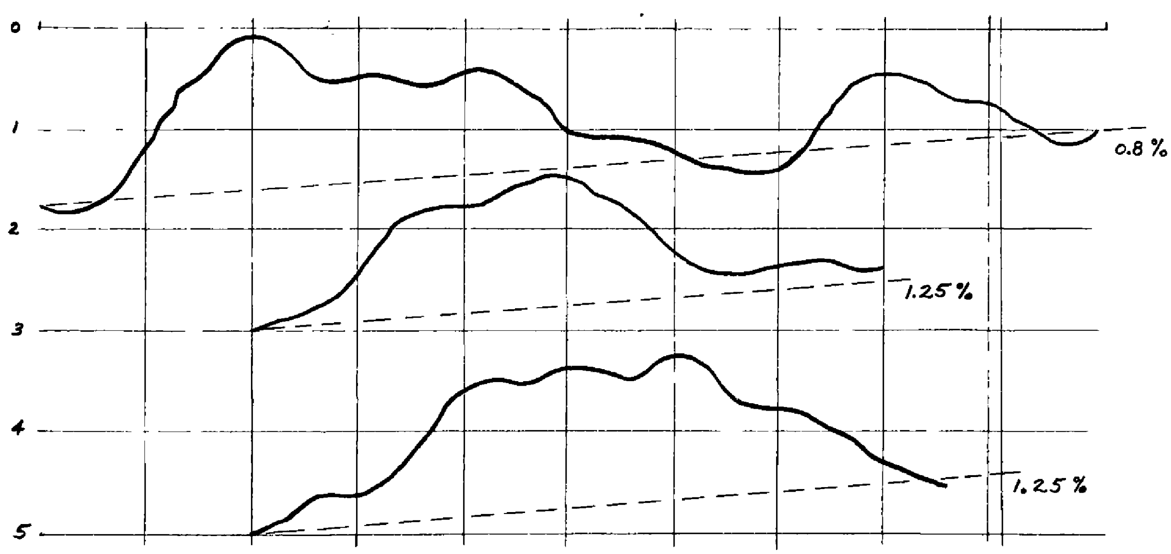
Briggs North

Figure 7. Profiles of the ground surface of spots in two locations.

Arrows indicate spot boundaries apparent on the surface. Vertical distance is greatly exaggerated to show detail. Each line is from a different site in the designated location. % figures show the general slope of the site concerned. March 1963.



Badger Pass



West of Wisdom

Figure 7a. Profile of the ground surface of spots in one location and mounds in another.

Arrows in the Badger Pass diagram indicate spot boundaries. The mound boundaries in the West of Wisdom diagram appear self-evident. The two lower mound profiles are from one line. They are divided for convenience. % figures show the general slope of the site concerned. March 1963, September 1961.

however, parts of eastern Madison County were covered only by photographs on a two-inch scale. It is possible that at the two-inch scale a small location with the pattern might not be evident on these photographs. Patternization boundaries delimited from the aerial photographs corresponded very closely with the limits found in the ground survey. I did find, however, in the ground survey that two small patterned locations not shown by the photographs occurred near Wisdom and Wise River. It is possible that these locations may have been developed after the photographs were taken. Most of the pattern found on the photographs gave every evidence of inactivity, and often vegetative stabilization, at the time the photographs were taken in 1942 as shown by comparison of pictures taken in later years with conditions existing on the ground. I examined a few 1960 aerial photographs made by the U. S. Geological Survey covering part of the Blacktail Creek drainage where the vegetation on the spots is highly stabilized. There is no discerible difference between the 1960 and 1942 aerial photographs in this location indicating that the spots were inactive and stabilized in 1942. Elsewhere, similar comparisons can be made and, as brought out later changes in activity or vegetation can also be identified in some instances.

The map resulting from this patternization boundary determination is shown here as Figure 8. It may be noted that the pattern is largely confined to Beaverhead and eastern Madison Counties. The map determined the study area within which the several study locations were chosen.

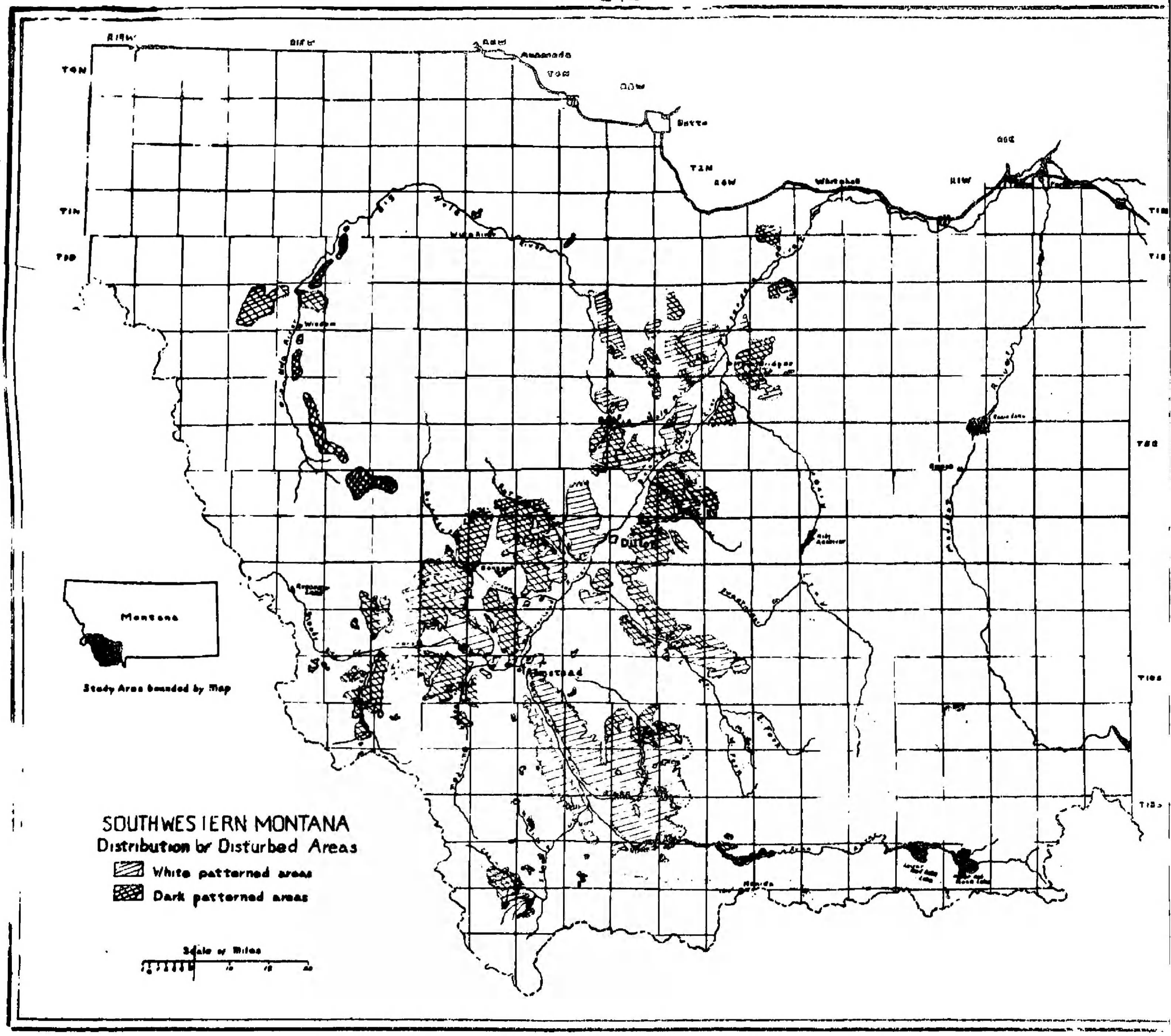


Figure 8. Location and distribution of patterned soil disturbance characterized by spotting of the landscape.

Determination of Causal Agent

To identify the biological agent responsible for the disturbance spots forming the pattern, I found subsurface examination to yield the best residual evidence of diagnostic character. I excavated individual spots in several locations. This digging provided information for mapping the horizontal and vertical components of inactive and stabilized spots together with specimens of crotovinal material and skeletal remains. Such evidence was compared to criteria based on study of the literature and since it occurred consistently in all spots excavated it led to the conclusion that the pocket gopher was the responsible agent for the original disturbance.

Figures 9 and 9a show portions of an inactive, stabilized, grass-covered spot in the Briggs North study location. These figures illustrate several points of diagnosis. Tunnel systems of considerable complexity were present. Nests were present at a lower level than the feeding tunnel system. I found the skeletal remains of a pocket gopher which could be identified as to species (Thomomys talpoides) in the walled-off nest as shown in Figure 9. A food storage chamber was adjacent to the nest and contained seeds of Agropyron smithii. All crotovinal material whether it was found as loosely packed debris filling unused tunnels (Crouch 1933, Scheffer 1931) or from the main mass of the soil body composing the disturbed spot yielded quantities of pocket gopher fecal pellets, typical grass leaf cuttings, and short pieces of small woody or semi-succulent roots. I found spiral drop tunnels such as described in the literature (Tryon 1947). Other tunnels I found appeared to be more of an alternating-direction

Aids in interpreting diagrams of subsurface tunnel systems

1. All tunnels and chambers are closed (filled with crotovinal material) unless specified as open. Small portions of an open system may be shown as closed by crosshatching.

2. "X" indicates the location of skull or body bones found during the excavations.

3. a) Solid lines indicate the plane of view nearest to the observer.
   b) Dashed lines indicate the plane of view at an intermediate distance from the observer.
   c) Dotted lines indicate the farthest plane of view or, in some cases, the part of one tunnel crossing below another.

4. a) The portion of these diagrams above the "O" base line is a vertical view of the horizontal tunnel and chamber development.
   b) The portion of these diagrams below the "O" base line is a side view of the vertical tunnel and chamber development.
   c) In both views more than one plane is usually included. These are distinguished as in 3a,b,c above.
   d) In some cases, only the horizontal view of the vertical face of the excavation cut is shown. These are specified in the individual caption.

5. Numbers shown indicate distance in feet unless otherwise specified.

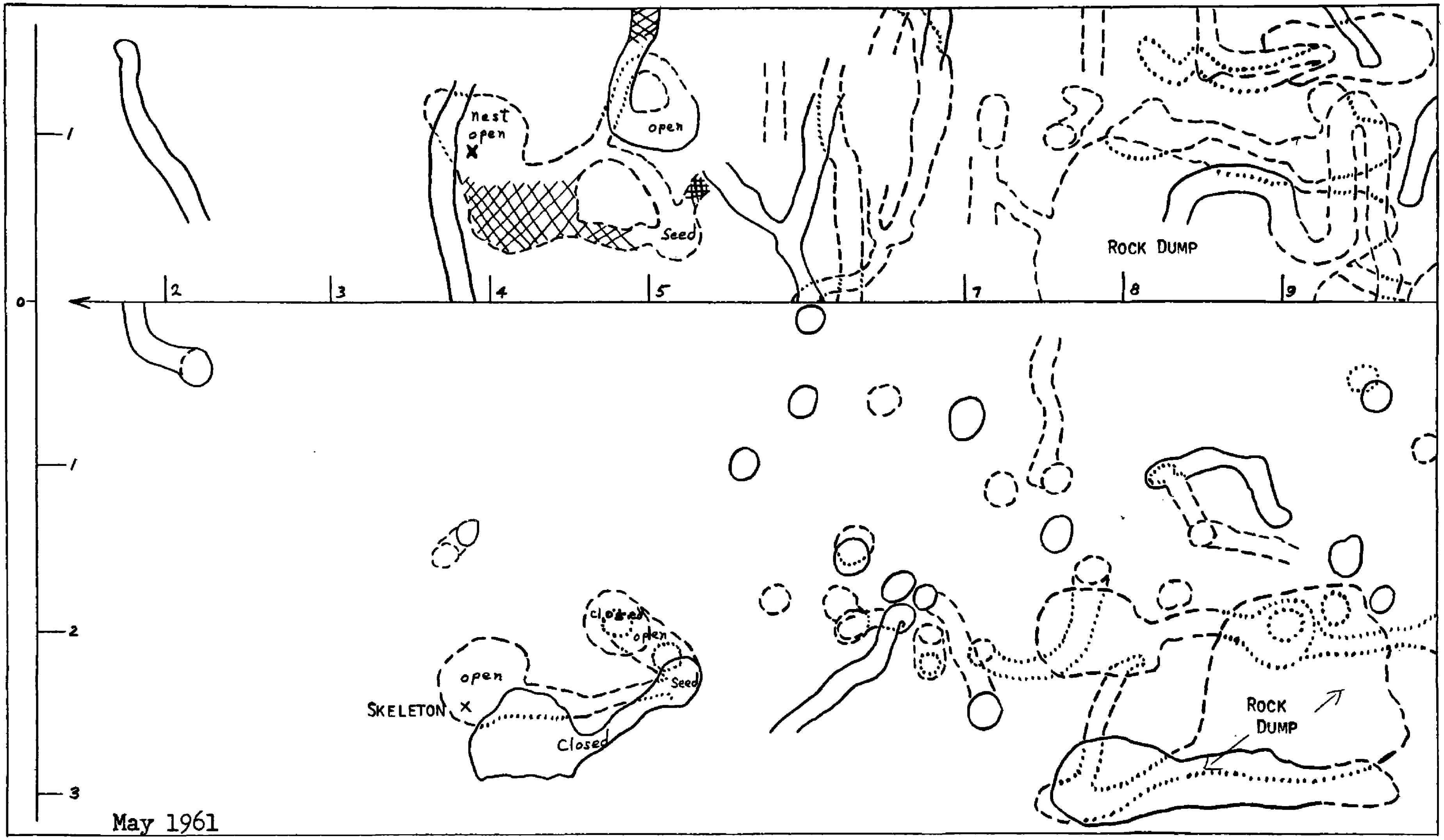


Figure 9. Briggs North excavation Number 1: Inactive spot.

Side and vertical views of underground tunnel development, nest site, and rock dump chambers. All tunnels and chambers closed except as noted. Only a part of the excavation is shown here. (5/26-31/61)

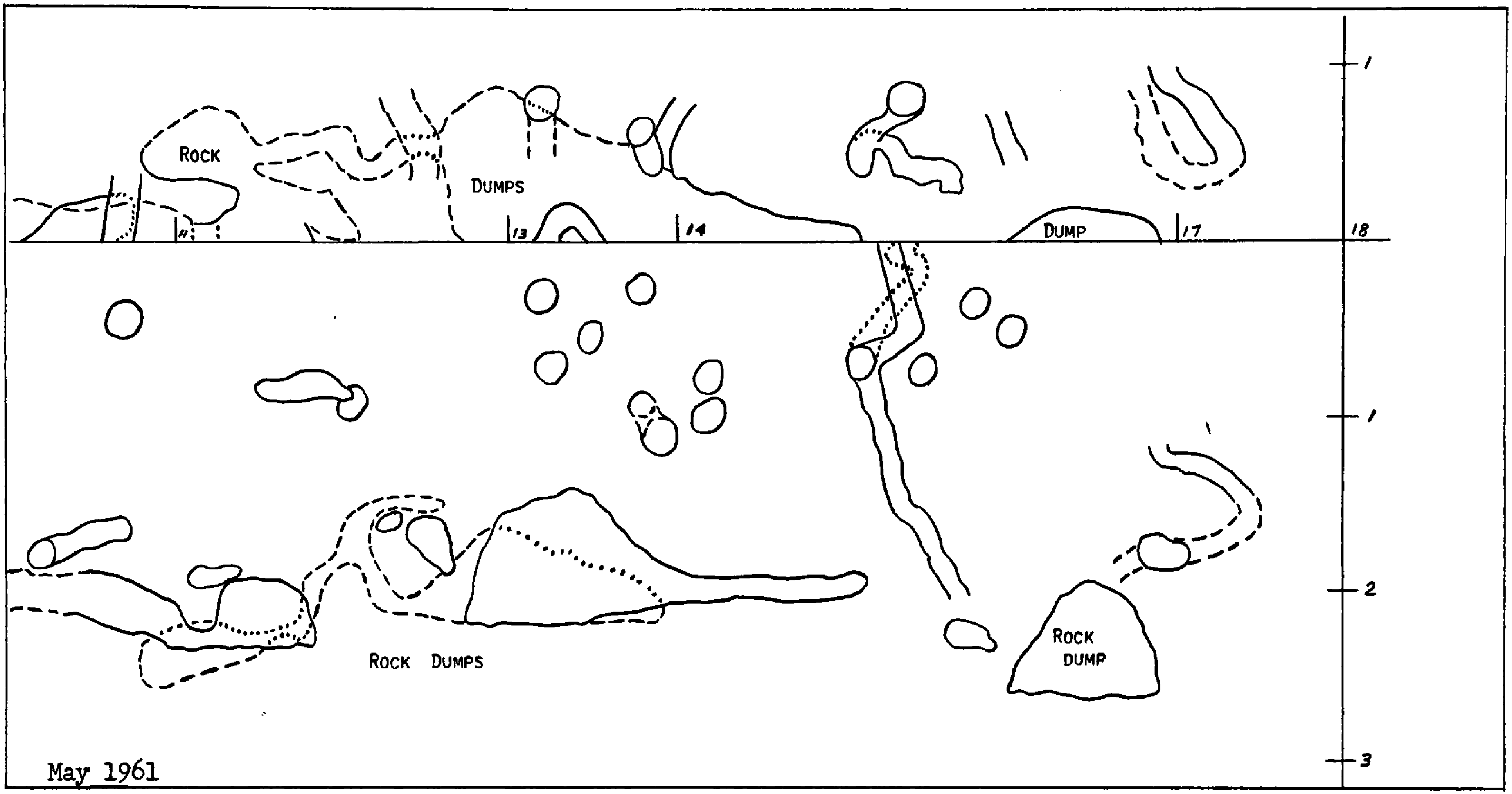
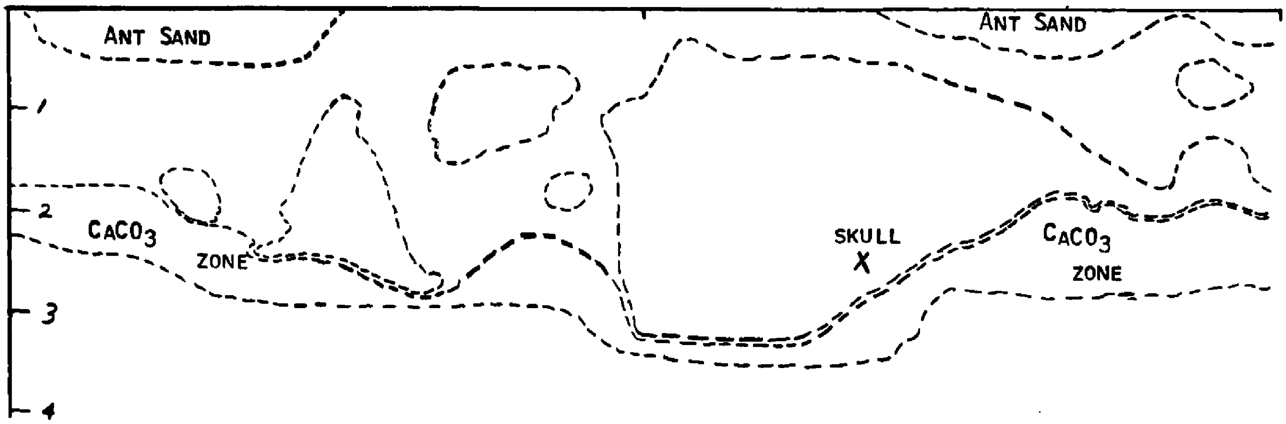


Figure 9a. Briggs North excavation Number 1: Inactive spot.

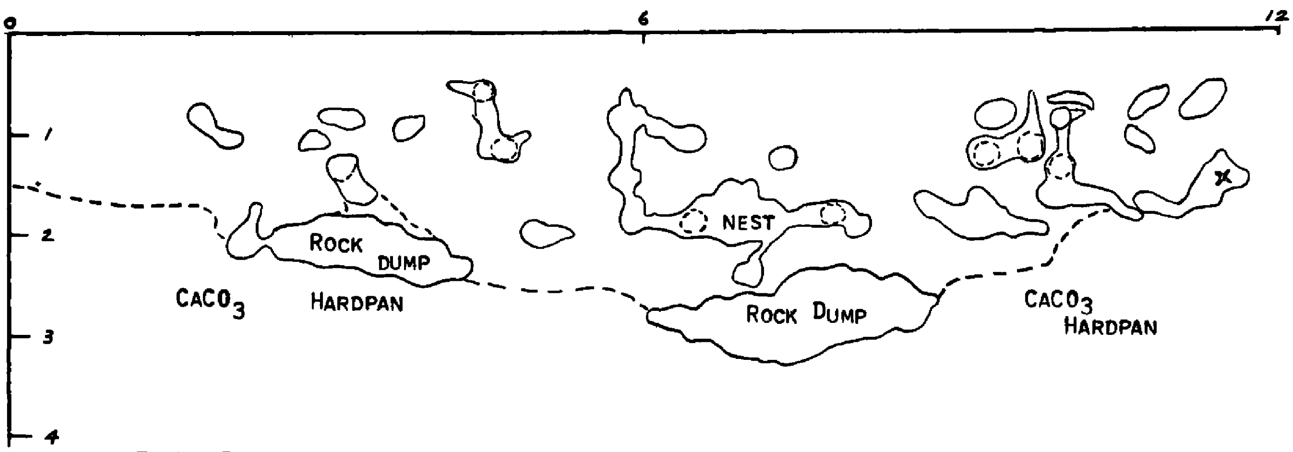
Side and vertical views of part selected to show the rock dump system in detail. All chambers and tunnels are filled with rock and crotovinal material. (5/26-31.61) ramp type structure and in the case of many tunnels going down to the rock dump chambers at the base of the disturbance, better shown in Figure 9a, the drop was almost vertical and the tunnel nearly straight. The rock dump chambers seem to compare well with the cobble or rock layer mentioned by Arkley and Brown (1954) as occurring at the base of the friable material. These authors also state that they found only one and one-half to two inch gravel in the upper part of the mounds they studied. This size and smaller material was all that I found in the disturbed spot above the rock-dump chambers. The smaller rock and gravel was coated with calcium carbonate and showed displacement. Because much of this material had the coated side up and because the quantity near the surface was greater than in the adjacent undisturbed ground, it seems reasonable to assume that this caused the spots to appear lighter in color on the aerial photographs than the surrounding ground. Material in the rock-dump chambers is up to several inches in diameter and apparently was removed by the pocket gopher from the heavily worked nesting area since digging in the ground immediately adjacent but undisturbed shows rock of the same size still in place and present to about the same degree from the surface down. Calcium carbonate coatings on the bottom of the undisturbed rocks indicate no movement while those in the rock-dump chambers exhibit displacement since the coated side lies in any orientation.

Presence of a hardpan formed of cemented calcium carbonate is a common characteristic throughout the study area. As shown in Table 2, depth to the hardpan is somewhat variable in different locations but soil pits dug in undisturbed sites indicate a possibility that abrupt localized differences also exist within a single location. The differences in local depth seem to be associated with surface conditions of the site concerned. As an example, soils under small Bouteloua gracilis patches, circular Opuntia polyacantha patches, or under active anthills had an abruptly shallower depth to a cemented hardpan or to a loosely cemented and apparently newly developing zone of calcium carbonate concentration above and separate from the lower well-developed hardpan. The latter sort of situation might be termed a calcium carbonate compaction zone. The order of magnitude I found to be on the scale of eight to ten inches depth for the seemingly restrictive surface conditions as compared to the usual fifteen inches depth to the hardpan under most other surface conditions in undisturbed sites in the study location most closely examined in this manner. There is also an indication that such shallower concentration may be reversed at least where the tight sod layer of Bouteloua gracilis is being replaced by a bunchgrass.

Of greater importance in this investigation is the consistent penetration of the hardpan which I found in the spots of disturbance excavated for internal examination. Figure 10, giving two views of the same section of a spot with sagebrush in the eighty to one hundred year age class present, illustrates the hardpan zone at twice the depth normal for undisturbed soil in that site (eighteen to twenty inches). The upper part of this spot exhibits a developing "compaction" zone such as described in the paragraph immediately above. This development may be related to the age of the spot or



Gross appearance of fresh vertical face of excavation



Detail of tunnels and chambers after location by probing

Figure 10. Badger Pass excavation Number 1.

Side views of the same vertical face of the cut before and after probing to find tunnels and chambers. Upper view is before probing. The volumes within the dotted lines in the upper view not shown as ant sand or calcium carbonate hardpan zone are composed entirely of pocket gopher crotovinal material. These inclusions in the soil body contain the tunnels and chambers shown in the lower view. "X" indicates the locations of skull finds. Sagebrush present above the ground is from 60 to 96 years old on this spot. September 1961.

to the anthills situated at the surface. I did find shallower development of calcium carbonate concentration immediately under the anthills than under the center part of the section shown. As can be seen in the upper half of Figure 10, I did not find complete penetration of the hardpan zone here as I found in study locations of more shallow hardpan occurrence. Nikiforoff (1941) found openings in the hardpan under some of the mounds he studied but Arkley and Brown (1954) did not.

The main feature of the two views in Figure 10 is the tunnel and chamber development contained within a body of much older crotovinal material. The upper half of the diagram shows the larger masses of disturbed soil still capable of identity as pocket gopher debris with the lower half showing the tunnels and chambers contained within these crotovinal bodies. Skeletal remains, fecal pellets, grass and root cuttings were also present.

To compare the internal evidence present in the inactive spots examined with soil disturbance caused by known agents, I also excavated active anthills, ground squirrel tunnel systems, and active pocket gopher workings. Typical anthills in the study area conform to the measured detail of one I dug out in a location with the calcium carbonate hardpan zone beginning at twenty inches. I found sorted rock fragment material of the ant (<u>Pogonomyrmex</u> <u>occidentalis</u>) heap extending only two inches into the ground but with ant galleries continuing on to the seventeen and eighteen inch depth. No ant galleries were found to penetrate the hardpan. At this depth most of the ant activity was at the center of the area under the heap.

Major gallery work was closer to the surface and in profile a tendency toward a funnel shape was evident.

Excavated tunnel systems of ground squirrels (Citellus richardsonii) conformed to the diagrams shown in the literature (Edwards 1946, Seton 1928, Storer 1958). The only exceptions to this were occasional sites where a ground squirrel had taken over an abandoned pocket gopher tunnel or an unused badger (Taxidea taxus) tunnel in order to penetrate the ground to the depth desired before making its own usual tunnel system. This "co-use" resembles that described by Snead and Hendrickson (1942).

Neither of these two agents made disturbances bearing resemblance to that found in the inactive spots I excavated. Only active pocket gopher workings showed the necessary features. Figures 11 and 11a present the subsurface detail common to active pocket gopher tunnel systems. Deep workings in this gopher's location were centralized and feeding tunnels radiating away from the center were only at shallow depths. Small calcium-coated rock was again concentrated near the surface of the deep center with large rock deposited in the rock-dump chambers forming a floor at the base of the workings. The hard-pan in adjacent undisturbed ground here began at a ten inch depth. It was not present at all in the disturbance center indicating a complete penetration in this case. The resident gopher was trapped.

Because some clones of Agropyron smithii bore similarity in diameter and appearance to spots in the Paskett Pasture location, I dug out one of these for examination even though other surface features such as the stairstep effect and small disoriented or

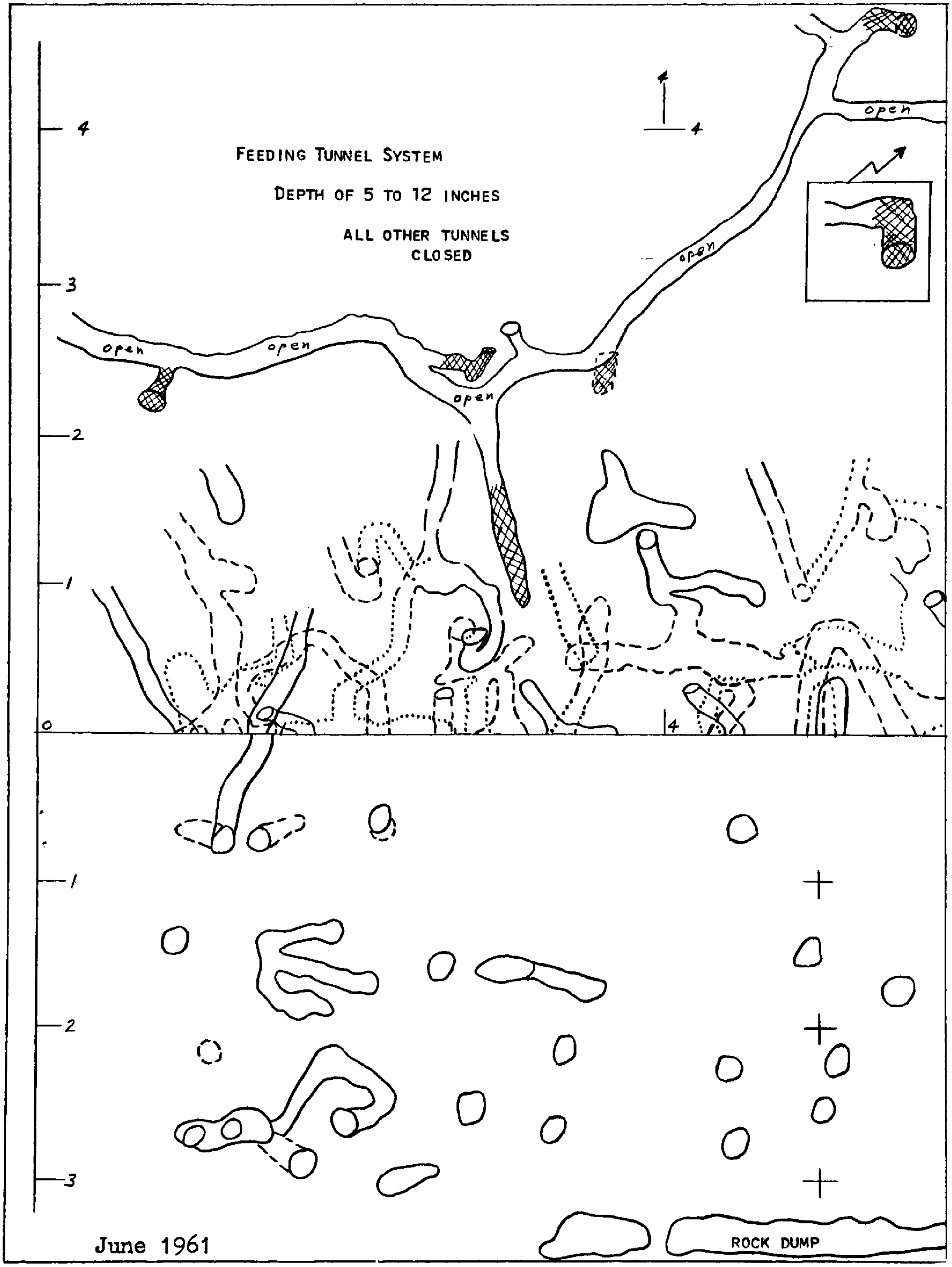


Figure 11. Briggs North excavation Number 2: Current activity.

Side and vertical views (of part) showing a feed runway, tunnel complexity, and the basal rock dump chamber. Resident taken by trap. (5/31-6/2/61, 6/14-15/61)

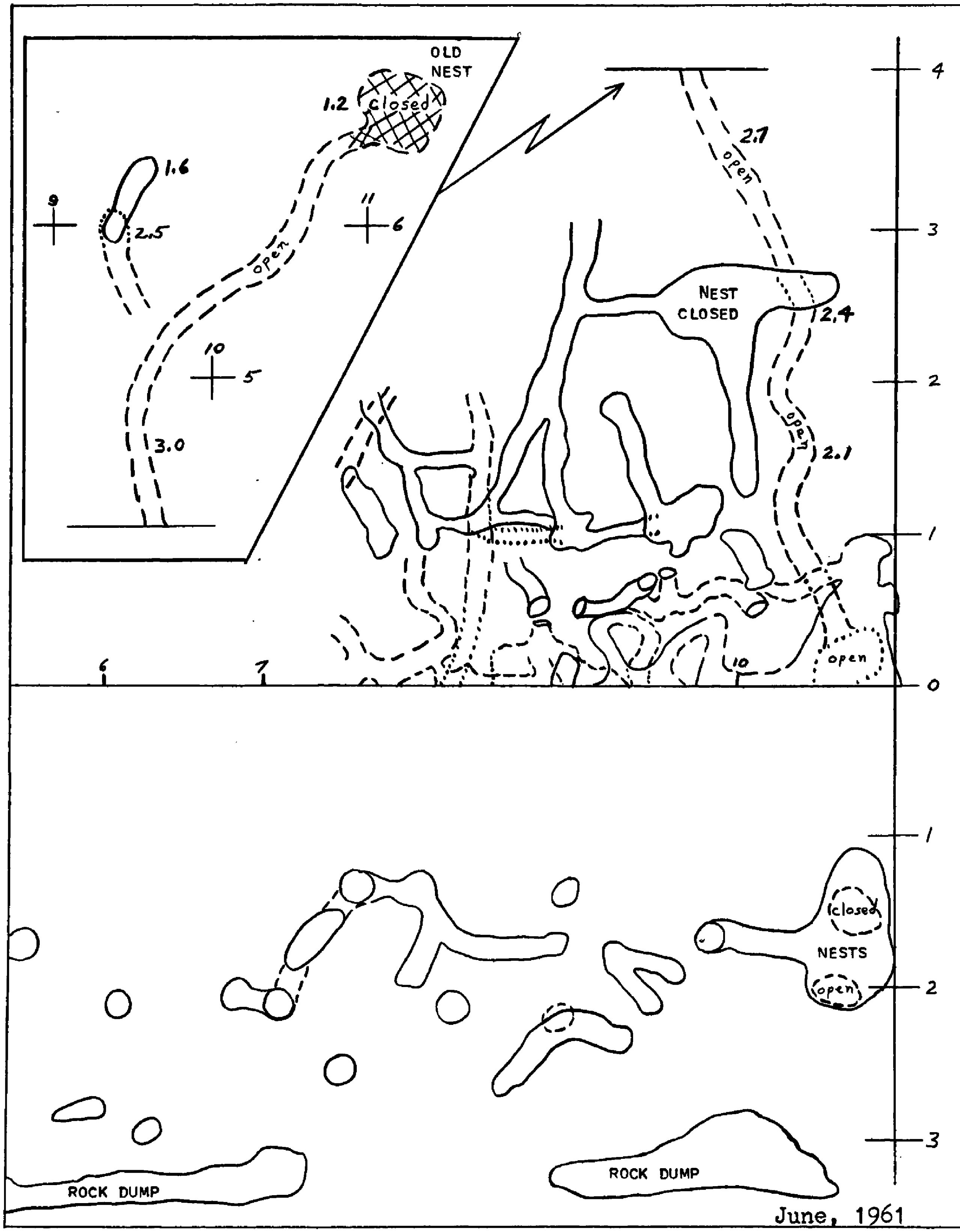


Figure 11a. Briggs North excavation Number 2: Current activity.

Side and vertical views of part showing nest systems and basal rock dump chambers. Dumps extend horizontally across the whole base of this spot and rest on red sandy parent material. Figures beside tunnel show depth in feet. (5/31-6/2/61, 6/14-15/61) displaced gravel were not present. I found here that no evidence of subsurface soil disturbance existed and the hardpan zone showed no discontinuity from that outside the clone. An adjacent inactive spot which I excavated had the usual internal disturbance features present and also met all surface criteria. The clones are infrequent and do not appear on the aerial photographs as light spots. This seemed to support the idea that the light spots were due to the calcium-coated gravel concentration at the surface of the soil disturbances. Cosby (1960) has reported similar clones formed by various species of plants.

Because of the regular spacing of spots, spacing distances of ant, ground squirrel, and pocket gopher workings were measured. Ground squirrels were eliminated on the basis of their localized colonial habit. The highest density of anthills did not exceed ten per acre and this was not comparable to spacing of the spots especially since spacing is not at all regular among the ant heaps. In addition, diameters of clearings around anthills are much smaller than the disturbed spots. The largest ant clearing found in any location measured only eight by eight and one-half feet.

Although pocket gophers are now relatively scarce in the study area, data taken from locations of current gopher activity indicate local populations comparable to those outlined in the review of literature (see Table 1). Applying procedures described by Howard (1961) to a study location north of Dillon, I counted an average of twenty-four gophers per acre with deviations of plus or minus four. Since the swale portions of the transect lines showed the greatest concentration of activity with upper slopes progressively less active to the point of no current population present, the parts of the lines pertaining to the swale site were extracted from the total data and averaged separately. Swale population then was found to average thirty-three gophers per acre with ranges from thirty to thirty-nine. Table 4 below summarizes the data from some of the measurements made to determine spacing in two locations.

Table 4. Date from lines run to determine current gopher activity spacing.

Location	Line	No. of lines	Distance (feet)	Number of Gopher centers	Average Spacing (ft.)
1	Straight	3	4059.0	51	118.80
	Random	1	1963.5	17	116.82
2	Straight	2	2706.0	35	76.56
	Random	1	3234.0	17	189.42

As can be seen from the last column, spacing varies among the populations present. The inference drawn from the apparent difference in spacing between the patternization spots and current gopher centers is that at the time of pattern formation the pocket gopher population was much higher than now. Such regular spacing of spots seems to indicate at least a territorial saturation point in the past.

Since active pocket gophers make an irregular surface disturbance, some investigation was necessary to see if the irregularity could develop into the nearly circular spots forming the pattern studied. Results of this phase of investigation are shown in the next four figures. Figure 12 shows the area of surface disturbance I diagramed in one site. Solid lines show the soil material pushed

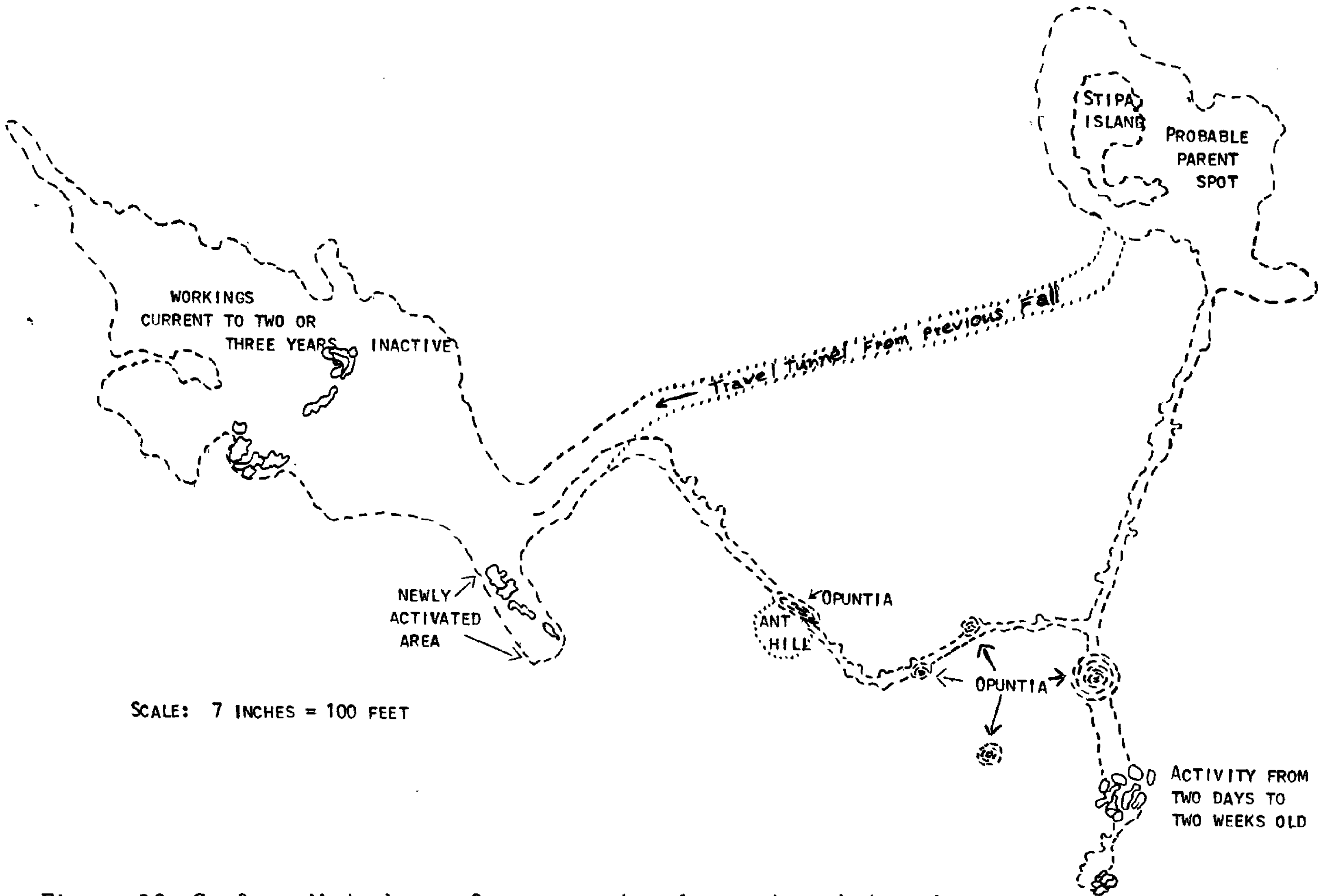


Figure 12. Surface disturbance from current and recent pocket gopher activity: East of Badger Pass.

Disturbance is either on contour or at right angles to contour. Dashed circles indicated as Opuntia are patches of heavily worked Opuntia polycantha apparently used for food during the dry summer season just ended. Solid lines show the location of gopher activity current on the day the diagram was made. Four pocket gophers are indicated as resident. September 1962.

up by the resident gophers on the day diagramed. The localization of such activity indicates four pocket gophers present. The balance of the area within the dashed lines encloses disturbance up to three or four years old judging by the various stages of revegetation in progress. Figure 13, diagramed in another study location, exemplifies the extent of surface disturbance caused by what seemed to be only one gopher during one season of activity. The locations of deep workings are indicated in this diagram. Gophers in this study location were highly dispersed.

Figure 14 shows a half acre area diagramed in a third location. I marked the parts of this surface disturbance indicating deep workings since these would seem capable of developing into spots after cessation of gopher activity. These places of deeper digging have the somewhat circular form comparable to spots. The balance of soil working here appeared to be shallow.

Some indication of progressive changes can be seen in Figure 15 which shows three one-acre strips diagramed in two adjacent study locations. The sample in the most active site shows irregularity with more regularity of disturbance outline as activity decreases and inactive stabilization occurs.

From the above described data and findings I conclude that the pocket gopher (*Thomomys talpoides fuscus*) is the agent responsible for the original soil disturbance developing into spots forming the pattern found in southwestern Montana. Results of this investigation support the findings of Dalquest and Sheffer (1942) and Arkley and Brown (1954).

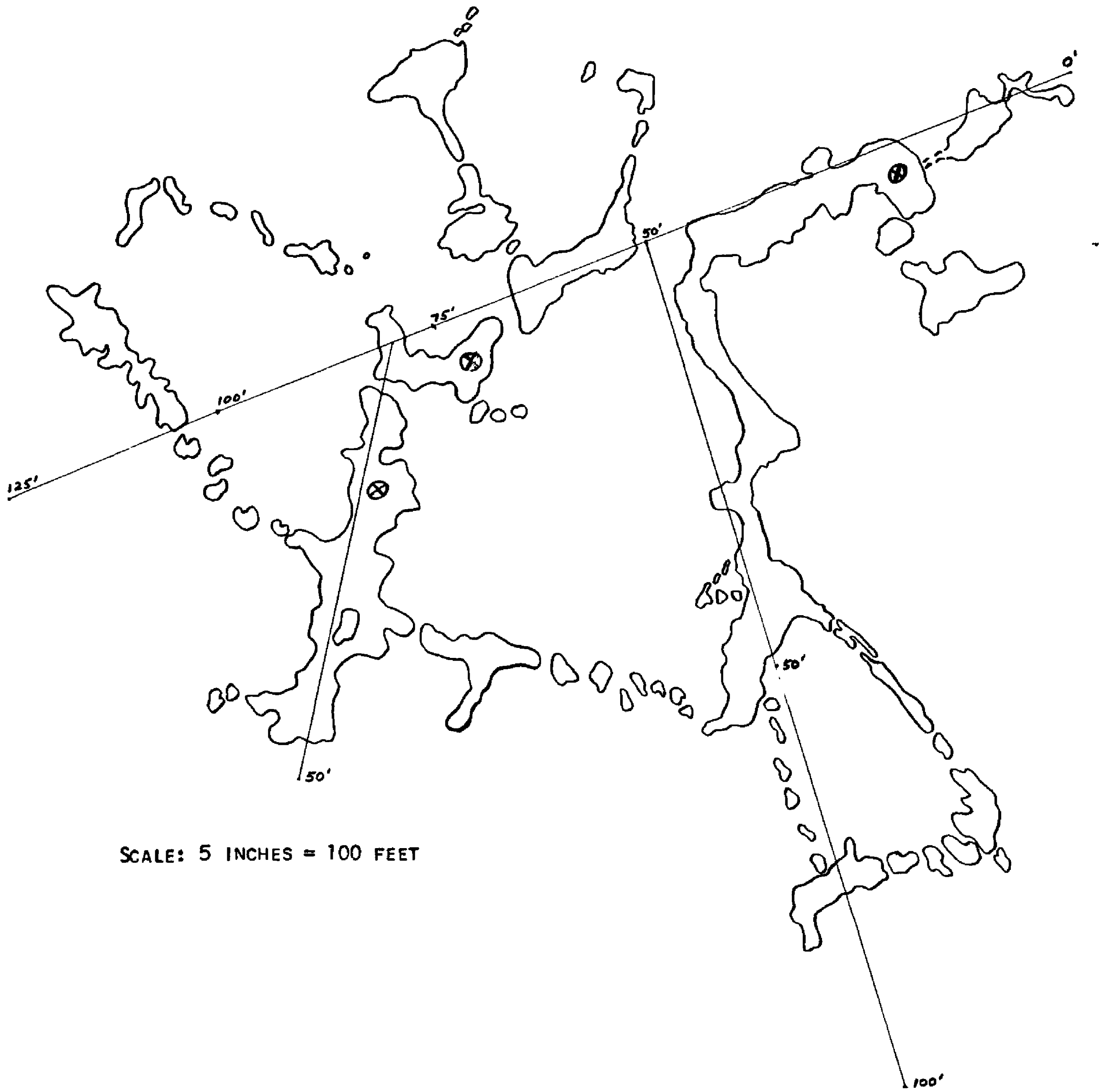


Figure 13. Surface disturbance from current and recent pocket gopher activity: Stone Creek.

Disturbance is either on contours or at right angles to the contour. This appears to be the seasonal work of one pocket gopher still active in this site. (X) indicates centers of deep workings. The balance of the activity is primarily shallow feeding tunnel disturbance. March 1963.

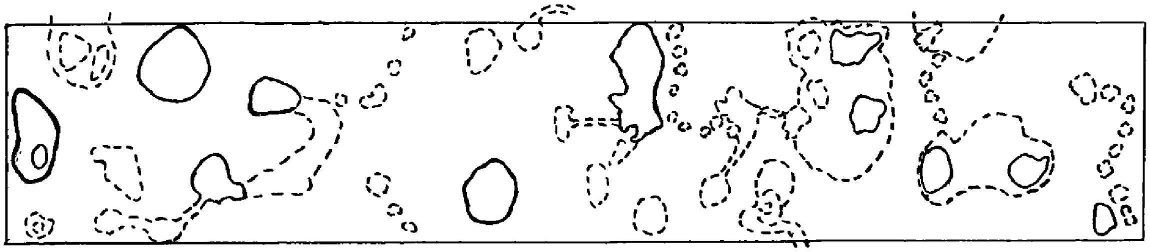


Figure 14. Surface disturbance from current and recent pocket gopher activity: Hagenbarth East.

Area included is one-half acre (66 feet by 330 feet). Solid line indicates deeper parts of the disturbance which are most likely to develop into spots upon stabilization. Dashed lines indicate shallow workings not likely to be recognizable after the inactive stage is reached. December 1962.

PLANT SUCCESSION

One of the major points of interest discovered during preliminary investigations leading to this study is the difference in plant composition shown by comparing aerial photographs taken in 1942 with those taken in 1955 for the same location. Such comparison revealed that an increase of Artemisia tridentata was apparently in progress. Contrast of two photographs for the two dates, 1942 and 1955, of the same location illustrating this difference in vegetation is shown in Figures 16 and 17. This contrast also indicates a relation of compositional changes to the spots of soil disturbance forming the pattern under study.

To examine vegetative relations connected with this patternization, I measured and recorded all possible detail as outlined in the methods of study previously described in this report. Line intercept and transect data for plant species of primary occurrence inside and outside the individual spot boundaries on a frequency basis are presented in Tables 5 and 6 following.

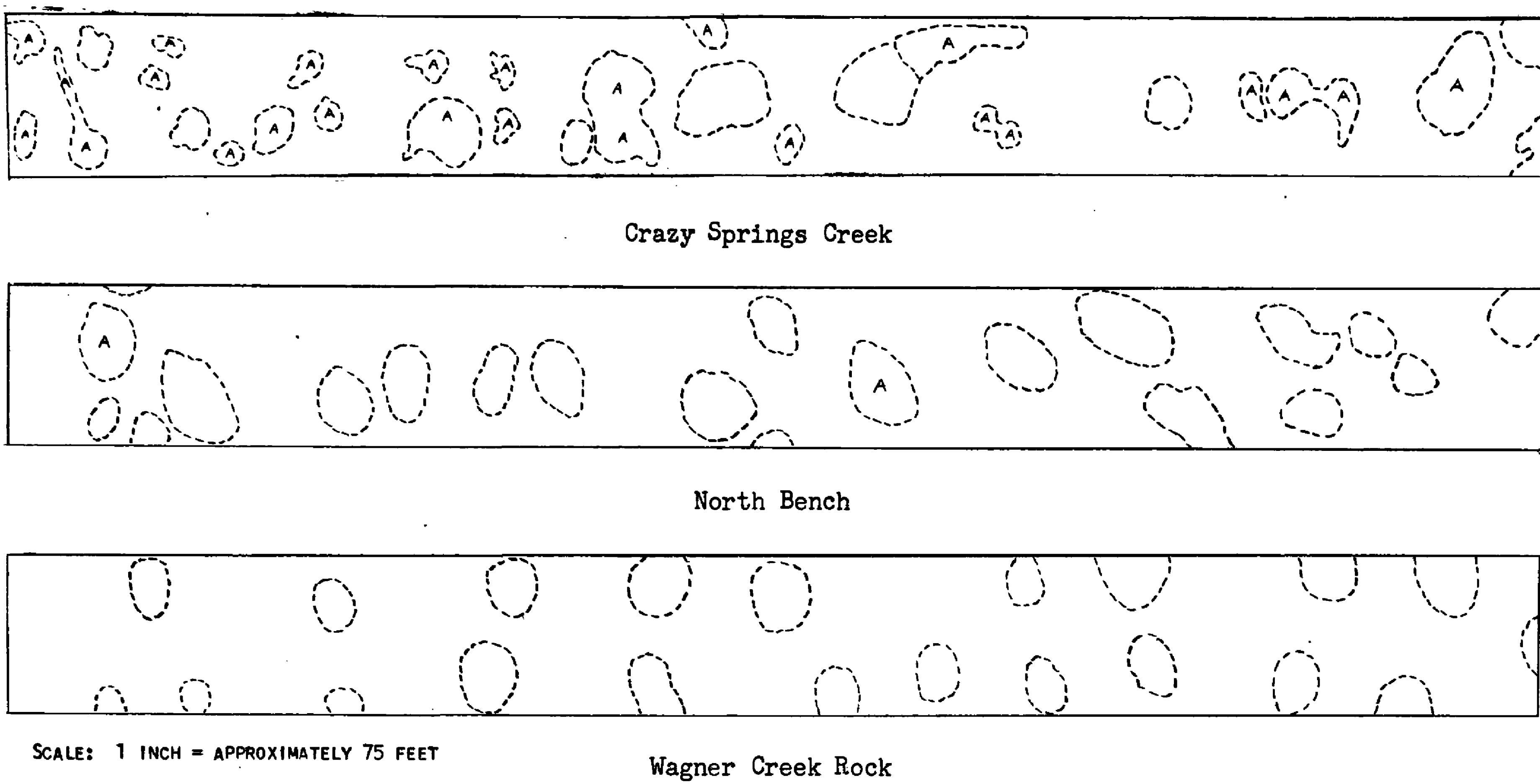


Figure 15. Comparison of surface disturbance in three locations in the Blacktail drainage.

Each strip is one acre in area. "A" shows both deep and shallow current pocket gopher activity. The Crazy Springs Creek sample is adjacent to a cattle concentration area at a waterhole and is currently active. The North Bench site is generally inactive except for the two spots noted. The Wagner Creek Rock location is well stabilized. This shows decreasing irregularity of disturbance boundaries from the active to the stabilized stages in spot development. August 1961

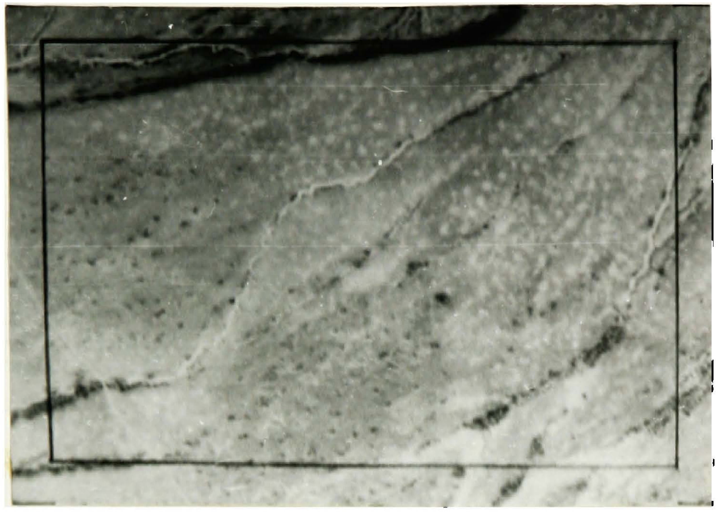


Figure 16. 1942 aerial photograph showing the vegetation then present. Most spots appear light in color. Approximate width of picture inside the solid border is one-half mile. Date of flight, August 21, 1942.

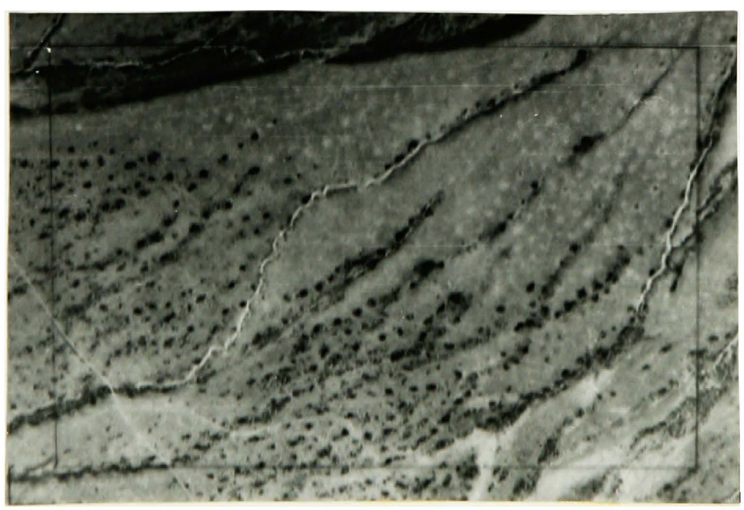


Figure 17. 1955 aerial photograph of the same area as the figure above. Many more spots appear dark. Approximate width of picture inside the solid border is one-half mile. Date of flight, July 20, 1955.

These figures show differences in spot appearance in the same location in two different years. The change illustrates the expansion of <u>Artemisia tridentata</u> into previously unoccupied areas by means of the spot disturbances.

TABLE 5.--FREQUENCY[A] OF SPECIES OF PRIMARY OCCURRENCE ON TRANSECT LINES IN LOCATIONS WITH STABILIZED SPOTS DOMINATED BY GRASSES.

LOCATION	GRASSES												OTHER PLANTS											
	STIPA COMATA				AGROPYRON SPICATUM				AGROPYRON SMITHII				CHRYSOTHAMNUS VISCIDIFLORUS				EUROTIA LANATA				ARTEMISIA FRIGIDA			
	INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE	
	F[B]	F%[B]	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%
RECENT SPOTS:																								
E. OF BADGER PASS																								
T - 1	3/21	14	36/38	95	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4/38	11	--	--	10/38	26
HAGENBARTH EAST																								
T - 3	35/37	95	63/63	100	--	--	--	--	--	--	--	--	--	--	--	--	4/37	9	4/63	6	--	--	--	--
INACTIVE SPOTS:																								
HAGENBARTH EAST																								
T - 1	9/29	31	15/37	40	--	--	--	--	--	--	--	--	--	--	1/37	3	7/29	24	3/37	8	--	--	--	--
T - 2A.	6/7.5	80	35/39.5	89	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2/39.5	5	--	--	--	--
T - 2B.	12/16	75	28/34	82	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
PASKETT PASTURE																								
T - 3A.	7/21	33	1/27	4	10/21	47	11/27	41	--	--	--	--	--	--	--	--	--	--	--	--	1/21	5	9/27	33
T - 3B.	7/20	35	1/28	4	9/20	45	11/28	39	--	--	--	--	--	--	--	--	--	--	--	--	4/20	20	12/28	43
T - 4	16/31	52	4/37	11	12/31	32	16/37	43	2/31	6	--	--	--	--	--	--	--	--	--	--	1/31	3	3/37	8
CRAZY SPRINGS CREEK																								
T - 1A.	9/30.5	29	34/36.5	93	--	--	--	--	6/30.5	20	11/36.5	31	4/30.5	13	2/36.5	5	3/30.5	10	--	--	--	--	2/36.5	5
T - 1B.	9/19.5	46	27/47.5	57	--	--	--	--	6/19.5	31	5/47.5	10	4/19.5	20	1/47.5	2	3/19.5	15	1/47.5	2	1/19.5	5	2/47.5	4
T - 2A.	2/15	13	29/39	75	--	--	4/39	10	--	--	--	--	7/15	47	3/39	8	8/15	53	1/39	3	1/15	7	--	--
T - 2B.	3/22.5	13	22/31.5	70	1/22.5	4	4/31.5	13	1/22.5	4	1/31.5	3	7/22.5	31	2/31.5	6	6/22.5	27	1/31.5	3	2/22.5	9	1/31.5	3
T - 3	7/26.5	26	25/33.5	75	--	--	--	--	1/26.5	4	6/33.5	18	8/26.5	30	1/33.5	3	1/26.5	4	--	--	--	--	--	--

[A]FREQUENCY - NO. OF FEET IN WHICH THE SPECIES OCCURRED IN THAT PORTION OF THE TRANSECT DESIGNATED "INSIDE" OR "OUTSIDE" THE SPOT AS THE CASE MAY BE.

TABLE 5.--(CONTINUED)

LOCATION	GRASSES: STIPA COMATA				GRASSES: AGROPYRON SPICATUM				GRASSES: AGROPYRON SMITHII				OTHER PLANTS: CHRYSOTHAMNUS VISCIDIFLORUS				OTHER PLANTS: EUROTIA LANATA				OTHER PLANTS: ARTEMISIA FRIGIDA			
	INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE	
	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%
INACTIVE SPOTS (CONT.)																								
NORTH BENCH																								
T - 1A	15/22	68	18/32	51	--	--	3/32	9	--	--	5/32	16	--	--	--	--	6/22	27	--	--	--	--	7/32	22
T - 1B	21/23	90	19/31	61	--	--	--	--	--	--	4/31	13	--	--	--	--	5/23	22	--	--	--	--	8/31	26
STONE CREEK																								
T - 1	4/20	20	2/20	10	--	--	--	--	3/20	15	16/20	80	14/20	70	4/20	20	--	--	--	--	6/20	30	4/20	20
BRIGGS NORTH																								
T - 1	16/16	100	84/84	100	--	--	--	--	--	--	57/84	68	--	--	--	--	16/16	100	57/84	68	--	--	4/84	5
STABILIZED SPOTS:																								
PASKETT PASTURE																								
T - 1	23/29	79	5/51	10	1/29	3	17/51	33	7/29	24	10/51	20	--	--	--	--	--	--	--	--	--	--	--	--
T - 2A	16/30	53	--	--	7/30	23	10/30	33	2/30	7	1/30	3	--	--	--	--	--	--	--	--	1/30	3	3/30	10
T - 2B	11/25	44	7/35	20	10/25	40	23/35	66	--	--	2/35	6	--	--	1/35	3	--	--	--	--	--	--	4/35	11
WAGNER CREEK																								
T - 1	29/35	83	23/34	68	5/35	14	7/34	20	2/35	6	--	--	--	--	--	--	--	--	--	--	1/35	3	4/34	12
T - 2A	20/29	70	20/31	65	--	--	--	--	--	--	10/31	32	--	--	2/31	6	2/29	7	--	--	--	--	13/31	42
T - 2B	23/27	85	19/33	58	--	--	3/33	9	2/27	7	3/33	9	--	--	3/33	9	3/27	11	--	--	1/27	4	8/33	24
T - 3A	28/31	90	13/37	35	3/31	10	2/37	5	--	--	4/37	11	--	--	1/37	3	1/31	3	--	--	2/31	6	13/37	35
T - 3B	26/30	87	13/38	34	1/30	33	9/38	24	--	--	4/38	11	--	--	--	--	1/30	3	1/38	3	--	--	13/38	34
T - 4A	24/26.5	91	12/33.5	34	--	--	3/33.5	9	1/26.5	4	--	--	3/26.5	11	6/33.5	18	--	--	--	--	2/26.5	8	7/33.5	21
T - 4B	19/27.5	69	11/32.5	34	8/27.5	29	8/32.5	25	--	--	5/32.5	15	--	--	3/32.5	9	--	--	--	--	4/27.5	15	10/32.5	31

TABLE 6.--FREQUENCY[A] OF SPECIES OF PRIMARY OCCURRENCE ON TRANSECT LINES IN LOCATIONS WITH SPOTS DOMINATED BY SAGEBRUSH.

LOCATION	GRASSES												OTHER PLANTS											
	STIPA COMATA				AGROPYRON SPICATUM				AGROPYRON SMITHII				ARTEMISIA TRIDENTATA				GUTIERREZIA LONGIFOLIA				CHRYSOTHAMNUS VISCIDIFLORUS			
	INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE		INSIDE		OUTSIDE	
	F[B]	F%[B]	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%	F	F%
INACTIVE SPOTS: BRIGGS NORTH																								
T - 1	16/16	100	84/84	100	--	--	--	--	--	--	57/84	68	1/16	6	2/84	2	1/16	6	2/84	2	--	--	--	--
T - 2	35/36	97	63/64	98	--	--	--	--	17/36	42	45/64	70	15/36	42	--	--	--	--	2/64	3	--	--	--	--
STABILIZED SPOTS: BRIGGS NORTH																								
T - 3	8/31	26	58/69	84	--	--	--	--	20/31	65	53/69	77	24/31	77	20/69	29	18/31	58	25/69	36	1/31	3	--	--
MEDICINE LODGE																								
T - 1	10/33	30	42/67	63	16/33	48	42/67	63	--	--	--	--	32/33	97	36/67	54	3/33	9	35/67	52	--	--	8/67	12
T - 2	2/20	10	26/80	32	8/20	40	67/80	84	--	--	--	--	17/20	85	62/80	77	1/20	5	48/80	60	3/20	15	11/80	14
T - 3	5/40	12	16/60	27	31/40	77	58/60	97	--	--	--	--	34/40	85	31/60	52	2/40	5	27/60	45	1/40	2	3/60	5
BADGER PASS																								
T - 1A.	--	--	--	--	6/37	16	9/35	26	--	--	--	--	7/37	19	3/35	9	2/37	5	4/35	11	1/37	3	--	--
T - 1B.	--	--	1/36	3	7/35	20	4/36	11	--	--	--	--	6/35	17	1/36	3	4/35	11	2/36	6	--	--	1/35	3
T - 2	--	--	--	--	20/21	95	66/79	84	--	--	--	--	19/21	90	37/79	47	--	--	11/79	14	--	--	9/79	11

[A] FREQUENCY - NO. OF FEET IN WHICH THE SPECIES OCCURRED IN THAT PORTION OF THE TRANSECT DESIGNATED "INSIDE" OR "OUTSIDE" THE SPOT AS THE CASE MAY BE.

[B] F - 16/16 INDICATES SPECIES FOUND ON EACH OF 16 ONE FOOT INTERVALS OF A 16 FOOT TRANSECT; THEN F% IS 100, ETC.

As can be seen in both tables, species composition differed inside and outside the spots both in relative frequency and presence or absence of some species. In spots examined where a state of inactivity had not yet reached the point of vegetative stabilization, differences indicative of successional stages are apparent, particularly when shrubs other than Artemisia tridentata are considered. Salsola kali var. tenuifolia is not included in the tabulations although I found it to be present inside the spots in the early stages of succession after disturbance ceased. This plant is left out since most transects were measured on spots stabilized or inactive for a number of years. Salsola sp., however, was a consistent annual invader in the very early stages of revegetation. Species, other than Salsola sp., not included in Tables 5 or 6 are excluded since I did not find that they exhibited any definite correlation with the spot activity.

Vegetation on spots which had stabilized were either in grass cover or in sagebrush. The sagebrush spots occurred as aggregated islands of sagebrush in a grass matrix in some locations or as aggregations exhibiting greater density and size of sagebrush plants in the spots in a nearly closed sagebrush community. Both can be distinguished on aerial photographs.

In general, shrubby species of various kinds showed more plainly evident characteristics of invasion and changes according to successional stages than did grasses. Shrub or shrublike species which I found to be common invaders in different locations in the study area are listed in Table 7. Most often only one of these species is dominant in a given spot.

Table 7. Species commonly invading spots in southwestern Montana.

Persistent when established	Present during various stages of succession
Artemisia tridentata	Opuntia polyacantha
Artemisia nova	Chrysothamnus viscidiflorus
Sarcobatus vermiculatus	Gutierrezia longifolia
	Eurotia lanata

On analysing data from shrub count plots, two shrubs, Eurotia lanata and Artemisia frigida, showed correlation with spot conditions. E. lanata exhibited a positive association in being present to a greater degree on the spot than off and A. frigida a negative association. Artemisia tridentata and Chrysothamnus viscidiflorus also showed a positive relationship to the spot disturbances but these will be discussed separately. Tables 8 and 8a present the data summarizing measurements on E. lanata and A. frigida together with results of a Chi square test of significance. The species were tested separately since the presence or absence of one species did not appear to affect the relation of the other species to the disturbance.

The relations shown in Tables 8 and 8a are also evident in the last two columns of Table 5 which lists data from transects instead of shrub count plots. The most consistent appearance of these positive and negative relations seems to occur in intermediate stages of succession. As shown by the footnotes in Tables 8 and 8a, the basic relationships of both shrubs, but particularly E. lanata, are affected by the degree of recent activity, by stabilization, or by the presence of A. tridentata. The last case suggests a competitive situation wherein E. lanata cannot become established or if established cannot maintain

TABLE 8.--The Number of Individual Crowns of <u>Eurotia lanata</u> and <u>Artemisia frigida</u> Inside and Outside of Spots. Data From 200 Square Foot of Plot Area.

Location	Inside		Outside		Significance	
	Eurotia lanata	Artemisia frigida	Eurotia lanata	Artemisia frigida	Eurotia lanata	Artemisia frigida
Hagenbarth East						
Transect 1	108		44			
2	4		2	2	**[d]	
3	11		12			
Badger Pass						
Transect 1	a.[a]			16		**
2	a.			9		
Paskett Pasture						
Transect 1	s.[b]			17		
2	s.	33		93		**
3	s.	119		429		
4	s.	48		237		
Crazy Springs Creek						
Transect 1	96	28	5	37		
2	r.[c] 237	55	11	23	**	**
3	85	11	7	31		
North Bench						
Transect 1	123	12	9	194	**	**
Wagner Creek						
Transect 1	46	27	1	180		
2	37	7		469	**	**
3	75	22	6	465		
4		128		275		
Briggs North						
Transect 1	665	4	112	16		
2	a. 71		142	1	**	**
3	a.		170	6		
Medicine Lodge						
Transect 1	a.			67		
2	a.			43		**
3	a.			5		

[a]a. Spots dominated by <u>Artemisia tridentata</u>.

[b]s. Spots long stabilized in location of historically least heavy grazing.

[c]r. Spots of recent activity.

[d]* Significant at the 5% probability level; ** at the 1% probability level.

TABLE 8a.--The Number of Individual Crowns of Eurotia lanata and Artemisia frigida Inside and Outside of Spots. Data from 100 square feet of plot area.

Location	Inside		Outside		Significance	
	Eurotia lanata	Artemisia frigida	Eurotia lanata	Artemisia frigida	Eurotia lanata	Artemisia frigida
Hagenbarth East						
Plot Site 1	109		55	1		
2	82		53	2		
3	71		12		**[a]	
4	120		14	2		
Briggs North						
Plot Site 1	4	76	3	62		
2	r.[b] 11	36		33		
3	r. 124	11	15	12	**	**
4	33	31	1	82		
5	47	8	2	27		
Dell-Lima						
Plot Site 1	52	11	8	23		
2	27	9	11	121	**	**
3	132	1	9	13		
4	17		19	50		
Stone Creek						
Plot Site 1		3	1			
2	5				*	
3		1		2		

[a]* significant at the 5% level; ** at the 1% level.

[b]r. reactivated spots in a stabilizing condition.

itself against invasion by A. tridentata. Whether this is root competition or an intolerance of E. lanata to shade, I did not determine. This competitive effect on Eurotia lanata may also be part of the explanation for its absence on spots dominated by Chrysothamnus viscidiflorus, especially in the Stone Creek study location.

To investigate the increase in Artemisia tridentata suggested by comparison of aerial photographs for different years (Figures 16 and 17), spots were also examined for age relations of this plant when it was present. Table 9 and 9a summarize ring counts of A. tridentata in the three study locations I measured in greatest detail. The Briggs North location exhibits the greatest contrast of the three locations when comparing aerial photographs from 1942 and 1955 and gave the most information on the extent soil disturbance by pocket gophers and other agencies might have on movement of sagebrush communities into unoccupied areas. This is a major aspect of the study.

Ages of A. tridentata correlated reasonably well with the dates of aerial photographs used for comparison. In some cases, I found A. tridentata plants up to thirty years old on spots appearing as bare or grass spots in the 1942 pictures. These plants occurred singly or were few in number on the spots. Although these individual plants were eight or nine years old in 1942, I do not believe they were large enough at that age to appear on the photograph since all plants I measured in the five to ten year age class during the study did not exceed four to six inches in height.

Photographs having spots with A. tridentata apparent in 1942 showed an expansion of the aggregations in 1955. Ring counts here

TABLE 9.--Ring Count Aging Analysis of Oldest Artemisia tridentata, based on spots additional to those measured by transects across the plant community.

Briggs North			Medicine Lodge			Badger Pass		
Sample	Inside rings	Outside rings	Sample	Inside rings	Outside rings	Sample	Inside rings	Outside rings
Paired Site:[a] 1*[b]	35	--	Paired Site: 1	43 36 30 32	40 34 32 25	Paired Site: 1	60 59 46+[c] 46+	52 51
2*	35 34 20 8 6	-- -- -- -- --	2	49 39 37 34 32	34 29 28 25 24	2	62 60 56	61 55 52 51 47+ 47
3	--	--	3	--	--	3	56 55 49 46	54 47+ 43 39

[a]Ages paired by plants inside a spot compared to those adjacent and outside.

[b]No plants outside.

[c]+ indicates a missing center either from rot, weathering, or carpenter ant (Camponotus sp.) activity in the stem.

TABLE 9a.--Ring Count Aging Analysis of Oldest *Artemisia tridentata* Plants at 3 Locations, Based on Transects Across the Plant Community.

Briggs North			Medicine Lodge			Badger Pass		
Sample	Inside rings	Outside rings	Sample	Inside rings	Outside rings	Sample	Inside rings	Outside rings
Transect:[a]			Transect:			Transect:		
1**[b]	5	22	1	36	35	1	--	--
		18		33	29			
				32	28			
				29	19			
				29	18			
2***[c]	38	27	2	37	35	2	96	91
	30	22		34	35		75	80
	24	19		34	28		72	66
	20	18		30	24		71	63+[d]
	19	--		30	24		60	52+
3	37	35	3	36	60	3	--	--
	36	33		35	55			
	36	26		34	43			
	33	22		34	42			
	23	21		33	36			

[a]Plants aged along a transect line.

[b]** only three plants present.

[c]*** only four plants outside.

[d]+ indicates a missing center either from rot, weathering, or carpenter ant (*Camponotus sp.*) activity in the stem.

indicated development by younger plants aggregated around the older plants which caused a larger area of the spot to appear dark in the 1955 picture. In this manner, I could determine that sagebrush invasion of spots is taking place and that by expansion of aggregations already present on spots into the interspot areas, progress toward _A. tridentata_ crown closure forming a continuous sagebrush type is occurring.

The Medicine Lodge and Badger Pass locations are already closed sagebrush communities. The Badger Pass location had _A. tridentata_ in the same age classes on and off the spots. Since I found some of these plants in the ninety to one-hundred year age class both inside and outside the spots, I concluded that a second generation development had occurred in this community after its expansion to crown closure. The density of _A. tridentata_ was greater on the spots and aggregation is evident from both transect and shrub count data. The aggregations indicate that primary invasion occurred on the spots and later spread to form the present closed community possibly through grazing influence. No difference appeared in the 1942 and 1955 aerial photographs of this location. Some difficulty was experienced in making ring counts here since carpenter ants (_Camponotus_ sp.) were active in boring out stem centers for depositing eggs or the centers in old plants had rotted out. This is indicated by footnote in Tables 9 and 9a.

The Medicine Lodge location presents a more confusing picture since, even though it is a closed sagebrush community, the age classes here are relatively young. In an effort to clarify this picture, I aged a number of spots across the two-mile sagebrush zone in both the Medicine Lodge and Briggs North locations. These data are presented in Tables 10 and 11.

The Briggs North location is not a closed sagebrush community but the spots are largely dominated by sagebrush forming woody islands in the surrounding grass type. Few plants occur outside the spots here. Ages of these plants are slightly younger than those in the Medicine Lodge but indicate the age of sagebrush invasion as being comparable.

Only at the top of the Medicine Lodge sagebrush zone did I find the older sagebrush inside the spot to any extent. The intermediate and lower elevations were either nearly the same age inside and out or had the older plants outside the spots. The only apparent explanation I could deduce is based on consideration of the grazing history in the Medicine Lodge extending back almost to 1860 and the presence of a few grass-covered spots scattered through the sagebrush community. The grass spots might indicate that original vegetative stabilization occurred in a grassland type and subsequent overgrazing caused a disclimax developing into a uniform sagebrush stand.

If sagebrush is essentially an invader as this study indicates, some source of seed is necessary. From other ring counts I made, particularly in the Dell-Lima location, there is an indication that *A. tridentata* naturally occurs on rock-ledge sites and spreads from these places to disturbed locations. I found plants of the rocky ledges in the ninety to one-hundred year old age class while any plants connected with disturbance such as spots or other kinds in the general vicinity did not exceed forty to fifty years old and were usually under forty.

TABLE 10.--Medicine Lodge Sagebrush Ages[a]

Elevational Location	Age Inside Spots		Age Outside Spots		Remarks
I Foot of hill Bottom of Sagebrush Zone	44 43 43 42 40	Avg 42	57 57 56 56 54	Avg 56	Early day heavy livestock trailing and mining freight traffic--back to 1860.
II Plus .4 mile uphill	39 37 36 36 34	Avg 36	42 36 34 34 33	Avg 36	
III Plus .4 mile uphill	53 44 41 40 29	Avg 43	43 39 36 36 35	Avg 38	An old but annually used sheep camp site lies between Location III and Location IV
IV Plus .6 mile uphill	41 37 37 36 35	Avg 37	37 36 36 35 31	Avg 35	
V Plus .6 mile uphill Top of Sage-Brush Zone	64 63 44 35 26	Avg 46	51 45 32 30 28	Avg 37	Sparse spot occurrence here grading into a grass-land type

[a]The five oldest plants in each elevational location are shown with their averages. Distance totals 2 miles on the slope. Approximate grade is 8%.

TABLE 11.-Briggs Ranch Sagebrush Ages[a]

Location	I[b]	II	III	IV	V
Ages of *Artemisia tridentata* plants	44 43 41 40 31	43 40 36 32 31+	37 28 26	47 41 26	43 36 34 32 27
Average age	40	36	30	38	34

[a] Ages of the oldest plants in each elevational location are shown. No ages were taken outside the spots for lack of plants. Distance covered on the slope is approximately 2 miles. Approximate grade is 7%.

[b] Location I is lowest on the bench and V the highest; II, III, and IV are intermediate.

Analysis of transect data (Table 5) and other measurements correlated with stage of inactivity or stabilization and observations in the various locations permit some localized successions to be described in spots ending in grass cover when stabilized. Table 12 shows six of such sequences.

Several study locations are not included in Table 12. In the case of locations with extensive sagebrush community development, there is no way to identify the early stages of succession specifically and these stages can only be inferred. In some other locations of stabilized grass-spot nature, either intermediate stages are absent or unidentified. In the latter case, the spots are either all stabilized or have been secondarily disturbed by other animals or humans; again, sequence of vegetation changes are inferential.

Using study data and the inferential sequences just discussed, I have developed two tables to show the generalized probable successions in grass spots (Table 13) and sagebrush spots (Table 14). These will serve as summary of this consideration of plant succession.

DISCUSSION

Most of the spots studied did not have as well developed a hump form as those in the location west of Wisdom. These latter spots most resembled the Mima mounds described in the literature (Arkley and Brown 1954, Dalquest and Sheffer 1942, Hansen 1962, Nikiforoff 1941). The location is a naturally sub-irrigated, nearly level upland bench and the mounds form a pattern of spacing and diameter measurements comparable to those in the study locations already described. Internal features of

TABLE 12.--Localized Sequences of Vegetational Changes [a] Identified by Relating Period and Stage Subsequent to Gopher Activity to Transect Date, Shrub Counts, Aging Analyses, Aerial Photographs, Surface Observation and Subsurface Examinations.

	1	2	3	4	5	6
Changes in Vegetation	Bare soil Salsola (Cryptantha)[b] Eurotia (Chrysothamnus viscidiflorus or Aristida) Stipa comata	Bare soil plus Opuntia or Opuntia Salsola Eurotia (Chrysothamnus viscidiflorus) Stipa comata	Bare soil Salsola Chrysothamnus viscidiflorus Artemisia nova or Sarcobatus vermiculatus	Bare soil Chrysothamnus viscidiflorus and Eurotia Eurotia Stipa comata	Bare soil Eurotia (Chrysothamnus viscidiflorus) or (Gutierrezia) Stipa comata or Artemisia tridentata	Bare soil Eurotia Agropyron spicatum (Agropyron smithii)
Locations Showing the Above Succession	Hagenbarth East Hagenbarth West Staudenmeyer Ranch Malesich Hiway Pasture Crazy Springs Creek East of Badger Pass	Malesich Hiway Pasture Hagenbarth East Hagenbarth West	Stone Creek: Malesich Pasture Lowland Benches of the Blacktail Drainage	Stone Creek: Lasich Pasture	Briggs North Briggs South Dell-Lima	Briggs North Paskett Pasture

[a] Only the generic name of the plant species is given unless confusion between species might occur.

[b] Plant names in parentheses show those of alternate or of companion occurrence with the one above.

TABLE 13.-Generalized Probable Succession in Spots Ending in Grass. Based on Data From Transects, Shrub Counts, Aging Analyses, Aerial Photographs, and Observations Above and Below Ground.

Period Following Gopher Activity	Stage of Succession	Detail of Changes in Vegetation	Estimated Accumulative Time
Recent and Inactive	1	Salsola kali, var. tenuifolia partially covers bare soil left by pocket gopher (Thomomys talpoides).	1 year
		Salsola sp. invasion continues to a complete cover.	2 years
	2	Eurotia lanata fills in the center of the spot. Periphery is still in Salsola sp.	3 years
		Eurotia sp. forms a complete cover over the spot area of deep workings. It may also be partly present in areas of shallow workings and feeding tunnels.	4 years
	3	Stipa comata begins to reinvade. Eurotia sp. is persisting.	5 years
Inactive and Stabilizing	4	Stipa sp. increases with Eurotia sp. persisting but of decreasing frequency. (Agropyron spp. may be present with or in place of Stipa comata.)	
Stabilized	Final	Grass cover is solid and often of somewhat greater density than the adjacent undisturbed area. Some few plants of Eurotia lanata usually remaining.	15 years or more

TABLE 14.-Generalized Probable Succession in Spots Ending in Sagebrush. Based on Age Analyses, Shrub Counts, Transect Data, Aerial Photographs, and Observations Above and Below Ground.

Period Following Gopher Activity	Stage of Succession	Detail of Changes in Vegetation	Estimated Accumulative Time
Recent[a] and Inactive	1	Salsola kali var. tenuifolia partially covers bare soil left by pocket gopher (Thomomys talpoides).	1 year
		Salsola sp. invasion continues to be a complete cover.	2 years
	2	Eurotia lanata fills in the center of the spot. Periphery is still in Salsola sp.	3 years
		Eurotia sp. forms a complete cover over the spot area of deep workings. It may also be partly present in areas of shallow workings and feeding tunnels.	4 years
	3	Stipa comata begins to reinvade. Eurotia sp. is persisting. Agrophyron smithii may become established.	
		Artemisia tridentata often enters at this point if seed is available. Parent plant is usually single to two or three.	5 years
Expansion	4	Eurotia sp. persists. Grass cover increases (Stipa sp. by seed, Agropyron sp. by rhizomes or seed). Parent Artemisia tridentata is gaining its growth.	6 to 10 years
	5	Eurotia sp. maintains a high frequency. Parent Artemisia sp. is producing young plants with a colony beginning in the shelter of the parent.	10 to 15 years

TABLE 14.-(continued)

Period Following Gopher Activity	Stage of Succession	Detail of Changes in Vegetation	Estimated Accumulative Time
Expansion (cont.)	6	Eurotia sp. begins to diminish but still of high frequency. Stipa sp. and/or Agropyron sp. is present but not increasing. Parent Artemisia sp. produces more seed and young plants increase. Agropyron spicatum enters the spot.	15 to 20 years
Stabilizing	7	Eurotia sp. is greatly diminished. Stipa sp. virtually absent. Agropyron spp. show feeding by rabbits (Lepus spp. and Sylvilagus sp.). Gutierrezia longifolia (or Chrysothamnus viscidiflorus) enters around periphery of the Artemisia sp. aggregation. Artemisia sp. parent and young are all producing seed.	20 to 30 years
Stabilized	8	Artemisia tridentata covers the spot. Agropyron spicatum is well established. Eurotia sp. is gone from the spot with only a few plants persisting outside the spot. A narrow peripheral band of Gutierrezia sp. is often present.	30 to 40 years
	9	Artemisia sp. expand from the spots and eventually coalesce to form a closed type. Agropyron spicatum is the main grass species. A second generation of Artemisia may follow if conditions are suitable.	40 years or more

[a]Initial changes were not observed on any spot known to end in sagebrush cover but are assumed to be the same as spots ending in grass. This assumption is based on examination of spots in all stages of sagebrush invasion and expansion and on transect data and age-count relations at the Briggs North, Dell-Lima, and East of Badger Pass locations.

the mounds west of Wisdom could be seen in many mounds by means of road cuts and excavation here was not necessary. I found that sub-surface detail of the mounds differed from that in the more nearly level spots excavated in other locations. The mounds at Wisdom had only about twelve inches of dark chernozem-like soil (Formosov 1928, Formosov and Kodachova 1960) at the top of the mound. No residual evidence of pocket gophers was apparent below this upper zone of heavily worked soil. This lack of evidence in the lower zones presents a hypothetical possibility that the mounds were formed so long ago that any evidence has been completely incorporated in the soil body. The few pocket gophers now resident in this location confine their activity to the upper zone and do not penetrate the substratum. It is further possible that pocket gophers transported soil material to raise nesting areas out of the subirrigated wet zone and did not further disturb this lower zone soil. Arkley and Brown (1954) report data from Oregon showing mound elevation of twelve inches in twenty-two years (1929 to 1951). Both Cahalane (1947) and Larrison (1942) indicate that the gopher does build mounds in the case of water table restriction. Fossil pocket gophers from California have been reported by Grinnell (1923) and a Pleistocene specimen was found in Kansas (Hibbard 1951). Reported measurements of these ancient individuals are similar to present species.

Although internal features of the Wisdom mounds differ from the spots studied in other locations of the Montana area, a geographical continuity of patternization exists between the two. In addition, gradation between the two sorts of soil disturbance is found in an adjacent location north of Wisdom. Here, the mounds are found in the subirrigated draw bottoms and merge into the stairstep type on the hill sides. Both grass spots and sagebrush spots are present on the slopes but the mounds are chiefly of the grass-covered type with only a few supporting Artemisia tridentata. Because of these reasons the mounds are attributed to the same disturbance agent as the spots.

As already suggested in this report, gopher population during the formation of the spot disturbances making the pattern must have been near a saturation level in order to cause fairly even spacing of spots over any extensive area. This high population level does not now exist and the question of initial cause of dense pocket gopher populations is brought up. Reports on food habits of pocket gophers (Aldous 1951, Brauson and Payne 1958, Ellison and Aldous 1952, Garlough 1937, Koford 1958, Phillips 1936, Ward and Keith 1962) indicate a preference for forbs or plants fairly high in moisture. Many workers indicate that high rodent and ant densities are associated with overgrazed rangelands (Bond 1945, Moore and Reid 1951, Norris 1950, Phillips 1936, Sharp and Barr 1960); some suggest livestock-rodent relations are not clearly indicated (Ellison 1946, Taylor 1930, Technical Committee 1960); and others recognize rodents as a possible contributing factor to range depletion (Fitch and Bentley 1949).

In the study area, the most likely hypothesis for initial development of high gopher densities seems to indicate connection with grazing activities since semi-succulent forbs replace grasses when livestock use is heavily concentrated. All present gopher populations occur in areas supporting such weedy vegetation. The few stomachs I examined taken from gophers trapped during the dry summer season in the benchland area all contained material from Opuntia polyacantha pads. No grass material was found in the stomachs even though present and this suggests Opuntia plants as the mainstay during dry periods. In places where grazing pressure has been relaxed and a return to grasses has occurred, I found very few gophers. Ages of sagebrush spots measured by ring counts indicated some correlation with periods of settlement by white people. Youngest sagebrush ages were found where settlement was most recent. It is also conceivable that Indian horses might have caused overgrazing in instances where sagebrush ages indicate gopher activity and sagebrush establishment prior to white settlement. We know that Indians had horses in numbers in this area at least by 1800 (Sampson 1952, pp. 113-115) and that Lewis and Clark traded for horses at Horse Prairie Creek in 1805. Further study is needed to determine the validity of the grazing influence hypothesis described here.

Disappearance of pocket gophers in sagebrush locations probably is connected with the increase of woody vegetation. Thomas (1962) discusses tree establishment in grasslands in Africa due to the presence of termite mounds providing an invasional site. Tevis (1956) found such invasion by Abies magnifica on gopher worked sites. Thomas (1962) continues by saying the forest advance into grassland was by coalescence of islands of woody vegetation around the termite mounds and that the termite colonies die out once a forest cover is formed. Sagebrush expansion in the study area appears to be facilitated by rabbit (Lepus californicus, Sylvilagus idahoensis) grazing at the periphery of the spot colonies. A narrow edge of depleted grass or sometimes Gutierrezia longifolia is found at the edges of sagebrush spots. This same sort of reduction of grass competition by rabbits is seen along drainage channels and roadsides where A. tridentata is present. This rabbit grazing assists in expansion of A. tridentata colonies until coalescence takes place. The degree to which this development of sagebrush communities is facilitated by rabbits was not investigated.

It is hoped that this investigation will add to the information already reported by Larrison (1942), Laycock (1958), and Tevis (1956) on plant succession connected with pocket gopher activity. This information does show another means of sagebrush movement into previously unoccupied areas than those described by Morris and Pace (1963).

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APPENDICES

Appendix A. Locations of study areas and sampling sites.

Name	Location	Vegetative Classification (Table 2)
Hagenbarth East	15 mi. N. of Dillon E. of Hiway	I. Needlegrass-Ricegrass
Hagenbarth West	15 mi. N. of Dillon W. of Hiway	I. Needlegrass-Blue grama
Stone Creek	8 to 12 mi. N.E. of Dillon	I. Needlegrass-Ricegrass
East of Badger Pass	14 mi. S.W. of Dillon	I. Needlegrass-Wheatgrass
Badger Pass	18 mi. W. of Dillon	II. Wheatgrass-Sagebrush
Medicine Lodge	30 mi. S.W. of Dillon (upper slopes)	II. Wheatgrass-Sagebrush II. Wheatgrass-Needlegrass
Paskett Pasture	22 mi. S.E. of Dillon S. of Blacktail Creek	II. Wheatgrass-Needlegrass
Crazy Springs Creek	20 mi. S.E. of Dillon 2 mi. N. of Blacktail Cr.	I. Needlegrass-Wheatgrass
North Bench	19 mi. S.E. of Dillon 3 mi. N. of Blacktail Cr.	I. Needlegrass-Wheatgrass
Wagner Creek Rock	17 mi. S.E. of Dillon 5 mi. N. of Blacktail Cr.	I. Needlegrass-Wheatgrass
Briggs North	30-35 mi. S. of Dillon E. of Hiway (upper slopes)	I. Needlegrass-Wheatgrass II. Wheatgrass-Needlegrass
Briggs South	38-40 mi. S. of Dillon E. of Hiway	I. Needlegrass-Wheatgrass
Dell-Lima	46 mi. S. of Dillon S. of Sage Creek	I. Needlegrass-Wheatgrass
Wisdom	60 mi. N.W. of Dillon 2-4 mi. S. of Wisdom	III. Idaho Fescue-Sagebrush
Bighole	6 mi. W. of Wisdom near Bighole Battlefield	III. Idaho Fescue

Appendix B. Animals and plants encountered or known to be present in the benchland study area.

Scientific Name	Common Name
Mammals:	
Antilocapra americana (Ord)	American antelope
Bos taurus ______	Domestic cow
Canis latrans. Say.	Northern coyote
Citellus richardsonii (Sabine)	Richardson ground squirrel
Equus caballus	Domestic horse
Eutamias minimus (Bachman)	Least chipmunk
Lepus californicus. Gray	Black-tailed jackrabbit
Lepus townsendii. Backman	White-tailed jackrabbit
Ovis aries ______	Domestic sheep
Perognathus parvus (Peale)	Pocket mouse
Peromyscus maniculatus (Wagner)	White-footed (deer) mouse
Sylvilagus idahoensis (Merriam)	Idaho pigmy rabbit
Taxidea taxus (Schreber) (T. t. montana. Schantz)	American badger
Thomomys talpoides (Richardson) (T. t. fuscus (Merriam))	Northern pocket gopher
Birds:	
Buteo regalis	Ferruginous rough-leg hawk
Calcarius ornatus	Chestnut-colored longspur
Centrocercus urophasianus	Sage grouse
Eremophila alpestris	Horned lark
Falco mexicanus	Prairie falcon
Numenius americanus	Long-billed curlew
Pica pica	Black-billed magpie
Poaecetes gramineus	Vesper sparrow
Speotyto cunicularia	Burrowing owl
Insects:	
Camponotus sp.	Carpenter ant
Canthon sp.	Tumblebug (beetle)
Pogonomyrmex occidentalis	Prairie mound-building ant
Grasses:	
Agropyron smithii. Rydb.	Western wheatgrass
Agropyron spicatum (Pursh) Scribn. and Smith	Bluebunch wheatgrass
Agropyron trachycaulum (Link) Malte.	Slender wheatgrass
Aristida longiseta. Steud.	Red three-awn
Bouteloua gracilis (H. B. K.) Lag. ex Steud.	Blue grama

Appendix B. (continued)

Scientific Name	Common Name
Bromus tectorum. L.	Downy chess (cheatgrass)
Calamagrostis montanensis. Scribn.	Plains reedgrass
Danthonia intermedia. Vasey.	Timber oatgrass
Festuca idahoensis. Elmer.	Idaho fescue
Hordeum jubatum. L.	Foxtail barley
Muhlenbergia richardsonis (Trin.) Rydb.	Mat muhly
Phleum pratense. L.	Timothy
Poa pratensis. L.	Kentucky bluegrass
Poa secunda. Presl.	Sandberg bluegrass
Sitanion hystrix (Nutt.) J. G. Smith	Squirreltail
Sporobolus cryptandrus (Torr.) A. Gray	Sand dropseed
Stipa comata. Trin. and Rupr.	Needle-and-thread
Stipa richardsoni. Link.	Richardson needlegrass.
Stipa viridula. Trin.	Green needlegrass
Grasslike plants:	
Carex eleocharis. Bailey	Needleleaf sedge
Carex filifolia. Nutt.	Threadleaf sedge (blackroot)
Carex spp. (Rupp.) L.	Sedges (wet sites)
Shrubs:	
Artemisia cana. Nutt.	Silver sagebrush
Artemisia frigida. Willd.	Fringed sagewort
Artemisia nova. A. Nels.	Black sagebrush
Artemisia tridentata. Nutt.	(Big) Sagebrush
Atriplex nuttallii. S. Wats.	Nuttail saltbrush
Chrysothamnus nauseosus (Pall.) Britt.	Rubber rabbitbrush
Chrysothamnus viscidiflorus (Hook.) Nutt.	Douglas rabbitbrush
Chrysothamnus viscidiflorus var. lanceolatus (Nutt.) Greene.	Lanceleaf rabbitbrush.
Eriogonum microthecum. Nutt.	Slenderbush eriogonum
Eurotia lanata (Pursh) Moq.	Winterfat (white sage)
Gutierrezia longifolia. Greene. (or G. sarothrae (Pursh) Britt. and Rusby)	Matchweed (snakeweed)
Hymenoxys (Actinea) sp. Cass	Pingue (rubberweed)
Potentilla fruticosa. L.	Shrubby cinquefoil
Sarcobatus vermiculatus (Hook.) Torr.	Greasewood
Tetradymia canescens. D. C.	Gray (spineless) horsebrush

Appendix B. (continued)

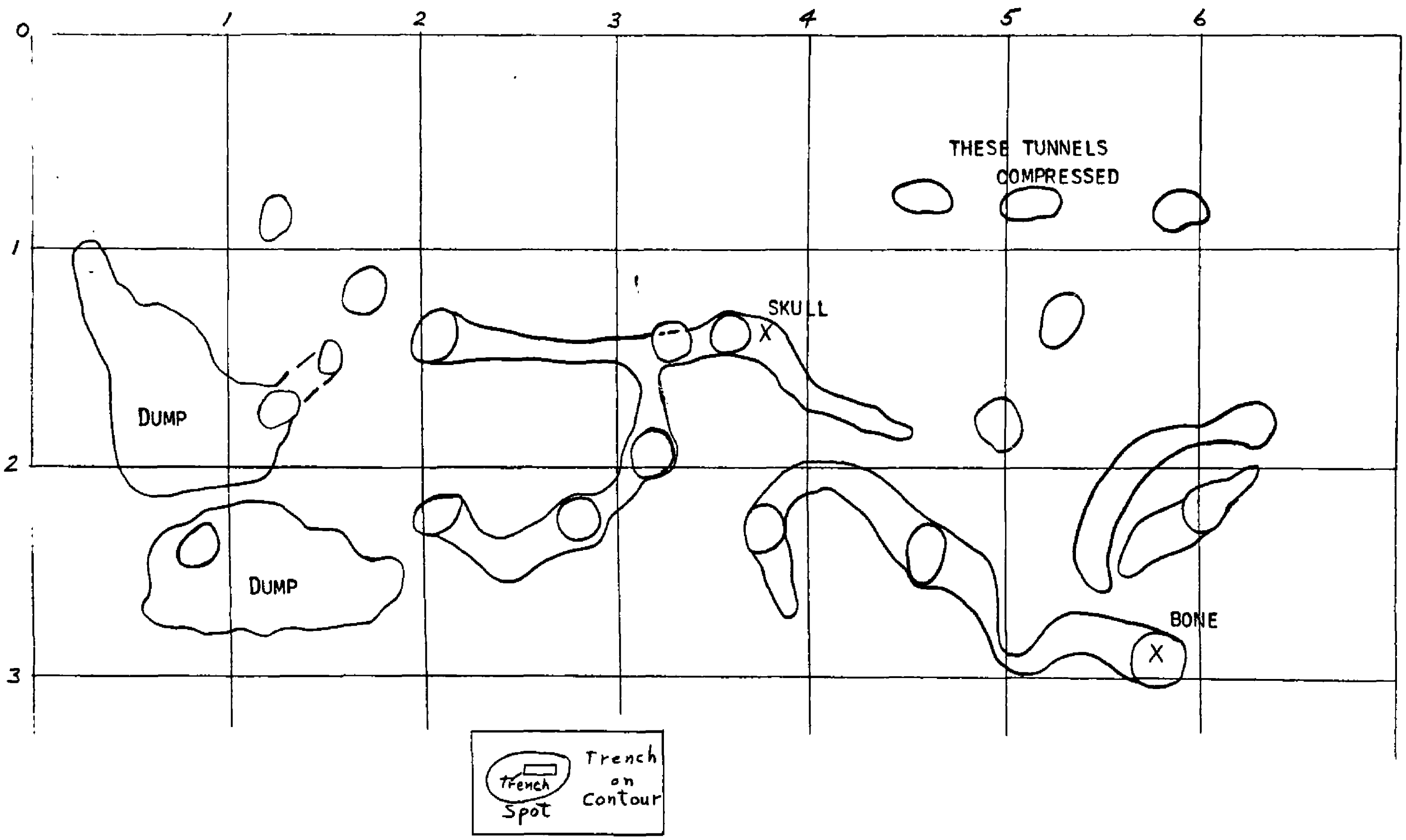
Scientific Name	Common Name
Suffrutescent plants:	
Applopappus sp. Cassini	Goldenweed
Aster commutatus crassulus (Rydb.) Blake (var.)	Aster
Aster scopulorum. Gray.	Aster
Erigeron divergens. T. and G.	Fleabane (daisy)
Grindelia squarrosa (Pursh) Dunal.	(Curlycup) Gumweed
Opuntia polyacantha. Haw.	(Plains) pricklypear
Phlox hoodii. Rich. (probably ssp. glabrata) (E. Nels.) Wherry)	Hood's phlox
Sphaeralcea coccinea (Pursh) Rydb.	Scarlet globemallow
Forbs:	
Abronia fragrans. Nutt. ex Hook.	Sand verbena
Achillea millefolium. L. ssp. lanulosa (Nutt.) Piper.	Yarrow
Antennaria sp. Gaertn.	Pussytoes
Arenaria congesta. Nutt.	(Ballhead) sandwort
Arenaria sp. L.	Sandwort
Aster spp. L.	Asters
Astragalus aridus. Gray.	(Rattlepod) milkvetch
Astragalus sp. L.	Milkvetch
Atriplex argentea. Nutt.	Silverscale saltbush
Chenopodium album. L.	Lambsquarter
Chenopodium leptophyllum Nutt. apud. Moq. D. C.	Narrow-leaved goosefoot
Cryptantha sp. Lehm. (probably C. Bradburiana. Payson. formerly Krynitskia glomerata (Pursh) Gray.)	Miner's candle
Eriogonum flavum. Nutt.	Yellow eriogonum
Geum triflorum. Pursh.	Old man's whiskers
Lappula sp. Moench.	Stickseed
Lesquerella sp. Watson	Bladderpod
Lupinus sp. L.	Lupine
Mamillaria spp. Haw.	Pincushion (ball) cactus
Orthocarpus sp. Nutt.	Owl's clover
Oxytropis spp. D. C.	Crazyweed (loco)
Phlox longifolia. Nutt.	Longleaf phlox
Polanisia sp. Raf.	Clammy weed
Potentilla spp. L.	Cinquefoil
Salsola kali, L. var. tenuifolia G.F.W. Mey. (var. tenuiflora. Tausch.)	Russian thistle

Appendix B. (continued)

Scientific Name	Common Name
Sedum stenopetalum. Pursh.	Wormleaf sedum (stonecrop)
Selaginella sp. Beauv. (probably S. rupestris (l.) Spr.)	Clubmoss
Sisymbrium spp. L.	Tumblemustards
Solidago graminifolia (L) Salisb.	Goldenrod
Taraxacum officinale. Wiggars	Common dandelion

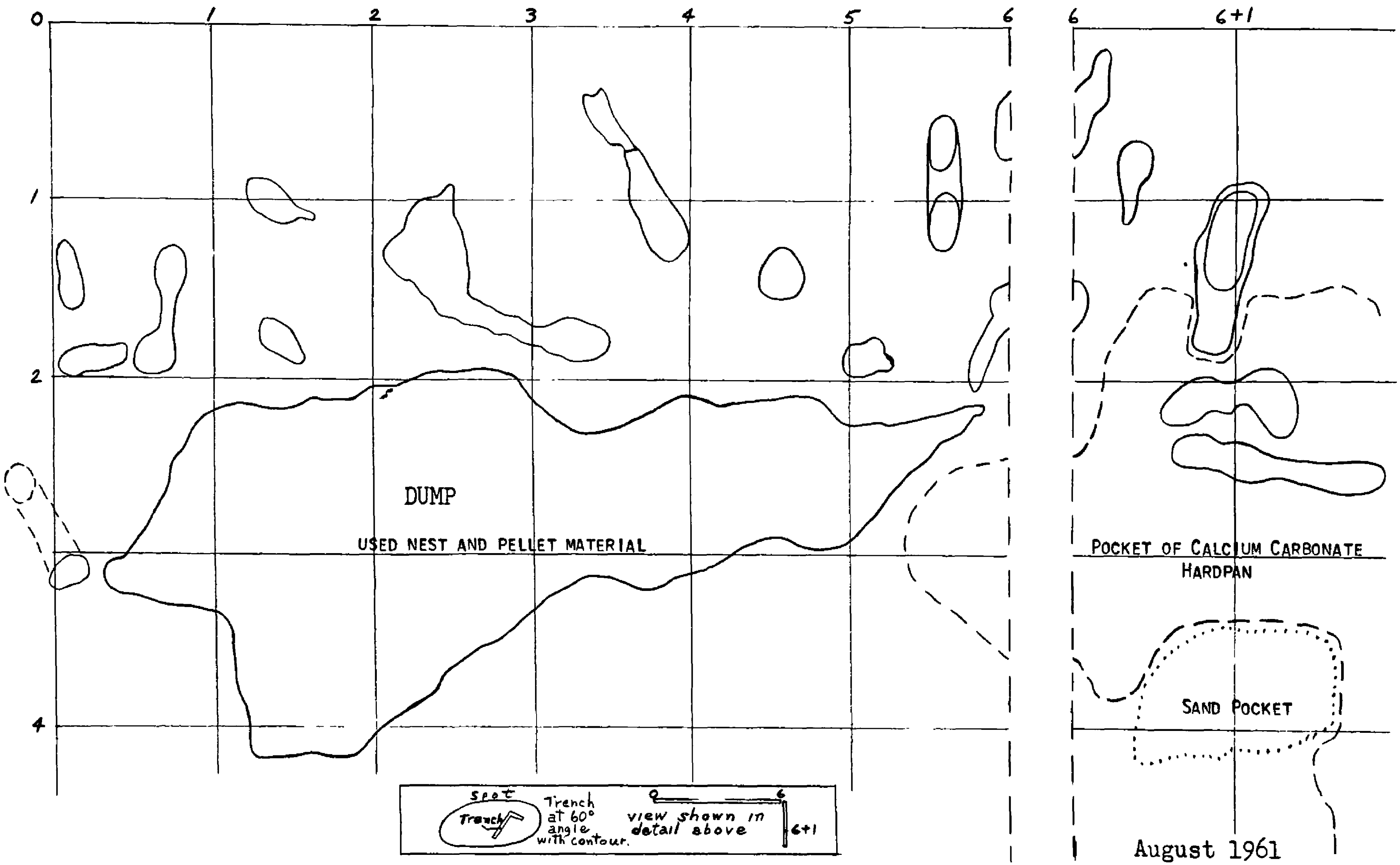
Appendix C. Other animals and plants mentioned.

Scientific Name	Common Name
Animals:	
Ctenomys spp. _______	Tuco-Tucos
Cynomys spp. Rafinesque	Prairie dogs
Geomys spp. Rafinesque	Eastern pocket gophers
Thomomys talpoides quadratus. Merriam.	Dalles pocket gophers
Thomomys spp. Wied-Neuweid.	Western pocket gophers
Veromessor pergandei (Mayr)	Harvester ant
(Not identified)	Termite (plant eating)
(Not identified)	Termite (fungus eating)
Plants:	
(Abies magnifica. A. Murr.)	Red fir
Agoseris sp. Raf.	Mountain dandelion
Artemisia discolor. Dougl. (now A. michauxiana. Bess. in Hook).	Sweet sage
Balsamorhiza sagittata (Pursh) Nutt.	Balsamroot
Bromus inermis. Leyss.	Smooth brome
Chrysothamnus parryi (A. Gray) Greene	Parry yellowbrush (rabbitbrush)
Cynodon dactylon (l.) Pers.	Bermuda grass
Festuca orthophylla. Pilger.	(Peruvian highlands)
Lupinus argenteus. Pursh.	Lupine
Lupinus spp. L.	Lupines
Medicago sp. L.	Alfalfa (medic)
Monarda fistulosa. L.	Horsemint
Picea sp. Dietr.	Spruce
Pinus ponderosa. Laws.	Ponderosa pine
Pinus sp. Duham.	Pine
Poa sp. L.	Bluegrass
Populus sp. L.	Aspen
Pseudotsuga menziesii. _______ (or P. taxifolia (Poir.) Britt.)	Douglas fir
Ribes spp. L.	Ribes (currants)
Stipa columbiana. Macoun.	Columbia needlegrass
Stipa lettermani. Vasey.	Letterman needlegrass
Trifolium sp. L.	Clover
Vicia spp. L.	Vetches
Viola sp. L.	Violet



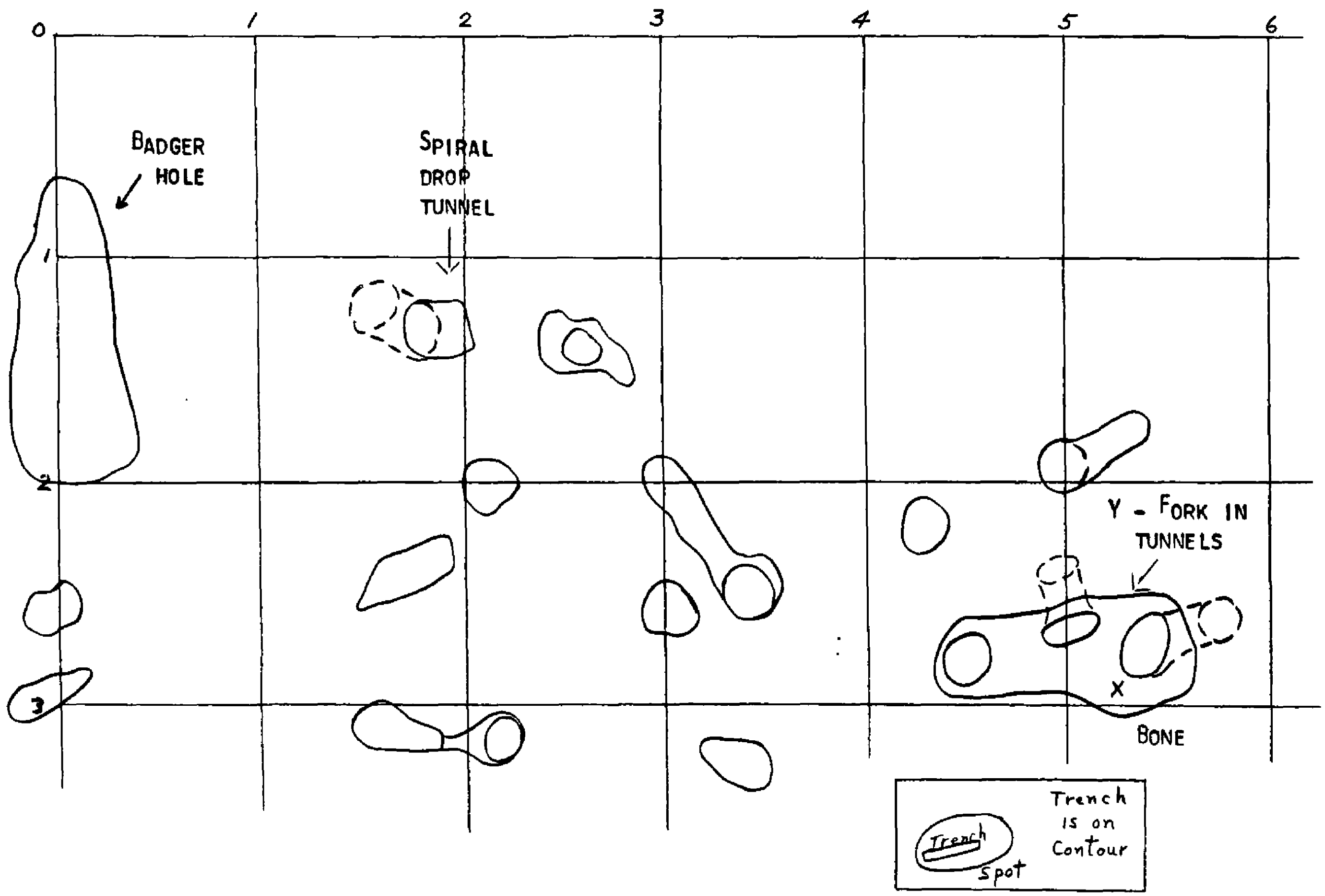
Appendix D. Wagner Creek excavation Number 1.

Side view of a vertical section showing tunnels and rock dump chambers. July 1961.



Appendix E. Wagner Creek excavation Number 2.

Side view of a vertical section. Large dump chamber, tunnels, and tunnels present in a hardpan pocket are shown. The entire development is within a body of crotovinal material except the hardpan and the sand pockets. August 1961.



Appendix F. Paskett Pasturs excavation Number 2.

Side view of a vertical section. The badger hole was filled with dirt and debris presumably blown into it. No pellets were present in this (predation?) tunnel. All other tunnels were filled with gopher debris including pellets. Location of body bones found is indicated in the diagram. July 1961.