
PRIMARY SUCCESSION OF VOLCANIC DEPOSITS
IN SOUTHERN IDAHO

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[Reprinted from ECOLOGICAL MONOGRAPHS 3:277-298. July, 1941]

CRATERS OF THE MOON NATIONAL MONUMENT





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PRIMARY SUCCESSION ON VOLCANIC DEPOSITS IN SOUTHERN IDAHO

INTRODUCTION

Some of the most recent volcanic deposits to be found within the United States are in that portion of Idaho known as the Snake River plains, or, as sometimes improperly called, the Snake River desert. Because the term "plains" is in common usage it is retained in this discussion, but the character of the region is such that "plateau" would be more descriptive. The plain has been built up by volcanic outpourings and has an elevation of from 3,000 to 6,000 feet, being highest in the north-central and eastern parts. The region is nearly surrounded by mountains. These are almost unbroken at the north and east; to the south there are north-south trending ranges. Mountains are fewer in the west where the plains merge with the Columbia Plateau. The length of the region is about 350 miles; the width varies between approximately 50 and 75 miles. An otherwise regular topography is broken by numerous volcanic cones; the largest, Big Butte, southeast of Arco (Fig. 1), rises 2,350 feet above the surrounding area (Russell, 1902). Near by are the smaller Twin Buttes (Fig. 1); elsewhere there are smaller cones. The Snake River flows westward across the entire length

of the plains. Its northern tributaries are few, even though there are vast mountain areas in which streams rise. Most of these streams disappear from sight and become "lost rivers" shortly after they reach the lava plains, owing to the porosity of the flows and the thinness of the soil mantle overlying them.

White men have known of the Snake River plains since 1810, when Wilson Price Hunt and his party crossed them on their way to the Columbia River (Irving, 1839). Within a few years the plains became a part of a regular highway for trappers and traders. Soon the region was traversed also by settlers who were following the Oregon Trail. For all people the trip across the plains was a difficult one; the Snake River was too turbulent to permit the use of boats and a shortage of water and game made the journey by land trying.

Settlement of the plains was begun in 1834 when Old Fort Hall was built near the Snake River in the eastern part. By 1854, when the Mormons are reported to have brought cattle to the Salmon River (Brosnan, 1935), grazing was probably established on a permanent basis in the region. It has continued to be the chief occupation of inhabitants over much of

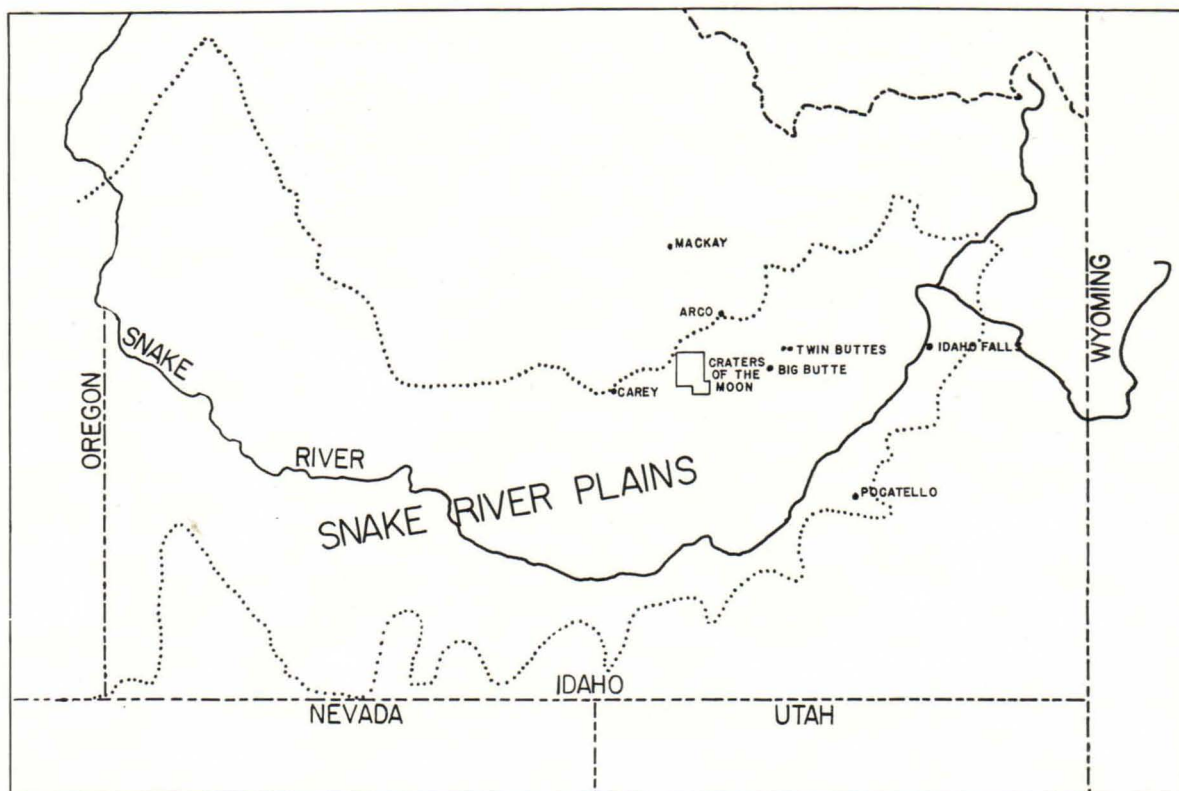


Fig. 1. Snake River plains and adjoining region.

the region, except in relatively small areas, chiefly near the Snake River, where water is available for irrigation, and in areas too rough and unproductive for grazing use, such as the one specifically discussed in this paper.

Sage (*Artemisia tridentata*),¹ is the dominant plant species over most of the plains. In addition other shrubs, as well as grasses and other herbs, occur. In limited areas trees make up a part of the vegetation. Junipers (*Juniperus scopulorum* and *J. utahensis*) occur in some places, and, more rarely, Douglas fir (*Pseudotsuga taxifolia*). Most important of the trees is limber pine (*Pinus flexilis*). The trees are found mainly in an area about 15 miles north and south by 50 miles east and west, lying between Big Butte and Twin Buttes on the east and the town of Carey on the west (Fig. 1).

The earliest available records giving information on vegetation of the plains are those of Captain Bonneville (Irving, 1843), who was in the region during the years 1832 to 1835. It is quite evident that sage was an important member of the vegetation at that time; grass was abundant near streams but not elsewhere. The next vegetation record is that of Israel C. Russell (1902) who did geologic work on the plains in 1901. He reported sage as the characteristic plant, with bunch-grasses between the sage bushes. His description applies in general today. Sage is and evidently has been a dominant member of the vegetation since the advent of the first white men into the region.

It is possible that vegetation disturbance has not been much greater since the coming of the white man than it was before. Grazing has undoubtedly increased, although the Indians had horses, and at times each year there were buffaloes in abundance (Irving, 1843). Fires have probably decreased. Bonneville reported that at certain seasons the sky was darkened for days at a time by smoke from fires set by the Indians (Irving, 1843).

The vegetation which occupies most of the Snake River plains has become established under the conditions of disturbance just mentioned. What effect the disturbance has had upon the character of the vegetation is not known. It may be that if fires and grazing were entirely eliminated for a number of years changes would occur in the floristic composition, or at least in the relative abundance of species now present. Weaver and Clements (1929) suggest that if the Snake River plains were kept free from fire and grazing they would come in time to support a grassland climax, similar to that of the Palouse Prairie in Washington. So far as is known to the writer, Palouse Prairie vegetation has not been adequately demonstrated to be the climax type in the Snake River region. The writer has seen only one

instance where an area not within the protecting influence of a cone, or near a stream, has a nearly pure grass stand. Two small kipoukas,² each less than 1/8 mile in diameter, located in the north-central part of the region, support vegetation of the type shown in Figure 2. These kipoukas are surrounded on all sides



FIG. 2. A kipouka surrounded by young lava flows. The predominant vegetation is bunch-grass; shrubs, though not absent, are small. Crater wall fragment in the distance. August 1, 1938.

by over a mile of fresh lava and have probably never been grazed, but one of them gave indication of having been partly burned recently. Although the evidence given here seems to confirm the opinion offered by Weaver and Clements (1929), it is not believed that one such instance is sufficient to warrant application to an entire region. Therefore, it is tentatively assumed that the grass-sage type of vegetation, which now occupies, and has occupied as far back as is known, most of the Snake River plains, is the regional climax.

One of the most interesting sections of the plains, from a botanical viewpoint, lies in the north-central part. In that area recent volcanic activity has occurred, some possibly less than a thousand years ago. It is there that trees occur in greatest numbers and that most variation exists in the vegetation of closely adjacent areas. Many parts have not been subjected to grazing because they are surrounded by fresh lava fields; the kipoukas mentioned above are an example. The major part of the region where the most recent volcanic activity took place lies within the Craters of the Moon National Monument, an area of about 75 square miles (Fig. 1). The Monument lies at the extreme northern edge of the plains, and is at the very foot of the mountains. The elevation over most of the Monument is between 5,300 and 6,000 feet; one tall volcanic cone rises to 6,515 feet above sea level.

The greater part of this study, which deals with primary succession on the volcanic material, was carried on within or not over two miles outside of the National Monument. Several reconnaissance trips were made into the surrounding country, within a radius of about 30 miles. The field work was done during the summers of 1936 to 1938, inclusive.

I wish to thank Professor W. S. Cooper and Dr. D. B. Lawrence of the University of Minnesota for

² A kipouka, sometimes spelled kipuka (Verhoog, 1937) is an island of old rock surrounded by young.

¹ Nomenclature of grasses follows Hitchcock (1935); that of trees, Sargent (1921); and that of shrubs, and herbs other than grasses, is according to Coulter and Nelson (1909), or Rydberg (1917), except in a few instances where neither manual describes a species, or when more recent work suggests a preferable name. Specimens of all species have been placed in the herbarium of the Botany Department of the University of Minnesota.

their assistance in the furtherance of this work. Especially valuable suggestions were obtained from the latter when he spent several days in the field in the summer of 1938 while the investigation was in progress; he has also offered helpful criticisms during the preparation of the manuscript. My wife, Dorothy S. Eggler, was my co-worker in the field. To former custodian A. T. Bicknell and present custodian G. E. McCarty of the Monument I extend my sincere appreciation for their interest and kindness.

CLIMATIC RELATIONS

The climate of the Snake River plains may in general be described as mid-continental in character, having scanty precipitation, rather cold winters and hot summers.

No long-time climatic data are available for the Monument itself, but it is believed that the use of records from the nearest stations of the Snake River plains is permissible, and that these give a fairly accurate picture of the weather conditions in the Monument. Records from the United States Weather Bureau stations at Aberdeen, Arco, Idaho Falls, Mackay, and Pocatello (Fig. 1) are introduced in the following report. Mackay is the only one of those stations not on the Snake River plains proper; it is in a tributary valley and the climate is quite similar to that of the Monument. Conditions at Arco, 18 miles east of the Monument, at about the same elevation, probably most nearly approximate those of the Monument. Wherever pertinent, my own observations made within the study area are added to supplement the long-time records.

PRECIPITATION

Over the region as a whole less than 40 percent of the annual precipitation of under 14 inches falls during the frostless season; at Arco less than 27 percent during that period. There are two periods of relatively high precipitation during the year, December and January, the time of greatest snowfall, and May and June, the time of maximum rainfall (Fig. 3).

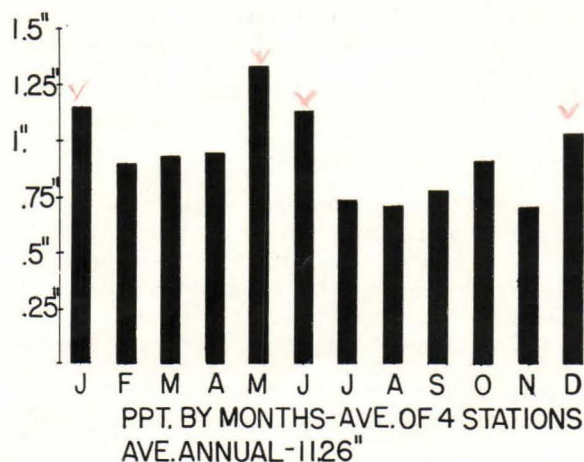


FIG. 3. Precipitation distribution; averages of records from Arco, Idaho Falls, Mackay, and Pocatello.

Some years there may be no precipitation during one or more months from July to September (U. S. Weather Bur. Bull. W, 1926). At Arco slightly less than half the precipitation falls as snow—4.28 inches of the total of 9.63 per year.

TEMPERATURE

Normal temperature records (Table 1) show winters to be moderately cold and summers moderately hot. The extremes which have been registered at Arco are -41° F. in February and 101° F. in July. The mean maximum for July, the hottest month, is 82.5° F.; the mean minimum for January, the coldest month, 1.8° F. Killing frosts may occur any month of the year; they have been recorded on July 18 and on August 18 (U. S. Weather Bur. Bull. W, 1926). Records for Pocatello were obtained directly from the station office; those for other stations from the Weather Bureau office at Boise, Idaho.

TABLE 1. Climatic data.

	January	February	March	April	May	June	July	August	September	October	November	December	Annual
Arco.....	14	20	30	43	51	57	66	64	55	44	31	18	41.2
Idaho Falls....	20	25	35	45	53	61	69	65	57	47	34	22	44.4
Mackay.....	17	21	31	42	51	59	67	65	55	45	32	20	42.1
Pocatello.....	24	29	37	46	54	62	71	70	60	48	37	27	47.1

	Period of Record Precip. Temp.	Elevation	Distance and Direction from the Monument
Arco . . .	31 yrs. 25 yrs.	5,318 feet	18 miles—East
Idaho Falls .	41 yrs. 28 yrs.	4,742 feet	83 miles—East
Mackay . .	25 yrs. 24 yrs.	5,897 feet	55 miles—Northeast
Pocatello .	39 yrs. 39 yrs.	4,477 feet	90 miles—Southeast

As is characteristic of semi-arid plateaus the nights are cool and the days warm in summer. Summer skies are clear, and there is no extensive cloud blanket to retard the rates of insolation and reradiation of heat. With such conditions rapid temperature changes are characteristic.

Air temperature measurements were made in the study area by means of a shaded thermograph during the period of June 17 to August 1, 1938. The maximum daily temperature was generally reached between two and four in the afternoon, the minimum between four and six in the morning. The highest temperature recorded during the period was 97.5° F., on July 22; the minimum, 25° F., on June 19. These two days exhibited the characteristically great daily temperature ranges of summer. At six o'clock in the morning on the day the maximum of 97.5° was attained the temperature was 48 degrees; the range for the day was 49.5° F. On the afternoon of the day when the 25° minimum was reached the temperature rose to 76.5° F., a range of 51.5° for the day. The average daily range during the June period was 38.2° F., during July 39.1° F.

Plants growing under these conditions must withstand what would seem to be a rather serious shock to their protoplasm twice a day, and this feature of the climate may play some part in determining the distribution of plants in this region.

WIND

Southwest winds prevail over the Snake River plains much of the time; at Arco it is the prevailing direction all months of the year.

At Pocatello, the nearest Weather Bureau station at which wind velocity measurements are made, the average hourly movement is 8.8 miles. The velocity is quite uniform during all months of the year (U. S. Weather Bur. Bull. W, 1926).

In the Monument, on a typical summer day, the wind usually rises during the morning and by noon or shortly after it often reaches a velocity of 15 to 20 miles an hour in unprotected places. Rarely it attains a velocity of 32 to 38 miles per hour, as estimated by the Beaufort Scale of wind force. The wind almost always dies down in late afternoon, and is quiet by sundown; nights are usually calm.

PRECIPITATION-EVAPORATION RATIO

The concept of a precipitation-evaporation ratio to express plant water relations has been used widely and has undergone several modifications since first employed by Transeau (1905). Transeau obtained the P/E ratio by dividing normal annual precipitation by the total evaporation record of a single year; on this basis he worked out climatic zones for the eastern United States. Annual evaporation data for Snake River plains stations are not available, so it is not now possible to compare the region with Transeau's climatic zones. P/E ratios are useful here as a means of comparing the moisture conditions among the months for which data are available. Such ratios are more useful than precipitation alone in that they give a measure of the water balance with which a plant has to work.

Records for calculating the P/E ratio were obtained for the months of April through September, 1914 to 1919, inclusive, from Aberdeen, Idaho, which is the only station in the region at which both evaporation and precipitation records have been made (Horton, 1921; U. S. Weather Bur. Bull. W, 1926). Aberdeen is about 50 miles southeast of the Monument, at an elevation of 4,400 feet. Amount of precipitation and seasonal distribution there are quite similar to those at Arco. P/E ratios are given in Table 2.

TABLE 2. P/E ratios computed for Aberdeen, Idaho.

	April	May	June	July	Aug.	Sept.
1914.....	0.150	0.074	0.380	0.058	0.000	0.243
1915.....	0.113	0.444	0.066	0.060	0.016	0.268
1916.....	0.073	0.212	0.009	0.049	0.048	0.000
1917.....	0.432	0.632	0.022	0.032	0.002	0.048
1918.....	0.118	0.073	0.108	0.174	0.055	0.208
1919.....	0.135	0.034	0.000	0.044	0.018	0.363
Average.....	0.170	0.245	0.198	0.070	0.023	0.190

May has definitely the most favorable moisture conditions for plant growth, and August the least. Despite the good moisture conditions in May it is probable that it is then too cold for best growth because freezing weather is common. June normally has

no freezing weather after the first week, but already moisture conditions are becoming less satisfactory. It is probably the best month for growth because the moisture-temperature combination is nearest an optimum.

CHEMICAL AND PHYSICAL CHARACTER OF
LAVA AND CINDERS

The plains character of the Snake River country is due largely to the manner of accumulation of volcanic material and little to subsequent erosion. Vents have supplied material in many places over a long period of time, from Miocene to Recent (Russell, 1902) and the surface in the large is nearly level. The youngest lava within the boundaries of the Monument is believed to be "more than 250 years but perhaps not more than 1,000" in age (Stearns, 1930) and it still retains an unweathered appearance. All volcanic material exposed at the surface within the Monument is basaltic in nature, as is the more recent over all the plains, and as a result there should be marked chemical uniformity in the various deposits regardless of their physical characteristics. The volcanic ejecta occur chiefly as two types, flows and cinders. Flows are essentially solidified lava streams. Individual flows range in area from a few acres to a few square miles. Within the Monument there are about 30 flow exposures, varying in age, degree of weathering, and amount and kind of vegetation.

The flows are of two types: (a) a broken, jagged, fragmental kind, known as "aa" (Fig. 4), and (b) a smoother, ropy or billowy type called "pahoehoe," which is generally somewhat cracked and fractured (Fig. 5).

The area occupied by cinders is small in comparison to that covered by the flows. Cinders are massed in



FIG. 4. An aa lava flow. August 22, 1938.



FIG. 5. North Crater Flow, a pahoehoe flow. August 27, 1938.

cinder cones, which are, according to Stearns (1930), "heaps of lava froth or spray formed by the fire fountains which played at the time of the eruptions." There are about 35 distinct accumulations in the Monument, ranging in height above the surrounding lava from approximately 50 to 800 feet, with basal diameters up to a mile. A majority of these cones are aligned in a zone with a northwest-southeast trend (Fig. 6), which has been given the name "The Great

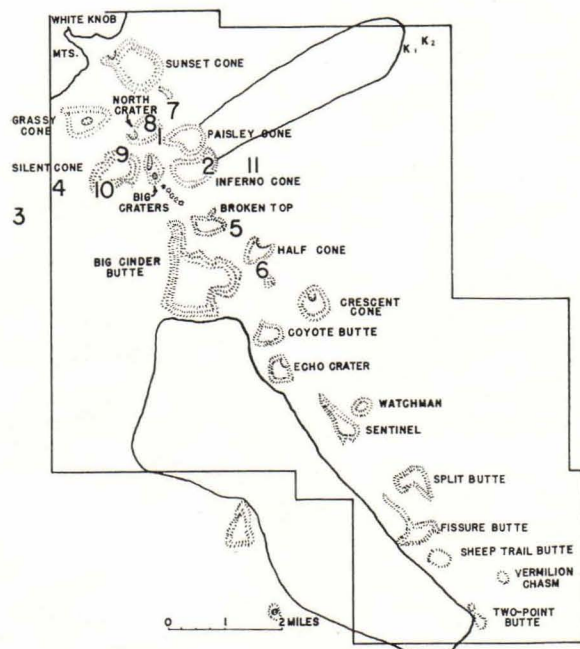


FIG. 6. Craters of the Moon National Monument. Cinder cones are aligned in a zone, the "Great Rift." Between the cones, and at the sides, are flows. Enclosing lines mark the locations of regions of good tree growth. Numbers mark the sites of detailed studies.

Rift." This zone has been the scene of great volcanic activity and was the source of most of the lava flows of the Monument, as well as the cones. Like the flows, the cinder cones vary in age and hence in degree of weathering and in vegetation.

PAHOEHOE LAVA FLOWS AND THEIR VEGETATION

GROWTH CONDITIONS ON FLOWS

GENERAL FEATURES

The 30 or more lava flows which are entirely or partly within the Monument represent together an age span of several thousands of years, and upon them can be found vegetation representing all the stages of primary succession from pioneer to the regional climax. Some flows are extremely fresh in appearance in that *superficially* neither soil nor vegetation is visible. Closer examination shows, however, that even the youngest flows have some soil present in depressions and that in these a few vascular plants are becoming established; only scattered lichens grow on the general flow surface. Other

flows show their great age by being almost completely mantled with soil and vegetation, and only here and there does the bare lava protrude. Between the two extremes in age are flows which are partly soil-covered but which have a considerable amount of bare lava exposed. These are intermediate also in the character of their vegetation.

FOUR VEGETATION HABITATS OF YOUNG FLOWS AND HOW THEY CHANGE AS FLOW AGE INCREASES

A young pahoehoe flow is of such character that it presents four types of habitat. Each is sufficiently distinctive in growing conditions it provides that it is invaded by a definite set of plants. Succession beginning in each habitat type will be considered as a subsuccession of the whole.

The habitat which occupies the greater part of a young pahoehoe flow is the nearly level lava surface. Here growing conditions are unfavorable; water runs off almost immediately; the surface is openly exposed to wind and sun. Soil accumulates very slowly, and it is only after all crevices and depressions are filled that wind-blown soil collects on the flow surface. It therefore continues as a xeric habitat without much improvement in growing conditions until late in the process of succession.

The other three habitats are forms of crevices or depressions in the flow, and their subdivision is based on depth and width of the crevice. They are here given the descriptive names "joint," "shallow crevice," and "deep crevice." Joints are too narrow to hold much soil, so moisture conditions, at least near the surface, cannot be very good. When the flow surface about them becomes soil-covered they too are covered and pass out of existence as a distinct habitat. Until that time in the life of the flow it seems unlikely that growth conditions in joints would change much.

A shallow crevice is any depression of sufficient depth to permit soil to accumulate to a thickness of an inch or more but not deep enough to enable a mature shrub to grow with most of its aerial portion below the general flow surface. A depression of the latter character is here considered a deep crevice. A depth of about 2 feet is usually the dividing point between deep and shallow crevices but it varies somewhat with the steepness of the walls. Deep crevices generally have steep sides, consequently soil does not blow out easily, but accumulates. They are usually fissures in the flow. Shallow crevices may be fissures but are more often depressions between folds or "ropes" of pahoehoe flow where a little soil can lodge (Fig. 7).

Conditions in shallow crevices are probably intermediate, in relation to moisture, between those in deep crevices and the flow surface. There is concentration of precipitation in them, but being open to exposure, water loss by evaporation is rapid. Shallow crevices usually do not have soil to a depth of over 2 or 3 inches, and so the soil-water reservoir is small. The fate of shallow crevices is to be leveled with soil, but usually not until the deep ones are first nearly filled. Moisture conditions in deep crevices are the most

favorable to be found in any of the four habitats of young flows. Deep crevices provide the best lodging place for both organic and inorganic soil, so they tend to fill rapidly. Addition of soil would improve moisture conditions by increasing the water reservoir. However, the value of the increased soil layer is offset as soon as the accumulation is sufficient to raise the aerial parts of plants above the general flow surface; then water loss from plants becomes too great for their survival. The nearer the crevice soil approaches the flow surface the more it is desiccated. In this way the deep-crevice habitat gradually ceases to exist as flow age increases.



FIG. 7. Very ropy lava of Indian Tunnel Flow. Soil has accumulated in depressions and pioneer plants have started. August 1, 1938.

FLOW SOILS

It has been found that the amount of soil on a flow is the most important single factor in determining the vegetation a flow can support. Therefore a consideration of flow soils is necessary before the development of the vegetation can logically be discussed.

These soils are fine in texture, and, according to Russell (1902), are mostly wind-transported, the sources being alluvial deposits near the mountain bases, ancient lacustrine beds in the western part of the plains, and dust and lapilli from cinder cones. He called the soil loess. Mechanical analyses of three samples taken at widely separated places on the Snake River plains, each at a foot depth, were made by him. The materials of all samples were found to be predominantly quartz and of uniformly fine texture, 75 to 80 percent of soil passing through a screen with 200 meshes per inch.

In the present work three samples of surface soils were taken from locations where the accumulation is thin. One site was an old flow about 5 miles east of Carey, and 22 miles west of the Monument, where the soil layer was approximately 6 inches thick; another was Silent Cone Flow, at Station 3 (Fig. 6), where the layer varies from 0 to 2 feet in depth; the third was from crevices in the young flow between Half Cone and Crescent Butte (Station 6, Fig. 6), and thus represents the first soil found on a flow.

Mechanical analyses of these soils (Table 3) showed them to be, in general, as fine in texture as were Russell's. Nearly three-fourths of the material in each sample was small enough to have been wind-

TABLE 3. Textures of three soils, as determined by mechanical analyses; values expressed in percentages.

	Surface of old flow east of Carey	Crevice in flow between Half Cone and Crescent Butte	Surface Silent Cone Flow
2 - J mm.....	6.42	2.11	5.08
1 - .5 mm.....	1.78	3.23	2.04
.5 - .25 mm.....	1.87	5.01	3.24
.25 - .1 mm.....	6.38	18.90	12.38
.1 - .05 mm.....	14.59	22.76	16.88
Less than .05.....	68.95	47.98	60.38

blown. The crevice material was slightly less fine than the other two, suggesting a colluvial origin, at least in part. Pieces of angular basalt, products of mechanical weathering of the flows, made up about 25 percent of the crevice soil; other soils contained less. The pieces ranged in diameter up to an inch or two. Nearly all those observed gave indication of having undergone some chemical weathering.

Microscopic examination of a sample failed to reveal the presence of diatoms, which should be found in a lacustrine deposit. The soil particles were angular in shape and looked like volcanic ash. Examination of many samples, taken at various places on the Snake River plains, would be necessary before it could be said that lake material is unimportant as a soil source in this region, but this one sample is suggestive.

FATE OF PRECIPITATION

The distribution of precipitation which falls upon a young lava flow has a marked influence on the distribution of its vegetation. There is no surface runoff, and, except for what evaporates, all water sinks downward into cracks and crevices. Thus there is an unequal distribution of water, which favors plants growing in crevices at the expense of those not so favorably located.

It is not known if a similar concentration of water would be found on old, soil-covered flows, but, since the lava surface under the soil retains much of its original pahoehoe character, it is likely that water in passing downward must tend to move toward the depressions, when once it has reached the impervious layer. As the thickness of the soil mantle increases, less and less of the precipitation would be expected to reach the rock surface, so that the distribution of moisture must become more and more uniform as a flow increases in age.

A phenomenon which suggests a source of water for certain flow plants is the presence of water, at 33 to 35° F., in numerous depressions and catch-basins on younger flows, during a part or all of the summer. Stearns (1930) discusses the source of this water as follows: "In these depressions a considerable amount of snow collects in winter. Some of it sifts down into crevices between the rocks and remains sheltered from the hot atmosphere during the long summer days. In addition, water during thawing periods in autumn or spring may drip downward into the crevices, where it is frozen by cold circulating air.

During the long cold winters ice forms. Some of it melts in summer, but in favored locations it never melts entirely away. Just as the solid lava is a poor conductor for the upward movement of heat from the molten lava beneath, so it is a poor conductor for the downward passage of heat from the sun. Usually a small amount of ice melts during the summer and forms a pool of water. On digging down into the loose rock in a water hole of this type, ice will always be found beneath the water." It is possible that water from melting ice in cracks may be available to certain deep-crevice plants growing on young flows, or those with roots in joints, but this point has not been verified.

TEMPERATURE AND EVAPORATION ON FLOWS

Not only is precipitation concentrated in cracks but temperature and wind conditions are such that evaporation from crevice floors is much less rapid than from the general flow surface.

To obtain a measure of atmospheric conditions in crevices, as contrasted with those in exposed places, temperature and evaporation measurements were made. An air-soil thermograph was placed on North Crater Flow, with the brass-colored bimetal air element $3\frac{1}{2}$ inches above the general flow surface and not shaded in any way, and the soil element laid on the floor of a deep crevice. The crevice was 31 inches deep, 10 inches wide at the top and three inches wide at the bottom. Weekly records were kept for the period from August 1 to September 5, 1938. The temperature range was found to be greater and changes more rapid just above the flow surface. The temperature there was about 30 degrees higher at the daily maximum and 10 degrees lower at the minimum. Figure 8 gives a typical week's record.

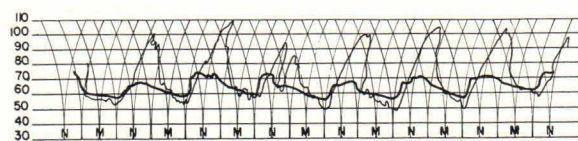


FIG. 8. Thermograph record for a typical week during the period Aug. 1 to Sept. 5, 1938. Narrow line—temperature $3\frac{1}{2}$ inches above the surface of North Crater Flow; wide line—temperature at the bottom of an adjacent 31-inch crevice. N = noon, M = midnight.

During the period from August 6 to 27, 1938, comparative evaporation measurements were made in this same crevice and above the surfaces of two other flows of the Monument. One Livingston white spherical porous-cup atmometer was placed in the crevice, the bulb being 10 inches below the general flow surface. Two similar atmometers were placed on each of the other two flows during the same period, the bulbs being 17 inches above the surface. Comparison of evaporation in the crevice with that at the surface immediately above would have been preferable, but was not possible with the available equipment. It is believed the surface evaporation on North Crater would have been essentially the same as on the two flows where measurements were made.

Figure 9 gives a comparison of evaporation during the three weeks' period in the crevice and above the surfaces. It can be seen that the rate of evaporation 10 inches below the surface was about half that 17 inches above, for the same period.

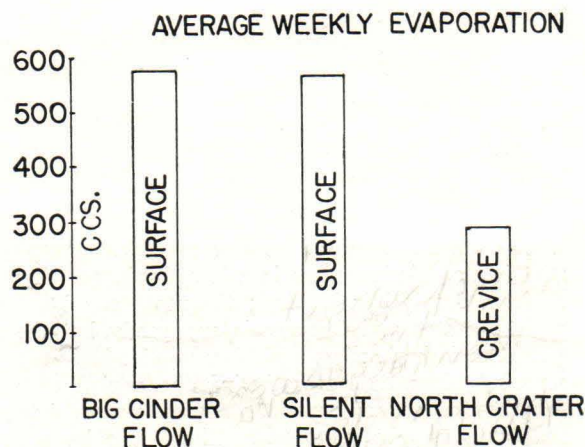


FIG. 9. Evaporation for the period Aug. 6-27, 1938; North Crater Flow—10 inches below the surface; Big Cinder Butte and Silent Flows—17 inches above the surface.

While temperature and evaporation rates are to some extent a measure of the same factor, evaporation is more inclusive in that it shows also the effects of wind and humidity. Judging from these evaporation measurements plants in deep crevices would transpire less rapidly than more exposed plants. Soil too must dry less quickly.

VEGETATION CHARACTER AND SEASONAL LENGTH OF PHOTOSYNTHETIC PERIOD

While it has been possible to obtain some quantitative idea of temperature and evaporation conditions above the rock surface, edaphic influences have largely gone unstudied in this kind of habitat. In view of the impossibility of obtaining adequate instrumental data on subterranean water relations, the ecological character and growth habits of the vegetation itself were studied in the hope of gaining at least some indirect information concerning moisture conditions about the roots. To that end the following facts were compiled for the more important flow species: (a) how much of the summer season each has green leaves, (b) general facts regarding character of leaves—whether thick or thin, large or small—features associated with the terms xerophyte and mesophyte, and (c) the distribution and general habitat preferences of the species as reported in the various available "floras" dealing with this general region. Observations concerning seasonal activities were made at approximately weekly intervals during the period June 20 to September 15, in 1937 and 1938.

Conditions of growth, especially in relation to moisture, were interpreted from these data as far as was possible. The order of presentation parallels that to be used in the section on succession, starting with the rock surface habitat.

Plants of Bare Flow-surface Habitat. The xeric nature of the lava surface is attested by the character of plants which grow there, only crustose and foliose lichens being found. It is only after soil has been added that vascular plants succeed in becoming established.

Plants of Joint Habitat. Only two plant species, *Aplopappus nanus* and *Chrysopsis hispida*, have been found growing in joints. Both grow with their stems fully exposed and without protection against sun and wind; their roots penetrate into narrow joints in the rock, being so tightly wedged that it has not yet been possible to excavate a root system from a flow. No information has been obtained regarding the depth of root system nor soil and water conditions extant in the joints. *Aplopappus* is a low shrub, growing here from 6 to 18 inches tall; the roots and basal part of the stems of *Chrysopsis* are woody but the upper stem is herbaceous. Neither species has been observed to lose its leaves during the period over which observations were made, and they appeared to be carrying on photosynthesis. The leaves have a xeric appearance.

Plants of Shallow Crevice Habitat. None of the shallow crevice species is green and active over the entire summer; many cease activity early in July, all but *Pentstemon deustus* by August 10. A few plants of that species have been observed with a small number of green basal leaves until the end of August.

With one exception, all of the more important species are said to grow elsewhere at elevations corresponding to their location in the Monument. The exception is *Drymocallis pseudorupestris*, the most abundant species in shallow crevices, which definitely has the appearance of a mesophyte. It is reported to grow from the submontane to the subalpine zones (Rydberg, 1917). Another interesting but rather rare species here is *Erigeron trifidus*, which is an alpine plant (Tidestrom, 1925; Rydberg, 1917).

There is no significant correlation, here, between altitudinal distribution, leaf character, and drought resistance. Apparently there is ample water for all species, both mesic and xeric, during spring and early summer; in middle and late summer there is no available water for any of them.

Plants of Deep Crevice Habitat. Two deep crevice species, *Chamaebatiaria millefolium* and *Sericotheca glabrescens*, have green leaves throughout the season of observation. *Woodsia scopulina* had largely ceased vegetative activity before June 20, *Brickellia grandiflora* var. *minor* by the end of July; *Philadelphus Lewisii*, varying somewhat with individuals, stopped activity and lost most of its leaves between July 10 and August 10. *Dryopteris Filix-mas* grows until cold weather comes; some have been observed late in September, still very green.

Most of these species are normally found at higher elevations, where moisture is a less critical factor than in the region of the Monument. *Sericotheca* is reported to grow in the piñon and yellow pine belts; *Philadelphus*, *Brickellia*, *Woodsia*, and *Dryopteris* in the submontane and montane (Abrams, 1923; Ryd-

berg, 1917; Tidestrom, 1925). Only *Chamaebatiaria* is reported for the *Artemisia* belt. It grows also at higher elevations (Tidestrom, 1925).

Judging by usual distribution and ability to continue growth throughout summer, *Chamaebatiaria* and *Sericotheca* are the most drought resistant of the deep crevice plants. The distribution and general character of the other four species would lead one to call them mesophytes, and it is surprising to find such an ecological type represented in a region so definitely xeric. Their presence in the deep crevices indicates that moisture conditions are favorable, and this corroborates the evidence obtained from temperature and evaporation measurements.

Plants of Old Soil-covered Flow Habitat. A greater number of individuals on old flows and character of the dominant species indicate that an accumulation of soil has materially improved moisture conditions. It may be possible that there is more water, at least early in the season, in deep crevices; but the more uniform distribution of vegetation and the fact that a majority of its dominant shrubs are green all summer suggest that water is available for a longer time and in greater total amount on the old flows.

Three shrubs whose leaves have been seen to keep their greenness until September 15 are *Artemisia tridentata*, *Purshia tridentata*, *Chrysothamnus nauseosus*, and *Eriogonum microthecum*. Two other dominant shrubs, *Leptodactylon pungens* and *Eriogonum heracleoides*, cease vegetative activity early in August.

Floristically, an old flow community is composed of species which grow in the *Artemisia* belt. All of the important herbs, and five of the six first-ranking shrubs are so reported (Rydberg, 1917; Tidestrom, 1925). The only exception is *Eriogonum heracleoides*, which is reported for the submontane and montane zones.

SUCCESION ON PAHOEHOE FLOWS

FLOW AGE CORRELATED WITH SPECIES NUMBER AND SPECIES DENSITY

Vegetation succession was studied by selecting pahoehoe flows of various ages, upon which quadrats were laid out. Tabulations of all vascular plants found within the plots were made. This work was done late in June, 1938, when both spring ephemerals and summer flowering plants were visible.

The only published geologic work on the Monument is that of Stearns (1930) and his conclusions regarding age of the lava have been largely followed in this work. He tabulated 27 of the lava flows in order of "approximate eruptive sequence." Six representative flows, including what he believes to be the oldest and the youngest, were selected for these successional studies. The quadrats were laid out as follows: flows are listed in order of increasing age: 1. Indian Tunnel Flow, 10 10-by-10 meter plots (Station 11 of Fig. 6); 2. North Crater Flow, 10 10-by-10 meter plots (Station 7 of Fig. 6); 3. Northwest Big Craters Flow, six 10-by-10 meter plots (Station 4

of Fig. 6); 4. Flow between Half Cone and Crescent Butte, 10 five-by-five meter plots (Station 6 of Fig. 6); 5. Northeast Flow from Big Cinder Butte, 10 five-by-five meter plots (Station 5 of Fig. 6); 6. Silent Cone Flow, five five-by-five meter plots (Station 3 of Fig. 6).

To eliminate personal bias in selecting the locations for the plots, they were arbitrarily spaced a predetermined distance apart, in most cases 20 meters from center to center. The greater uniformity of vegetation on older flows warrants the use of smaller and fewer quadrats there.

To facilitate comparison between the various flows, the densities are expressed uniformly on a basis of 1,000 square meters for each (Table 4). (Density as used here refers to the number of individuals of a species per 1,000 square meters of surface area.)

The total of 52 species of vascular plants occurring in the quadrats fall quite naturally into three groups: (1) those which increase for a time and then decrease as flow age increases, pioneers in general (Table 4a); (2) those which become increasingly important as flow age increases and attain their greatest density on the oldest flows, climax species (Table 4b); and (3) a group composed of species which follow no definite sequence or are too limited in number to give any indication of successional trends (Table 4c).

The youngest flow, having had the least time to progress from a sterile condition, has the smallest number of species, 12, and the lowest total density, 269 individuals per 1,000 square meters. On the other flows, which together represent an age span of several thousands of years, the number of species increases with flow age. There is also a substantial increase in total number of individuals with age increase; the oldest flow has 28 times as many as the youngest.

PROCESS OF VEGETATIONAL DEVELOPMENT

Rock Surface Prisere. Succession upon bare rock has been worked out many times, but it has usually been done in regions less arid than that under consideration here. As has been noted elsewhere, a rock surface prisere beginning with crustose lichens on the lava, and a crevice prisere where herbs and shrubs are the pioneers is found. But, in contrast to these other places, the rock surface prisere is found to be relatively unimportant. Fruticose lichens never come in and the smaller forms function mainly as aids in weathering. They do not grow densely enough to form a substratum for vascular plants. The crevice priseres are the most important.

Joint Prisere. The two species associated with joints, *Aplopappus nanus* and *Chrysopsis hispida*, persist a long time but their habitat is finally eliminated and they are succeeded by members of the climax community.

Shallow Crevice Prisere. The plants of shallow crevices are small and for the most part herbaceous; only one species is woody. The predominant species is *Drymocallis pseudorupestris* (Fig. 7). It has the

TABLE 4. Densities of lava flow species per 1,000 square meters on each flow.

	Indian Tunnel Flow	North Crater Flow	N. W. Big Craters Flow	Flow between Half Cone and Crescent Butte	N. E. Flow from Big Cinder Butte	Silent Cone Flow
4a—Species whose densities increase and then decrease with greater flow age.						
Trees						
<i>Pinus flexilis</i>	—	—	—	4	4	—
Shrubs						
<i>Aplopappus nanus</i>	—	13	102	108	120	—
<i>Chamaebatiaria millefolium</i>	1	61	89	32	24	—
<i>Pentstemon deustus</i>	47	320	114	500	472	128
<i>Philadelphus Lewisii</i>	5	72	130	—	—	—
<i>Sericotheca glabrescens</i>	—	20	—	32	4	—
Flowering herbs, except grasses						
<i>Brickellia grandiflora</i> var. <i>minor</i>	—	12	13	—	—	—
<i>Drymocallis pseudorupestris</i>	181	1001	240	604	548	—
<i>Erigeron trifidus</i>	—	28	20	—	—	—
<i>Pteris terebinthina</i> var. <i>foeniculacea</i>	2	394	—	100	48	—
<i>Stephanomeria myrioclada</i>	12	15	28	40	60	—
Grasses						
<i>Stipa occidentalis</i>	—	1	17	368	224	120
Ferns						
<i>Dryopteris Filix-mas</i>	2	—	—	—	—	—
<i>Woodsia scopulina</i>	3	—	2	24	—	—
4b—Species whose densities increase with greater flow age.						
Shrubs						
<i>Artemisia tridentata</i>	—	—	27	396	324	896
<i>Chrysothamnus nauseosus</i>	1	1	3	4	20	64
<i>Eriogonum heracleoides</i>	—	—	2	260	8	792
<i>Eriogonum microthecum</i>	—	—	—	292	184	112
<i>Leptodactylon pungens</i> including var. <i>Hookeri</i>	—	76	—	224	300	232
<i>Purshia tridentata</i>	—	23	2	128	112	432
Flowering herbs, except grasses						
<i>Eriogonum aridum</i>	—	2	—	36	44	64
<i>Eriogonum ovalifolium</i> var. <i>celsum</i>	—	—	—	—	4	152
<i>Gayophytum ramosissimum</i>	—	—	—	—	—	928
<i>Navarretia Breweri</i>	—	—	—	—	—	240
Grasses						
<i>Agropyron inerme</i>	—	—	—	—	—	512
<i>Agropyron Vaseyi</i>	—	—	—	—	—	648
<i>Poa secunda</i>	—	1	23	220	132	1632
<i>Sitanion hystrix</i>	5	12	145	264	280	208
4c—Incidental species which exhibit no apparent successional trends.						
Shrubs						
<i>Eriogonum effusum</i>	—	—	66	—	76	—
Flowering herbs, except grasses						
<i>Achillea lanulosa</i>	—	—	2	—	—	—
<i>Castilleja Vreelandii</i>	—	—	—	12	—	—
<i>Chaenactis Douglasii</i>	—	—	—	—	56	24
<i>Chrysopsis hispida</i>	—	—	—	—	40	—
<i>Cirsium Hookerianum</i>	—	1	3	—	1	—
<i>Cryptantha flexuosa</i>	—	—	—	36	216	64
<i>Delphinium megacarpa</i>	—	—	—	—	—	96
<i>Eriogonum depressum</i>	—	—	—	12	88	—
<i>Eriogonum subalpinum</i>	—	34	—	36	4	24
<i>Lithospermum pilosum</i>	—	—	—	—	—	8
<i>Lomatium triternatum</i>	—	—	—	—	—	32
<i>Mentzelia albicaulis</i>	—	—	—	—	20	—
<i>Opuntia polyacantha</i>	—	—	12	—	—	24
<i>Oreocarya sericea</i>	—	—	—	60	68	—
<i>Pentstemon cyaneus</i>	—	—	—	—	—	24
<i>Phacelia leucophylla</i>	5	—	—	—	72	—
<i>Phoenicautis Menziesii</i>	5	—	30	—	—	—
<i>Polygonum Douglasii</i>	—	—	—	—	—	8
<i>Senecio altus</i>	—	—	—	—	—	96
<i>Senecio canus</i>	—	—	—	—	—	24
<i>Senecio uintahensis</i>	—	—	—	12	—	—
Grasses						
<i>Bromus tectorum</i>	—	—	—	—	—	8
<i>Orizopsis hymenoides</i>	—	1	—	24	72	—
Total species sampled on each flow.	12	19	21	24	28	28
Total individuals sampled on each flow.	269	2088	1070	3824	3651	7600

highest density and occurs on all but the oldest flow. The species with the second highest density is *Pentstemon deustus*. It has woody roots and about 2 to 4 inches of woody perennial stem. Following these two, in approximate order of importance, come

Pteryxia terebinthina var. *foeniculacea*, *Stipa occidentalis*, *Stephanomeria myrioclada*, and *Erigeron trifidus*. There is less confinement of these species to a restricted habitat than is true of deep crevice species. *Drymocallis* grows exclusively in shallow crevices on flows, but the other species grow also on cinder cones.

Some difficulties were encountered in compiling density values for *Leptodaetylon* because it was not realized while the field work was being done that certain variations in the group were constant enough to warrant a separation of the material into a species and a variety of that species. Further consideration has shown that there are two forms growing on the lava. The plants on old soil-covered flows, such as Silent, are largely *L. pungens*. *L. pungens* var. *Hookeri* is a shallow crevice plant, and all on North Crater Flow are probably of that variety. It is believed that both the species and its variety are found on flows intermediate in age, but because this was not recognized in the field there has been no separation in the density tabulations (Table 4b).

Several other shallow crevice plants were found in the plots on the flows, but only in small numbers. Two of these, *Achillea lanulosa* and *Castilleja Vreelandii*, grow more abundantly in the mountains north of the Monument, and the disseminules probably come from there. Three other incidental species have been observed only on young flows, *Cirsium Hookerianum*, *Phoenicautis Menziesii*, and *Senecio uintahensis*. Other species more commonly associated with cinder cones occur on the flow in small numbers, and include *Eriogonum depressum*, *Mentzelia albicaulis*, *Oreocarya sericea*, and *Phacelia leucophylla*. One grass, *Oryzopsis hymenoides*, comes into this category also.

The roots of shallow crevice plants probably contribute humus to the soil, but it is likely that most of the above-ground parts blow away and lodge in deep crevices. In some places considerable amounts of vegetation are carried into crevices by conies (*Ochotona* sp.), which store them for winter food.

Exposure to winds retards the accumulation of soil in shallow crevices, so they persist as long or longer than near-by deep crevices. It is not uncommon



FIG. 10. North Crater Flow, showing vegetation in three habitats; rock surface at the right, shallow crevice in the center, and a nearly filled deep crevice at the left. July 16, 1938.

mon to find parts of old flows bearing some pioneer stages of both bare rock and shallow crevice types that must have been maintained in that primitive condition for hundreds of years. Under such circumstances exposed lava surfaces with lichens, a shallow crevice with characteristic vegetation, and a deep crevice filled with soil and supporting a few *Purshia* shrubs of the climax vegetation, may all be found within a radius of a few feet (Fig. 10).

Deep Crevice Priseres. Seven species are characteristic of deep crevices; five of them here grow exclusively in such situations. Two of the five are shrubs: *Philadelphus Lewisii* and *Sericotheca glabrescens*; the other three are herbs: *Brickellia grandiflora* var. *minor*, and two ferns—*Woodsia scopulina* and *Dryopteris Felix-mas*. *Chamaebatiaria millefolium*, a shrub, is found in deep crevices but attains its best development on cinder cones. The seventh species, limber pine, occurs sparingly on pahoehoe flows (Fig. 11).



FIG. 11. Big Cinder Butte Flow, with scattered, dwarfed limber pines. In the distance is the Devil's Orchard where trees are larger and more abundant. June 21, 1938.

Individuals soon outgrow the crevices in which the seedlings start, and most of the tree is then exposed above the flow surface. Such pines are generally dwarfed and contorted and do not appear thrifty; reproduction is scanty.

The three shrubs, *Philadelphus*, *Chamaebatiaria*, and *Sericotheca*, are dominant in the deep crevice community; they supply the largest individuals and have the greatest density.

Deep crevice plants react upon their environment by supplying organic material which, in part at least, turns to humus. Considerable quantities of dead stems and leaves have been seen in the crevices, and it is likely that even in this dry climate much of it undergoes humification. The humus, along with the residual soil from flow weathering and the wind-transported soil, tend as time goes on to fill the crevices. In that way these species contribute to their own destruction, for when the crevices are filled, the physical protection that is afforded against the desiccating influence of wind and insolation ceases to exist and they are succeeded by the apparently more drought resistant climax species (Fig. 12).

Convergence of Priseres to Climatic Climax. All successions lead directly to the grass-sage climax as

rapidly as soil accumulates to a depth sufficient to support its deep-rooted members. Deep crevices are filled first, accompanied by a disappearance of their characteristic vegetation, while shallow crevices still



FIG. 12. Big Crater Flow at the left, Silent Cone Flow at the right. There is close correlation between amount of vegetation and age of flow. June 21, 1938.

persist. Eventually minor depressions are filled also and shallow crevice plants disappear. Coverage of intervening surfaces is aided by shrubs in the crevices; these impede wind movement sufficiently to cause deposition of aeolian material. Thus these flat flow areas that formerly maintained nothing higher than foliose lichens gradually come to support the regional climax (Fig. 13).



FIG. 13. Silent Cone Flow with vegetation which is probably the regional climatic climax type. June 20, 1938.

This final stage is dominated by six shrubs: *Artemisia tridentata*, *Purshia tridentata*, *Eriogonum microthecum*, *E. heracleoides*, *Chrysothamnus nauseosus*, and *Leptodactylon pungens*. A less important shrub is *Eriogonum aridum*; another is *E. effusum*, which is very similar to *E. microthecum* in habit and close to it taxonomically. Just as typical of this community as the shrubs are certain herbs which occupy spaces between them. Five grasses are important: first is *Poa secunda*, then in order are *Agropyron Vaseyi*, *A. inerme*, *Sitanion hystrix*, and *Stipa occidentalis*. *Gayophytum ramosissimum* and *Navarretia Breweri* are the most important dicotyledonous herbs.

There are numerous herbaceous species which, here,

attain their best development and greatest abundance on cinder cones, but which are also present on old lava flows. They appear to be a regular part of the climax vegetation. This group includes: *Chaenactis Douglasii*, *Cryptantha flexuosa*, *Delphinium megacarpa*, *Eriogonum ovalifolium* var. *celsum*, *E. subalpinum*, *Lithospermum pilosum*, *Pentstemon cyaneus*, and *Polygonum Douglasii*. Three other herbs, *Lomatium triternatum*, *Senecio altus*, and *S. canus*, have been seen only on old flows. Prickly pear, *Opuntia polyacantha*, grows on old flows and also on old cinder cones.

Old flows in this area, like all accessible grass-supporting flows on the Snake River plains, have been grazed to some extent, but probably less than is usual; the disturbance thus produced may be responsible for the introduction of certain weedy plants, such as *Bromus tectorum* (Table 4c).

AA LAVA FLOWS AND THEIR VEGETATION

RATES OF SUCCESSION ON PAHOEHOE AND AA LAVA FLOWS

Succession on the aa type of lava flow has not been studied statistically in the Monument. A general survey indicates that pahoehoe flows tend to become completely covered with the grass-sage climax before aa flows of like age. A specific instance is a flow about 5 miles east of Carey which contained both lava types. The pahoehoe portion supported the typical grass-sage community members; the aa had some of these species in places, but more of its vegetation was characteristic of earlier successional stages. *Chamaebatiaria* and *Sericotheca* were there, growing between blocks of lava, suggesting that conditions were similar to those of deep crevices on smooth flows. Much of the aa flow remained void of soil and hence it bore less vegetation than the pahoehoe.

The greater advance of vegetation on pahoehoe is evidently due to the fact that less soil is required to cover this nearly smooth and level kind than an aa flow with its great surface irregularity. Surfaces of some aa flows are serrate in profile and the ridges may be bare of vegetation and soil while low areas between, where soil has accumulated, support a good growth. As a major part of the soil mantle that accumulates on the flows is transported, the time required to complete the process would be proportional to the amount of soil required.

Elsewhere, in regions of greater precipitation and where more residual soil accumulates, conditions may well be quite different. Stearns (in correspondence) reports that he has observed flows in Hawaii and also in Oregon where aa has a dense vegetation covering, while equal-aged pahoehoe is still quite bare. He believes the subject of succession rate on pahoehoe and aa is "too variable to be covered in any general statement." Nevertheless, it seems worth while to report conditions as they are in individual cases. From many such it may be possible eventually to generalize.

RELATION OF LIMBER PINE DISTRIBUTION TO
FLOW PHYSIOGRAPHY

DISTRIBUTION ON PAHOEHOE FLOWS

Limber pine is sparingly present on certain pahoehoe flows, including Big Cinder Butte Flow, and the flow between Half Cone and Crescent Butte. On others, such as Indian Tunnel Flow, only a very few pines are found; on still others, as Silent Cone Flow, there are none (Fig. 13). This is shown by the density studies as given in Table 4.

No obvious reason for the erratic distribution of pine on flows presented itself, but it was thought successful establishment might be correlated with protection by cinder cones against drying winds. This assumption was reached because Big Craters Flow with few trees and Silent Cone Flow with none lie to the west (to windward) of the line of cinder cones; the two flows having fair tree growth lie in the lee of the cones (Fig. 6). To test this theory evaporation measurements were made. Livingston white sphere anemometers were placed on Silent Cone Flow and on Big Cinder Butte Flow, a pair on each (Stations 5 and 3, Fig. 6). Records were kept for four weeks in July, 1938. Evaporation rates at the two sites were almost identical for the period, as is recorded by the first two units of the histogram (Fig. 9). Thus the manner of distribution of pine does not seem to be due to a difference in evaporation.

DISTRIBUTION ON AA FLOWS

Further investigation throughout the Monument and adjacent region revealed that the best pine stands on lava—those with the largest trees, the most individuals, and having the best reproduction—are mainly in two areas, as bounded within the black lines of Figure 6. One area extends northeast from Inferno and Paisley Cones and includes the area popularly known as the Devil's Orchard; the other lies west (to windward) of the line of cinder cones, starting at approximately the south end of Big Cinder Butte, and extending in a south and easterly direction to the end of the Monument, paralleling the lines of cinder cones. The presence of this area of pines to the west (windward) of the zone of cones further shows that the establishment of trees has no relation to the position of cones.

Both regions of best pine growth consist almost entirely of extremely rough aa flows. Most of the larger one to the south may be described by the term "sawtooth." Here are long, nearly parallel ridges with depressions 6 to 20 feet deep in between. Soil and snow collect in these depressions, and it is here that vegetation is found. Monoliths or fragments of old crater walls frequently protrude through the flows, and these further add to the topographic irregularities (Fig. 4).

Because the best development of trees on flows is associated with extreme surface irregularity, it was logical to look for a causal relationship. A reasonable explanation is that these flows offer the conditions necessary to the success of seedlings, namely, a reduc-

tion in evaporation intensity and an increase in soil moisture. It was not possible to make measurements of evaporation on these flows, but it may be expected that it would be reduced in depressions several feet below the general surface, or in the shade and protection of a crag 6 to 30 feet high. Monoliths frequently are of the latter height.

The probable benefits received by seedlings from even small increases in soil water can be seen in the results of a tabulation of the positions of 125 trees, exclusive of seedlings, selected at random on Derelict Flow, a large aa flow in the southern tree area. Trees grow here in depressions where snow would accumulate in considerable quantity in winter; in addition it was found that in a majority of cases they grow where run-off from exposed rocks would collect. Seventy-eight of the trees were growing at edges of rock outcrops; 14 others grew within 4 feet of such outcrops. Only 33 were more than 4 feet away.

It is thus evident that trees occupy positions on aa flows where water collects and where evaporation is reduced, and it is probably the case on pahoehoe also. Pine on pahoehoe is a typical deep crevice plant; its seedlings apparently must start in protected sites in order to succeed. When deep crevices which afford these conditions disappear, pines, like other deep crevice plants, also disappear, and the grass-shrub regional climax is finally attained. This is well illustrated on Silent Cone Flow.

The problem of why there are almost no trees on certain young flows, as Indian Tunnel Flow and Big Craters Flow, is still unanswered. A possible explanation is that the flows are too young and there has been insufficient time for them to become established.

CINDER CONES AND THEIR VEGETATION

GROWTH CONDITIONS ON CONES

GENERAL FEATURES

In contrast to flows, which are nearly level, there appear on cinder cones the indirect effects of topography, which, in this semiarid region, are responsible for rather marked differences in the character of vegetation on north- and south-facing slopes. Another difference between flow and cinder cone vegetation is due to the physical character of the lava itself. Vascular plants do not grow on flows until soil accumulates; then they are limited to crevices for a long time. The very youngest cinder cones support vascular plants quite generally, and there is no reason to believe that any change in cinders was necessary before these plants could start.

Three community types include essentially all vegetation to be found on the cones. A pioneer community of herbs occupies a major part of young cones (Fig. 14); it decreases in proportion of area covered as cones become older, until finally it is restricted to only the most exposed parts of southwest slopes. A second community, in which trees are dominant, is confined to protected sites, chiefly on north-facing slopes (Fig. 15); it occasionally is found in

depressions on south slopes also. The third type is dominated by shrubs and occupies south slopes of old cones; it may be entirely absent from young cones (Fig. 16).



FIG. 14. South side of North Crater. Alternating light and dark zones indicate low, wind-formed ridges. Small white spots are *Eriogonum depressum*; in the foreground they grow in old wagon tracks. July 20, 1938.



FIG. 15. North side of North Crater. Depressions support trees while ridges have only herbs. July 16, 1938.



FIG. 16. Shrub community on southwest side of Silent Cone. July 19, 1938.

HABITATS OF CONES AND HOW THEY CHANGE AS CONE AGE INCREASES

Growth conditions on young cones are modified slowly, and then only as a result of change in soil and in micro-climatic influences brought about by the vegetation which succeeds in getting started. Without vascular plants of sufficient size to serve as windbreaks weathered material does not remain in place, but blows away, and even after some hun-

dreds of years cinders at the surface of little vegetated parts of cones are unweathered. Vegetation also adds humus, resulting in a greater ability of soil to supply water to plant roots. Such superior



FIG. 17. Road cut with plants growing in a narrow seam of weathered soil; unweathered cinders above and below support little vegetation. July 8, 1938.

water-supplying ability of fine-textured soil over that of unweathered cinders was demonstrated in a striking manner in a road-cut in the Monument, near Station 7 (Fig. 6). A seam of weathered material about 3 inches thick lay between unweathered cinders, below and above. As can be seen in Figure 17, plants are nearly absent from the cut except in the narrow seam of fine soil, where many are found. Finer texture evidently gives this soil better moisture conditions than are present in the coarser, unweathered cinders adjoining.

Accompanying the change in soil texture is one in color, which goes from black to gray or light brown, as weathering products accumulate. The effect of this alteration is to reduce light absorption, and thus soil temperature on bright summer days.

CINDER CONE SOILS

Unweathered cinders are coarse, some being as much as 3 to 4 inches in diameter, but the average is about one-fourth inch. There is usually more or less interstitial material of sand size mixed throughout. Cinders are usually light in weight, porous, and are sometimes soft enough to be crushed between the fingers.

Although large areas on cinder cones have remained devoid of vegetation, except for small herbaceous species which are not very effective as soil-binders, there has been little mass movement of cinders. No deposit approaching the size of dunes is found. The surface in some herb communities is rippled, but these ripples are only 4 to 6 inches in height (Fig. 14).

FATE OF PRECIPITATION

Here, as on the flows, there is little or no surface run-off. There flatness of surface and frequency of crevices is responsible, but on the cones it is due to porosity of cinders. Water usually sinks in immediately. Rarely, during extremely violent rains, rivulets flow for 100 or 200 feet before disappearing.

CRATERS OF THE MOON NATIONAL MONUMENT

Absence of water loss would be expected to result in conservation of much of it for use by vegetation. But the same property which gives a cinder soil almost limitless ability to absorb water probably permits much of it to sink deeply, beyond the reach of plant roots.

Prevailing southwest winds cause winter snows to be concentrated on northeast sides of cones at the expense of the supply on southwest sides. Because of its protected position and greater initial quantity this snow persists, and furnishes moisture to vegetation after that on exposed southwest slopes has melted. This is strikingly shown by a photograph taken on April 3, 1939, by Helen K. Sharsmith (Fig. 18) which also illustrates the close correlation between position of snow and vegetation.



FIG. 18. Snow persisting on northeast sides of cones when southwest sides are bare; positions of snow and vegetation coincide. Spatter cones in foreground; Half Cone and Crescent Butte, left distance; Broken Top, center; Big Cinder Butte, right. Photograph by Helen K. Sharsmith. April 3, 1939.

SOIL MOISTURE

Water-retaining Ability of Cinder Soil. Water relations of unweathered cinders cannot be compared with those of gravel or other soils of comparable particle size. Water is not confined to the outer surfaces of cinders, but penetrates within as well; thus water-retaining ability is higher than might be expected.

Measurements were made of water-retaining capacity of unweathered cinders of three different textures; also, for comparison, of a fine-textured soil from an old lava flow. Two of the cinder samples were prepared by combining 25 lots of unweathered cinders. This mixture was separated into two lots with a 2 mm. soil sieve. A third lot consisted of coarse, unweathered, unassorted cinder soil collected from North Crater (Fig. 19). Sample 4 was aeolian material from an old flow. A 500 cc. soil tube, 26.5 centimeters tall, was filled with soil from each sample. Each lot was kept wet for three days, excess water was then drained until presumably there was no gravitational water left. Water content was determined for each sample both as a percentage of its dry weight and of its volume. The values are recorded in Table 5.

TABLE 5. Water-retaining ability of four soils.

Sample	Soil type	Water as percentage of weight	As percentage of volume
1	Cinder material over 2 mm.	74.7	23.7
2	" " 2 mm. and less. . .	73.8	53.2
3	" " fresh, unassorted. .	89.6	26.2
4	Old flow surface soil (aeolian)	41.7	48.1

If calculated on a dry weight basis, the three cinder soils appear to have unusually high water-retaining capacities—values such as are associated with soils containing a considerable amount of colloidal matter. These values are excessively high because of the light weight of cinders; many have a specific gravity of less than unity. The coarser the soils, the greater is the difference between percentages of water computed according to the two methods. Sample 3 is probably the most porous in texture and its water content, in relation to its weight, is about $3\frac{1}{2}$ times as great as that in relation to volume. For the clay and silt soils—sample 4—the values approach equality. For cinder cone soils in general it is probable that the water content in relation to weight runs about two to three times that in relation to volume.

Braun-Blanquet (1932) and Livingston and Kotsu (1920) state that the water-supplying power of a soil is much more closely correlated with water content expressed on a basis of volume than on a basis of dry weight. The present work certainly tends to substantiate those reports.



FIG. 19. Northeast side of North Crater. Soil sample site 1 was in the woods at the right, 2 at the upper end of the herb community in the foreground. Pine seedlings were studied in this herb community. White spots are *Eriogonum depressum*. July 16, 1938.

Available Water. Soil of a south-facing slope, receiving greater insolation and being more exposed to the prevailing southwest winds, might be expected to have a lower water content than a protected north-facing slope. To test this, and also to learn the depths to which roots must penetrate to find available water, moisture content and wilting coefficient values were determined at six stations. These were located as follows: site 1, wooded northeast base of North Crater (Fig. 19); site 2, herb community, middle of northeast side of North Crater (Fig. 19); site 3, herb community, middle southwest side of

North Crater (Fig. 20); site 4, pine woods near base of Silent Cone; site 5, middle of north side of Silent Cone, also pine wood; site 6, herb community on southwest side of Silent.



Fig. 20. Southwest side of North Crater. July 19, 1938.

At intervals of about 2 weeks, in 1937, soil samples were collected at depths of 6 inches, 18 inches, and 36 inches, and in 1938 at 3 inches, 6 inches, and 18 inches. After determination of water content each sample was divided into two parts, and moisture equivalent of each determined. These two values were averaged and wilting coefficient calculated. Available water is the difference between water present and wilting coefficient of a soil.

A usual procedure in determining soil constants is to consider only the portion below 2 mm. diameter, assuming water relations of the larger particles to be unimportant. Because of the nature of cinder material no separation was made here, and anything that would go into a soil centrifuge cup was included.

Measurements of available water, computed on a gravimetric basis, are given in Table 6. While these values are, as suggested earlier, not as accurate as if computed on a volumetric basis they do show where water is available and indicate relative amounts.

Rather surprisingly there were no outstanding differences in amounts of available water between north and south sides of cones and between herb and tree communities. Sites 1, 4, and 5 in pine woods have little more available water than sites 2, 3, and 6 in communities of small scattered herbs. Very likely there would be conspicuous differences earlier in the season.

These data show that upper layers may be deficient in available water by midsummer; five of the six sites had none at the 3-inch depth during at least part of the summer of 1938. At 6 inches, four sites lacked water in 1937 and one the next year. At no time during the sampling period was water entirely absent at 18 inches, but there was under 1 percent at site 1 in 1937. At one sampling, following a rain, there was nearly 30 percent of water at site 3 at a depth of 3 inches. In 9 days time this fell to under 6 percent—less than the wilting coefficient value, and 7 days later there was essentially no water. Roots of slow-growing plants probably would not elongate

TABLE 6. Available water.

	Depth in inches	1937 VALUES				1938 VALUES			
		June 29	July 15	July 29	Aug. 13	July 3	July 13	July 21	Aug. 1
SITE 1									
Pine woods, northeast side of North Crater	3					0.00	9.30	0.00	0.00
	6	0.12	0.00	0.00		10.73	15.75	2.51	0.00
	18	6.98	4.51	0.36		16.97	15.57	1.49	6.30
	36	17.76	16.07	14.58					
SITE 2									
Herb com- munity, north- east side of North Crater	3					0.00	4.98	0.00	0.00
	6	29.55	20.65	20.63		34.73	23.92	10.90	24.49
	18	61.32	68.88	60.74	51.63	54.84	62.48	58.99	52.32
	36	75.80	65.58	72.59	64.29				
SITE 3									
Herb com- munity, south- west side of North Crater	3					0.00	18.68	0.00	0.00
	6	24.59	9.78	0.00	0.00	13.43	34.00	28.23	22.07
	18	42.80	38.90	33.51	41.18	34.14	53.92	40.90	57.38
	36	41.93	40.02	46.13	40.91				
SITE 4									
Pine woods, north side of Silent Cone	3					24.92		0.00	
	6	7.04	0.00	0.00	0.00	15.92		18.25	
	18	21.32	31.17	13.99	23.72	24.92		22.27	
	36	23.41	26.38	24.38	13.21				
SITE 5									
Pine woods, north side of Silent Cone	3					0.00		7.70	
	6	12.62	24.45	9.86		12.36		12.12	
	18	30.16	32.04	28.68		15.76		11.73	
	36	32.56	35.45	36.50					
SITE 6									
Herb com- munity, south side of Silent Cone	3					18.89		3.77	
	6	23.74	0.00	0.00		21.62		25.07	
	18	34.54	36.28	37.41		28.53		25.17	
	36	29.35	31.74	28.79					

rapidly enough to keep ahead of the lowering zone of available water.

Plants on cones make sufficiently close contact with cinders to enable them to utilize water from the internal as well as from the external surfaces. Examination of root systems of many plants reveals that they quite commonly grow directly through the individual cinders. This has been a major handicap in excavating roots for careful study; it has been almost impossible to prevent breakage when separating them from cinders. Figure 21 shows a specimen of *Galium Watsoni* from North Crater, with cinders through which its roots have passed.



FIG. 21. Roots of *Galium Watsoni* passing through cinders. June 30, 1937.

SOIL TEMPERATURE

To find the magnitude of daily temperature fluctuations and to compare the rate of change of soil temperature with that of the air above, an air-soil thermograph was placed on a southern exposure of

a cinder cone, in an area as free of vegetation as could be found. In the soil, measurements were begun at a 3-inch depth, and this was increased 3 inches each week, records being taken during the latter half of June and during all of July, in 1938. Air temperatures were taken in the shade, 3 inches above the soil surface, during the same period. As might be expected, surface layers of black, unweathered cinders heated readily when the sun was shining. At all hours of day and night temperature at a depth of 3 inches usually equalled or exceeded air temperature. The daily maxima, for a period of 10 days, ranged from 8° F. more than those of the air to 3° F. less; the average soil maximum was 2.6° F. higher than the air. The absolute maximum at a 3-inch depth was 94° F. These measurements were made in June; had they been made later in the season and at depths less than 3 inches, it is probable that much higher temperatures would have been recorded. At greater depths, 6 inches and over, temperatures were less extreme than those of the air.

Only a short time was needed for changes in air temperature to be recorded in soil also. At 3 inches the maximum and minimum usually came not more than an hour later than in the air; often they practically coincided. A close relation was observed at all depths. Even at 3 feet the soil temperature began to rise in the morning only about an hour later than the air. The small daily increase took place in from 2 to 4 hours. Decrease was less rapid during the night. The record for the week when measurements were made at 30 inches is presented in Figure 22.

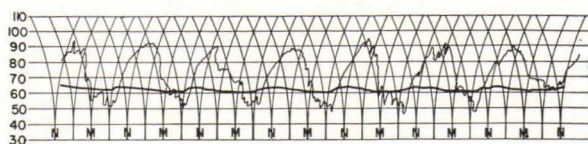


FIG. 22. Air and soil temperature records for the week of July 19-25, 1938, made on a cinder cone. Wide line is record at 30-inch depth; narrow line is shade temperature 3 inches above the cone surface. N = noon, M = midnight.

It apparently is rather unusual for soils to exhibit such rapid temperature changes at depths below the immediate surface. Weaver and Clements (1929) present records for a Nebraska prairie soil, taken at depths of 3 and 12 inches. The temperature trends and time of change at 3 inches followed the air quite closely, but those at a foot depth were several hours behind, the maximum being reached about midnight and the minimum shortly after midday.

It has been pointed out that in the region of this study daily air-temperature ranges are so great that shock may occur to the protoplasm of the above-ground parts of plants. Parts in upper soil layers are probably equally exposed to this danger, or even more so. High temperatures in this black soil may be fatal to tender plants, especially seedlings.

EVAPORATION

Direct effects of wind are not important in determining survival of plants upon cinder cones. There are a few contorted trees, and some breakage occurs, but a more important result is in increase in water loss—transpiration from plants and evaporation from soil.

Evaporation measurements were made for a period of 4 weeks in July, 1938, at three sites midway between the base and summit of North Crater. One site was on the southwest side of the cone in an area of herb vegetation (Fig. 20); one on the northeast side, also in an herb community (Fig. 19); the third was at the same elevation as the second, 175 feet from it, and about 25 feet within a pine woods. Atmometers were set up in pairs, the water reservoirs being buried sufficiently to bring the bulbs 10 inches above the cinder surface.

For the whole period evaporation in the herb community on the southwest side was 2,378.8 cc., on the northeast 1,989.5 cc., a ratio of about six to five. In the pine woods it was 1,477.9 cc. Reduced evaporation in the pine woods as compared to the near-by herb community can be attributed to the effect of vegetation, in providing shade and acting as a wind-break. The ratio of evaporation in the southwest herb community to that in the northeast pine woods is eight to five. The greater evaporation in the southwest is due to wind differences and to effects of increased saturation deficit, resulting from direct insolation. The effect of this is more rapid loss of water from the above-ground parts of plants and more rapid drying of soil surface layers.

VEGETATION CHARACTER AND SEASONAL LENGTH OF PHOTOSYNTHETIC PERIOD

A study of growth habits and ecologic character of important species found on cinder cones was made in a manner similar to that followed for the lava flows. The following facts were compiled: (a) time of year when each flowers, (b) time of year when fruits mature, (c) time it has green leaves, (d) ecologic character of leaves, (e) distributional preference of species as reported in various "floras," and, for many of the species, (f) studies on the nature of root systems and their vertical extent.

Plants of Herb Community. Members of the pioneer community are few in number of species and individuals, and small in size. Only a small part of the cinder surface is covered by plants. Five important species fall into three distinct groups, based primarily on differences in length of season of vegetative activity of leaves and depth of root systems; anatomical characters of leaves differ somewhat within groups, especially the third.

Eriogonum depressum, the most abundant species in the community (Figs. 14 and 19), is in a class by itself in that it is the only one which has green leaves throughout the summer. These have a xeric appearance; they are small, densely covered with white tomentum, and are crowded into a close cluster

near the ground; exclusive of the flower scape the plant is not over 2 inches tall. Its root system extends vertically downward with little branching. The longest one excavated went down $46\frac{1}{2}$ inches; several others were nearly as long. It is interesting that seedlings as well as mature plants have deeply penetrating root systems. Seedlings have been observed which, in their first growing season, had roots a foot long by August. This may partly account for the success of this species. Its reported distribution is from the montane to the alpine zones.

A second group includes two species: *Chaenactis Douglasii* and *Phacelia leucophylla*. Both are taller than *Eriogonum*, being from 8 to 14 inches high. Both have green leaves, xeric in appearance, until about midsummer. Those of *Chaenactis* are finely cut and somewhat floccose; those of *Phacelia* are thick and densely canescent. The root systems are less deep than those of *Eriogonum*; those of *Chaenactis* being from 8 to 12 inches, and *Phacelia*'s from 14 to 18 inches, in the individuals measured. Both species are here growing within the range of their usual distribution.

The third group includes *Mimulus nanus* and the bitterroot (*Lewisia rediviva*). *Mimulus* is an annual, and most individuals have fruited and died by July 15, many before that time. It has small, thin leaves which have a definite mesic appearance. Its root system is shallow and usually does not extend downward over 4 inches. *Lewisia* is a perennial. A crown of more or less cylindrical fleshy leaves expands very early in the spring when soil moisture is plentiful. Late in June, as the large, delicate flowers mature, the leaves gradually wither and dry. By early July, when the fruits are ripe, above-ground parts are scarcely visible. Its roots are also fleshy and extend laterally several inches, but vertically only about four. Both *Mimulus* and *Lewisia* grow here within their general altitudinal range.

These three groups exhibit a direct relationship between length of activity period of the leaves and vertical extent of root system. One can well suppose there is also a relationship to available water. Activity of shallow-rooted *Mimulus* until the end of June indicates the presence of available water to within about four inches of the surface. Deeper-rooted *Chaenactis* and *Phacelia* find water somewhat longer at depths of 8 to 14 inches. Measurements of available water (Table 6) showed it to be present at such depths most of the summer and the plants probably have not exhausted the supply by the time they cease growth. *Eriogonum depressum* can find ample water all summer at the depths to which its roots penetrate.

There are indications in some places in this community that surface conditions may be as influential in determining plant density as moisture. A cinder surface from which the fine-textured material has been blown away is an inhospitable germination bed, but slight disturbance, such as is brought about by the walking of man or other animals, or by the wheels of vehicles, seems to improve it. The location

of tracks may remain plainly marked for years by the perennials which become established in them (Fig. 14). It is not known whether the tracks merely cause a concentration of disseminules or whether they offer improved growing conditions. Soil may blow into the depressions, and it is probable that compacting of cinders improves water-retaining ability. In any event plants do grow more densely in these tracks than elsewhere and it shows that root competition may not be the critical factor which determines their wide spacing in the community.

Plants of Tree Community. The tree community, found mostly on north-facing slopes of cinder cones, is composed of three tree, and a small number of shrub and herb, species. Limber pine occurs on most cones, aspen (*Populus tremuloides*) and Douglas fir on a few old ones which have steep north slopes. The usual distribution of Douglas fir in zones from the submontane to the subalpine suggests that moisture conditions where it is found here are favorable. The similar distribution and mesophytic leaves of aspen further indicate this, as does successful maintenance of pine, when once it has become established.

Plants of Shrub Community. A consideration of herbs and shrubs in the tree community, and also in the shrub community of south slopes, yields little information on moisture conditions of their habitats. The species are less confined to a restricted habitat and most of the important ones are common to both of these communities; some are also in the climax community of old flows. Moisture conditions in the shrub community appear to be intermediate between those of the herb and tree communities.

SUCCESSION ON CINDER CONES

CONE AGE CORRELATED WITH SPECIES NUMBER AND SPECIES DENSITY

To demonstrate the changing character of vegetation with increasing cone age density studies were made of two communities on North Crater, a young cone, and of three on Silent Cone, an old one (Fig. 6). The herb communities were studied in meter-square plots. Six were spaced as equidistant as possible on two sides—northeast and southwest—of North Crater (Figs. 19 and 20), four others on the upper half of the south side of Silent Cone, the only part which supports the herb community type. For purposes of comparison densities have been computed on an areal basis of 6 square meters for each (Tables 7a and 7b).

The herb community on North Crater is composed of few species, only five being found in the plots; *Eriogonum depressum* has the highest density. In the community on older Silent Cone 10 species were found in the plots. *Eriogonum depressum* is absent, first place being taken over by *Chaenactis*. *Elymus condensatus*, a grass, has second place. The presence of seedlings of *Purshia* and sage suggests that shrubs are invading this last bit of herb community on Silent Cone and that it will, in time, be dominated by them.

Tree communities were studied near the northeast bases of the cones, where the densest growth occurs. On each cone eight 10 by 10 meter plots were spaced 15 meters from center to center; trees were tabulated in these and grouped in size classes as in Tables 7c and 7d. Shrubs were counted in 2 by 8 meter plots, one in a predetermined corner of each larger one (Tables 7e and 7f). Herbs were counted in 1 by 5 meter plots in the same corners (Tables 7g and 7h).

Older Silent Cone supports a denser tree growth than North Crater, there being 161 individuals to 53 in comparable areas. Douglas fir is present on Silent Cone and seems to prevent pine from attaining the size it does on North Crater, but there is little reproduction and this species probably will not become more important.

Both tree communities contain five shrubs, and in both *Purshia* is definitely dominant. The Silent Cone community has more herbs than the North Crater one, both in number of species and individuals. *Gayophytum* occupies first place in the latter while in the former *Agropyron inerme*, a grass, has that distinction.

North Crater has no shrub community while the south side of Silent Cone is almost covered by one (Fig. 16). Six 5 by 5 meter plots were laid out there for the study of shrubs; herbs were tabulated in a part of each (Tables 7i and 7j). *Artemisia* and *Purshia* are the dominant members. *Crepis acuminata*, *Mentzelia albicaulis*, and *Gayophytum* are important herbs. Four species of grasses occurred in the plots.

PROCESS OF VEGETATIONAL DEVELOPMENT

Herb Community. The herb community which covers a major part of young cinder cones is the earliest successional stage represented on them today. Judging by the present condition of the cinders, it is probable that it has existed almost since the formation of the cones.

Tree Community. On the north slopes the pioneers are being succeeded by a tree community, first in areas where moisture conditions are most favorable—in depressions and near the cone bases, then in adjoining parts having less protection. Pine and *Purshia* lead the way in the invasion. When these are established and moisture conditions improved other species join them.

To study the manner of limber pine migration and the degree of success of its seedlings, observations were made regularly during the summer of 1938 in an area on North Crater which is being invaded by pine. The plot was about 180 by 150 meters in size. It was bounded on three sides by pine woods and there were a few scattered trees on the fourth (Fig. 19); thus an ample seed supply was available. As the area lay near the northeast base of the cone moisture conditions were thought to be quite favorable. The positions of seedlings were mapped late

TABLE 7. Density values for species found in the communities on North Crater, a young cone, and Silent Cone, an old cone.

NORTH CRATER		SILENT CONE	
7a. Herb community; six 1 meter plots.		7b. Herb community; six 1 meter plots.	
<i>Chaenactis Douglasii</i>	6	<i>Artemisia tridentata</i>	2
<i>Eriogonum depressum</i>	22	<i>Bromus tectorum</i>	2
<i>Lewisia rediviva</i>	2	<i>Chaenactis Douglasii</i>	20
<i>Mimulus nanus</i>	6	<i>Delphinium megacarpa</i>	3
<i>Stipa occidentalis</i>	1	<i>Elymus condensatus</i>	14
		<i>Eriogonum vimineum</i>	5
		<i>Mimulus nanus</i>	3
		<i>Phacelia leucophylla</i>	2
		<i>Pteryxia terebinthina</i> var. <i>foeniculacea</i>	2
		<i>Purshia tridentata</i>	6
7c. Trees in tree community; eight 10 by 10 meter plots. Diam. at 4 feet.		7d. Trees in tree community; eight 10 by 10 meter plots. Diam. at 4 feet.	
<i>Pinus flexilis</i> Under 1 in.....	12	<i>Pinus flexilis</i> Under 1 in.....	66
1-3 in.....	14	1-3 in.....	64
4-8 in.....	19	4-8 in.....	24
9 in. plus ..	8	9 in. plus ..	0
		<i>Pseudotsuga taxifolia</i> Under 1 in.....	2
		1-3 in.....	0
		4-8 in.....	0
		9 in. plus ..	5
7e. Shrubs in tree community; eight 2 by 8 meter plots.		7f. Shrubs in tree community; eight 2 by 8 meter plots.	
<i>Artemisia tridentata</i>	1	<i>Chrysothamnus nauseosus</i> ..	11
<i>Chrysothamnus nauseosus</i> ..	4	<i>Leptodactylon pungens</i>	2
<i>Pentstemon deustus</i>	1	<i>Pentstemon deustus</i>	11
<i>Purshia tridentata</i>	127	<i>Purshia tridentata</i>	101
<i>Ribes cereum</i>	7	<i>Ribes cereum</i>	30
7g. Herbs in tree community; eight 1 by 5 meter plots.		7h. Herbs in tree community; eight 1 by 5 meter plots.	
<i>Eriogonum ovalifolium</i> var. <i>celsum</i>	1	<i>Agropyron inerme</i>	136
<i>Eriogonum subalpinum</i>	8	<i>Chaenactis Douglasii</i>	21
<i>Gayophytum ramosissimum</i> ..	74	<i>Crepis acuminata</i>	2
<i>Mimulus nanus</i>	26	<i>Cryptanthus flexuosus</i>	3
<i>Phacelia leucophylla</i>	4	<i>Delphinium megacarpa</i>	2
<i>Poa secunda</i>	5	<i>Drymocallis convallaria</i>	5
<i>Sitanion hystrix</i>	22	<i>Eriogonum depressum</i>	2
<i>Stipa occidentalis</i>	3	<i>Eriogonum subalpinum</i>	5
		<i>Gayophytum ramosissimum</i> ..	96
		<i>Mentzelia albicaulis</i>	53
		<i>Mimulus nanus</i>	11
		<i>Nicotiana attenuata</i>	11
		<i>Phacelia leucophylla</i>	22
		<i>Poa secunda</i>	11
		<i>Polygonum Douglasii</i>	19
		<i>Pteryxia terebinthina</i> var. <i>foeniculacea</i>	3
		<i>Sitanion hystrix</i>	21
		<i>Stipa occidentalis</i>	2
		7i. Shrubs in shrub community; six 5 by 5 meter plots.	
		<i>Artemisia tridentata</i>	85
		<i>Chrysothamnus nauseosus</i> ..	3
		<i>Purshia tridentata</i>	79
		<i>Ribes cereum</i>	1
		7j. Herbs in shrub community; six 1 by 5 meter plots.	
		<i>Agropyron Vaseyi</i>	2
		<i>Chaenactis Douglasii</i>	2
		<i>Crepis acuminata</i>	37
		<i>Delphinium megacarpa</i>	2
		<i>Elymus condensatus</i>	1
		<i>Eriogonum aridum</i>	1
		<i>Eriogonum ovalifolium</i> var. <i>celsum</i>	2
		<i>Eriogonum subalpinum</i>	6
		<i>Gayophytum ramosissimum</i> ..	30
		<i>Lithospermum pilosum</i>	5
		<i>Mentzelia albicaulis</i>	44
		<i>Mimulus nanus</i>	2
		<i>Phacelia leucophylla</i>	14
		<i>Poa secunda</i>	9
		<i>Sitanion hystrix</i>	14

in June and records of their vigor were kept periodically until August 18th.

A total of 105 seedlings were in the plot; seven grew singly, the rest in clumps of from two to eight. Most were within 25 meters of the seed trees; the farthest removed was 45 meters.

On July 5th, 14 seedlings were alive; on the 16th, 10; on the 27th, four; on August 3rd, four; on August 18th, the last time observed, three.

It is evident that seeds were produced in ample quantity to reproduce the species, that they were well disseminated, that many germinated, but that few, if any, survived through the first summer. The high mortality rate may be due to their shallow root systems or to high temperatures in upper soil layers. Most of the root systems had a vertical length of only about 3 inches at the time the plants died; the longest excavated was $5\frac{1}{2}$ inches.

Occurrence of seedlings in clumps, never associated with pine cone remains, suggests that rodents are the agents of pine seed dissemination, and that the clumps mark the sites of seed caches. There are two species of chipmunks and three of ground squirrels in the Monument which might carry pine seeds. Their food habits lead the writer to think that ground squirrels are largely responsible. The one most commonly associated with the younger cinder cones is Hollister's Ground Squirrel, *Citellus lateralis tesco-rum*.³ Limber pine seeds are wingless and wind dissemination would be unimportant but rodents spread them very well. An advantage of rodent dissemination is in the greater likelihood of germination when buried, but a disadvantage is introduced in that several seedlings together must compete for water.

The ground squirrel is an effective agent for *Purshia* dissemination also, clumps of seedlings being found almost as frequently as are pine. These often contain many individuals; 21 in one group were counted on North Crater. Competition for water in such situations must be very keen.

A measure of the rate of invasion of an herb community by pine was obtained by studying ages of trees near the edge of a southward advancing woods on the east side of Inferno Cone, one of the youngest in the Monument. A transect 25 meters wide was laid out in a north-south direction, extending inward 160 meters, from the southern margin of the forest. Ages of all trees an inch or more in diameter at a height of about 4 feet, were determined from increment borings. There were no large dead trees and it seems likely that the present living ones are the first to occupy the site.

The trees of the transect were found to be uneven-aged, ranging from over 150 years down to 13 years. They are located in three quite compact and distinct groups, each composed of trees of varying ages. Between the three main bodies the herb community still persists, or there are numerous pine seedlings and small trees. The northernmost forms the southern margin of the nearly continuous pine forest; the other two are outposts beyond it. This suggests that the forest advance has not been unbroken and uniform, but that one or more trees became established at a distance from the seed source and that then

others filled in about them. The southern tree island was apparently established before the center one, as it contains older trees.

The rate of invasion has been very slow. In more than 150 years the forest margin has advanced 37 meters; in over 121 years only 12 meters, and that only in the form of a single small tree under an inch in diameter. But this tree may be the nucleus for another island of trees.

Shrub Community. On south slopes the herb community is slowly succeeded by shrubs. *Purshia* is the pioneer in this invasion. It has an extensive root system and is able to withstand partial burial, by wind-borne cinders, to which isolated shrubs on cones are subject. Its branches apparently elongate sufficiently to keep above the surface, and they send out adventitious roots wherever contact is made with soil. Thus *Purshia* makes a very good surface stabilizer. Only after it has become sufficiently abundant to prevent further burial and has helped to bring about an accumulation of fine-textured surface material does sage become important in the community.

Convergence to Climatic Climax. As old cones are eroded away and approach flatness they come in time to support the regional climax type of vegetation. This is not now occurring in the Monument because cones of sufficient age are lacking, but it is evident in several instances in the vicinity of Big Butte (Fig. 1). Both the tree and shrub communities lead to the climax, the former by undergoing a complete loss of trees and an increase in grasses, and the latter through a reduction in shrubs and an increase in grasses.

SUMMARY

The Snake River plains of southern Idaho have been built up by many volcanic eruptions which have occurred over a long period of time, Miocene to Recent. Most of the volcanic material is in the form of lava flows, but cinder cones are common, especially in the area of the Craters of the Moon National Monument, in the north-central part of the plains. There some of the most recent volcanic activity has taken place, and cones and flows of various ages are present.

Primary succession on pahoehoe lava flows and upon cinder cones was studied within the Monument and in immediately adjacent areas. General observations were also made on the vegetation of aa flows. Consideration has been given to possible causes for the presence of trees on flows in certain restricted areas on the Snake River plains and their absence from others.

A young pahoehoe lava flow presents four distinct vegetation habitats. The most extensive of these is the xeric, bare flow surface, where lichens are pioneer plants. A second habitat, much more limited in area, is that in joints. Shallow crevices furnish a habitat with a thin soil deposit for vascular plants but there is no protection for aerial portions of plants. Deep crevices provide the best moisture con-

³ The writer is indebted to Philip M. Blossom, Associate Curator of the Museum of Zoology, University of Michigan, for the taxonomy of the rodents and for information on their food habits in the Monument.

ditions to be found on young pahoehoe flows, and in them several mesic herbs and shrubs are pioneers. Soil, partly residual, but mostly aeolian in origin, slowly fills all crevices and then deposits as a mantle over the flow surface. First deep crevice plants are eliminated because of the changing habitat, then shallow crevice plants, and finally joint and rock surface plants. They are all replaced by a grass-sage type of community which is probably the climatic climax of the Snake River plains region.

The Monument is near the center of an area of about 750 square miles where trees—mostly limber pines—grow scatteringly upon the flows. The best tree growth is on the roughest flows, mainly of the aa type, and old flows which are completely soil covered generally have none. Rough flows probably supply conditions which tree seedlings need for successful establishment: concentration of precipitation in depressions, and protection against strong desiccating winds.

North-facing and south-facing slopes of cinder cones present conditions of growth which are quite different, mainly in the rate of evaporation. On south-facing slopes, and on ridges and prominences of north-facing ones, a community of herbs provides the pioneers. Its members are well adapted to growth in this xeric habitat, by either ceasing growth early in summer, or in having deeply penetrating root systems. In depressions on north slopes trees are present. Only slowly are the herb communities succeeded by trees on north slopes and by shrubs on the south.

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