MANNER OF INVASION OF VOLCANIC DEPOSITS BY PLANTS, WITH FURTHER EVIDENCE FROM PARÍCUTIN AND JORULLO[1]

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INTRODUCTION

Volcanoes and their effects are of interest to the soil-scientist and ecologist, as well as to the volcanologist, geologist, and geophysicist. The first two are interested because volcanic activity brings forth problems having to do with rate of weathering of lava and cinders, accelerated erosion and its control, and problems of plant nutrition, including nitrogen fixation by microorganisms, growth of mycorrhizae, and general problems of composition of plant communities which are greatly modified, even to extinction, by volcanic activity.

Agricultural man has been interested in volcanoes and their activity for as long as he has grown crops in areas adjacent to them. Volcanic outpourings of any type cause him to lose the use of his agricultural land for from a few years to many centuries, depending upon the type of ejecta and the climate of the region. However, over a period of decades or longer, agriculture, per se, may profit by the addition of a layer of volcanic ash over old fields. Some of the most fertile soils are weathered volcanic ash. One example is that of the Snake River Plains in southern Idaho. Another is cited by Colton (1945), who states that following an eruption of Sunset Crater in Arizona, during the eleventh century, the quality of the soil in an area of about 800 square miles was improved by a layer of ash which varied from 1 ft to less than 1 in. in depth. Corn soon grew better than before and even to this day pine trees are claimed to grow at lower altitudes in this area than where there is no ash. The important influence of the ash is believed to be in improvement of water retention by the soil. As will be noted later in this report an ash mantle has improved growing conditions in some places near Jorullo Volcano, in Mexico.

Invasion of any bare area by plants involves two main processes. First, there must be transportation of disseminules into the area from an outside source. Second, germination of the disseminules must take place, followed by growth of the resulting plants to maturity, until they are able to reproduce by sexual or asexual means, and hence increase the number of individuals of a species and result in its establishment. In the invasion of any volcanic area these processes would seem to stand out especially acutely. Volcanic deposits are completely sterile because they originate from within the earth where there is no life and all organisms, including microforms, must be brought to the bare area from outside sources. The extreme situation would be that of a volcanic island, to which disseminules would need to be transported across a body of water. Volcanics carry no products of past life cycles, no fixed nitrogen from an organic source as might the

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materials associated with water-carried deposits in deltas, or wind-borne material in dunes. Everything begins anew; only inorganic nutrients are available, and some of them may be deficient, particularly fixed nitrogen.

Some questions which seem pertinent in a consideration of the problem of succession on volcanics are: 1) How quickly, after the volcanic material has been poured out does vegetation become established? 2) From how far away may disseminules be carried? 3) What kinds of plants are pioneers? 4) Are the pioneers capable of fixing nitrogen? Some of these questions have been answered in part, by others. Present information is not adequate to supply complete answers to all of these questions, but because some of the problems involve such basic biology it seems worthwhile to pursue them as far as is possible in the light of present knowledge.

The method of presentation will be to discuss the histories of two Mexican volcanoes in some detail and of some others very briefly, and to show what these have contributed toward the solution of some of the problems.

PARÍCUTIN VOLCANO

Parícutin Volcano (named after the nearest Mexican Indian village), in the state of Michóacán, Mexico, has been active during the present decade. Probably more is known about its eruptive history and the relation of this activity to vegetation than is known for any other volcano. Hence, it is appropriate that it should be the first volcano considered here. The author spent 3 months at this volcano in the summer of 1945 and made a return visit of about 6 weeks in the summer of 1950.

Parícutin is located in west central Mexico, about 180 mi. west of Mexico City. It is on the Central Mexico Plateau, but only a few miles from its southern edge. Parícutin is the most recently active of a whole belt of volcanoes which crosses Mexico, south-east and north-west, between 18 and 20° N. lat. Most of these volcanoes are small and were active for only a few years. Parícutin itself was active between 1943 and 1952. Jorullo, also recently active, between 1759 and 1775, is another of the small type. Some of the volcanoes are giants and must have been active for a very long time to have attained such great size. Included in this group are Colima, Popocatépetl, and Nevado de Toluca.

VEGETATION PRIOR TO START OF VOLCANIC ACTIVITY

Prior to the start of volcanic activity the area around Parícutin was approximately three-quarters forested. The rest was in fields and pastures, or was occupied by villages. Forest on the reasonably level plateau, with an altitude of about 7200 ft, between the many old volcanic cones, and that on the sides of old cones, up to an elevation of about 9,000 ft, was predominately pine (*Pinus pseudostrobus* Lindl., *P. leiophylla* Schl. & Cham., and *P. teocote* Schl. & Cham.). There was some admixture of oaks, in 8 different species, plus other trees, and shrubs and herbs. Between 9,000 and 10,000 ft, on cones reaching that elevation, fir (*Abies religiosa* (H.B.K.) Schl. & Cham.) was predominant, but there was also considerable oak and a little pine; above 10,000 ft pine was again dominant. Vegetation in the zone below 9,000 ft was the most variable in composition, probably because of the local agricultural methods.

In accordance with the practice of milpas agriculture which was largely followed in the area, fields were allowed to lie fallow when fertility had become depleted. Abandoned fields tended to grow up to pine. Also, oak was probably cut in the lower, easily accessible sites, for fuel and building timbers. Evidence for this opinion is seen in the fact that most of the oak trees at lower altitudes were on less accessible, steep hillsides which were not cultivated and were difficult to reach for timber cutting (Eggler 1948).

CLIMATE

Although located only about 19° from the equator, temperatures of the region are distinctly moderate, because of the altitude. The plateau area between old cones lies from about 7,200 to 7,500 ft altitude and the cones rise above that from a few hundreds, to several thousands of feet. The two tallest peaks near Parícutin are Cerro Angáhuan, rising to about 10,600 ft, and Cerro Tancítaro, to almost 13,000 ft. Snow and freezing weather do not occur, except at the tops of the highest mountains. Total annual precipitation near the volcano is probably about 60 in. Almost all moisture comes during the summer season when daily rains are the rule. Winters are dry.

GENERAL HISTORY OF VOLCANIC ACTIVITY

Parícutin began eruption on February 20, 1943, and remained active until March 4, 1952. There was almost continuous ejection of bombs, ash, and cinders during the first 2 yrs; then activity became more intermittent, with periods of violent activity being interspersed with periods of comparative quiescence. At maximum volcanic activity ash and cinders rose to heights of fifteen to twenty thousand feet before they spread out and drifted, finally settling down on many square miles of area. A cone of ash, cinders, and bombs rapidly built up around the vent and reached a height of almost 1,500 ft in the second year and 1,700 ft by 1946 (Bullard 1947). Lava first began to issue on the second day of activity (Bullard 1947), and many flows have emerged since that time. All flows formed aa[2] lava upon cooling. Many of the early flows have been partially or completely covered by later ones, or by wind or water-borne ash. At any particular time, since from almost the start of activity, the surface of the volcanic area has presented a mosaic of lava flows of various ages, a large cinder cone, and ash-mantled fields and

[2] Aa lava is clinkery and fragmental. It breaks into angular pieces as it moves and cools. The word is Hawaiian in origin.

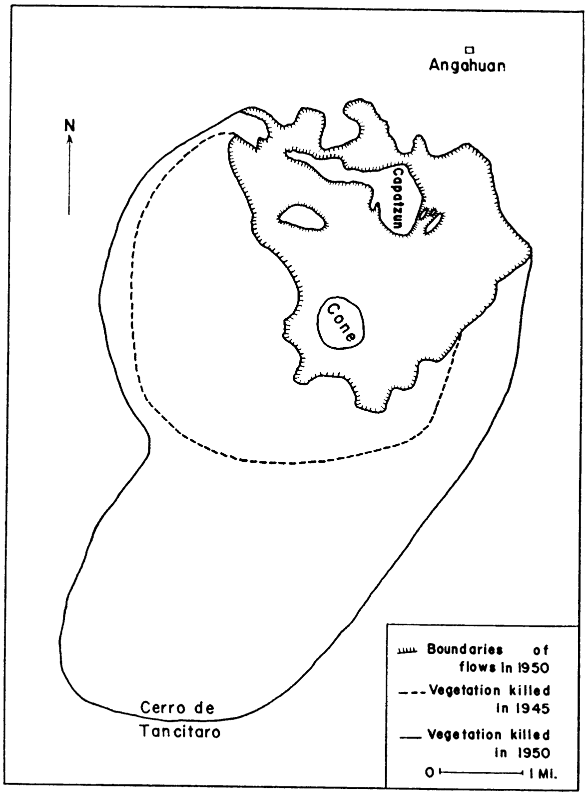

FIG. 1. Parícutin Volcano with extent of lava flows, and areas in which pre-volcanic vegetation was destroyed.

woods. Fig. 1 indicates the arrangement of these features as they appeared in 1950.

When the author visited the volcano in 1945 ash, cinders, and bombs were still being ejected intermittently. Some days the sky was clear and quite free from ash fall; at other times ash fell as thick as rain. A mantle of accumulated ash extended several miles in all directions, being thickest south of the vent. A mile from the base of the cone ash was 8 to 10 ft deep; 4 mi. from the cone it averaged about 1 ft in depth. In the summer of 1945 about 5 sq mi of area was covered by lava, most of it north and east of the cone (Eggler 1948). The flows making up this lava differed in age. Some lava was 2 yrs old, some about 1 yr, and some was new, being still in the active condition in 1945.

VEGETATION IN 1945, AFTER TWO AND A HALF YEARS OF VOLCANIC ACTIVITY

In 1945 the observable effects of the volcano upon vegetation were largely destructive in character. All vegetation had been destroyed in an area estimated at about 18 sq mi. The main cone of the volcano, along with a small satellite, Zapícho, covered about 1 sq mi of area; lava flows covered about 5 sq mi, and deep ash had killed all vegetation in an area of about 12 sq mi. Nowhere, in 1945, was there any indication that any of this completely denuded area was being invaded by plants. Primary succession had not begun.

Outside of the area of complete destruction, there was partial destruction over a much larger area, of possibly 100 sq mi. Here, tree survival depended upon depth of ash, kind of tree, size of tree, and upon length of time ash deposit remained upon the leaves. Among the pine trees those from 5 in. to about 1 ft in diameter near the base survived best, often remaining alive in ash to 4 ft deep; trees over 1 ft in diameter survived next best, in ash to about 32 in.; then came those 3 to 5 in. in diameter and, finally, the smallest ones, which rarely survived in ash 1 ft deep.

Oaks survived burial in ash somewhat better than pines in 1945, but the different sizes withstood it in relatively the same order as those of pine. Small hawthorne trees (*Crataegus pubescens* (H.B.K.) Steud.), which usually grew along old stone fences, survived burial better than almost any other tree species, considering their small size. Alder (*Alnus jorullensis* H.B.K.) usually had all branches knocked off, but new leaves came directly from the main stem.

Some shrubs of *Baccharis pteronoides* DC. withstood burial very well, and continued to grow in ash up to 22 in. deep; adventitious roots were sometimes present on buried parts of branches of this shrub. *Cestrum terminale* var. *latifolium* Francey, continued growth in ash as much as 4 ft deep.

In plants of several kinds stems had been killed back to the old soil level, and later the plants resprouted. Conspicuous in this group were two small shrubs, *Bouvardia ternifolia* (Cav.) Schlecht. and *Fuchsia pringlei* Robino. & Seat.; and two herbs, *Argemone platyceras* Link. & Otto, and *Mirabilis longiflora* L.

Two grasses, *Digitaria velutina* (DC.) Hitch. and *Cynodon dactylon* (L.) Pers., were able to continue growth during accumulation of ash and to keep ahead of it, if the total depth was not more than 18 to 20 in. The grasses were actually spreading somewhat where ash was not over 15 in. deep. Other herbs continuing in old fields, where ash was not over about 20 in. deep, were *Asclepias neglecta* Hemsl., *Erigeron scaposus* DC., and *Pteridium aquilinum* (L.) Kuhn.

Reproduction of plants from seeds buried under ash was not taking place in 1945, even where ash was only an inch or two in depth. But where overlying ash had been removed by erosion a good crop of weeds usually soon appeared, indicating that many seeds were still viable. A covering of ash inhibited seed germination, possibly by retarding aeration.

VOLCANIC ACTIVITY BETWEEN 1945 AND 1950

Lava continued to pour from the volcano between 1945 and 1950, but output of ash and cinders was much reduced. Most of the lava erupted during this period moved out over older flows and increased the total lava thickness, but some flows moved on beyond old limits and covered new areas. (See Fig. 1.) Total land surface covered by flows by 1950 was approximately 8 sq mi. It is believed that ash and cinders emitted between 1945 and 1950 actually had little influence on existing vegetation nor on the establishment of new vegetation.

Vegetation in 1950, After Seven and a Half Years of Volcanic Activity

During the period between 1945 and 1950 the plant life about Parícutin volcano changed in several ways. More plants of all types died. This was due, in a relatively small area, to burial under new lava flows, but in most places it came about as a result of the cumulative influence of partial burial under ash for so many years. However, most pre-volcanic plants which survived actually looked greener and healthier in 1950 than they had in 1945. During this period many plants had started from seeds or spores. These new plants were generally located under trees or shrubs or perennial herbs already present, or in old soil which had been uncovered by erosion, or in playa areas. Present in smaller numbers, but certainly of much interest to the ecologist, and presaging what is likely to come during the next few years, were plants growing on new lava flows. In very extensive former wooded areas and old fields where pre-volcanic plants failed to survive, there was still no plant life in 1950. Pure ash alone was still not a "soil" and plants were not becoming established.

MORE PLANTS DEAD

Between 1945 and 1950 lava flows covered additional areas totalling about 3 sq mi. Plants in this area were buried and destroyed. Elsewhere, to distances of 10 to 15 mi. from the volcano plants continued to die wherever ash still lay upon the old soil. This was not because of new ash fall, but rather was the result of long-time partial burial under ash or, in some cases, was the result of physical breakage suffered during the early years of the eruption, when ash-fall was very heavy.

The most obvious evidence of more plant fatalities was the fact that the area of complete destruction extended about 4 mi, in a southerly direction, beyond where it was in 1945. (See Fig. 1.) Most trees were killed as far south as the summit of Cerra Tancítaro. Fir had been an important tree species on this mountain but all were now killed on the north-facing side, where only scattered pines, oaks, and alders still remained alive. The zone of complete kill was also extended somewhat both east and west, but not at all to the north, where some plants still remained alive to the edge of the lava flows.

Throughout the whole area oaks had been less abundant than pines before volcanic eruption began. It appeared in 1945 that they were surviving partial burial by ash somewhat better than pines but by 1950 scarcely any oaks remained alive where ash was 1 ft or more deep. In the zone of partial destruction quite a number of alders were still alive in 1945 but very few remained in 1950. Likewise, *Arbutus xalapensis* H.B.K., *Symplocos prionophylla* Hemsl., and *Clethra obovata* Hook. & Arn., all small trees, were practically all dead by 1950. In the case of pines the mortality rate continued to be highest among small trees, and next highest among large ones over 1 ft in diameter. In 1945 very conspicuous were scores of small pines which were bent over under the weight of ash. The tops were buried but the trees continued to live. By 1950 only a few of these bent-over trees survived.

The population of most kinds of shrubs was also less in the zone of partial destruction in 1950 than in 1945. In this group were Cestrum, *Symphoricarpos microphyllus* H.B.K., *Arctostaphylos rupestris* Rob. & Seat., *Bouvardia*, and *Fuchsia pringlei*. This last plant formed nearly-closed stands on the floor of some areas of pine forest just northeast of the lava flows in 1945, but in 1950 only a few plants remained. But they were more than twice as tall as those of 1945, which had been unusually small for the species. Most individuals in 1950 were growing close to trees, in which position they apparently had some advantage in protection or in a supply of nutrient. Baccharis had decreased in some places, but in others it was reproducing from seeds under old bushes, and was spreading.

Argemone and *Mirabilis*, two herbs which had been conspicuous in old fields, were now much reduced in number. But in some places Mirabilis was reproducing under, and close to, old plants. The two most abundant grasses in 1945, Cynodon and Digitaria, were generally spreading where established in ash not over 6 or 8 in. deep, but were doing less well in deeper ash; many clumps had died out completely.

REPRODUCTION IN ASH, NEAR LIVING PLANTS

In 1945 there was no reproduction of plants from seed anywhere about the volcano where ash was present in any measurable amount. By 1950 this was changed and there was reproduction of some species where pre-volcanic plants remained alive. A few examples will be cited. There was still no reproduction in ash alone where living plants were absent.

In pine woods, at the north edge of the lava flows, ash was still almost 2 ft deep in 1950 and many seedlings of pine, as well as various shrubs and herbs, were present (Fig. 2). These plants had not grown from seeds buried under the ash, but rather from recently scattered disseminules. Pine needles which were mixed in the ash were decomposing. Excavation of some of the pine seedlings gave indication that their roots had the typical structure which indicates the mycorrhizal condition. Fungi were obviously present in the ash mantle here. Judging by the number of nodes present on the main stems of the pine seedlings or the persistence of cotyledon leaves on some, it appeared that they began growth in 1948, 1949, and 1950. The old, pre-volcanic pine trees had formed no adventitious roots above the level of the old buried soil. But branches from lateral roots were growing vertically upward into the layer of

FIG. 2. One type of situation at Parícutin in which reproduction from seeds was taking place. Ash is 20 in. deep. Two pine seedlings are in the extreme right, center. Pine needles and branches, both within and on top of the ash, prevent erosion, act as mulch, and may aid in supplying nutrient. North of the lava flows. August, 1950.

new ash above. The surviving pine trees were apparently well adjusted to the layer of ash still piled to a depth of 2 ft about their bases.

Proximity of seedlings, such as *Mirabilis*, pine, and others, to already established plants, suggests that there is a very close and intimate relationship between seed germination, seedling survival, and the living plant. The plant is more than just a source of seeds.

Several ways in which living plants might aid seed germination and seedling survival suggest themselves. These would apply to both woody and herbaceous species. First, living plants reduce erosion. In the absence of a stabilizing influence erosion runs rampant in this volcanic area. When it rains running water erodes the unconsolidated ash, and when it does not rain the wind blows it. A surface layer of leaves and other plant parts seemed to be an effective soil stabilizer. Second, the same organic layer would constitute a kind of mulch to hold moisture and prevent the formation of a hard surface crust, through which seedlings would have difficulty in penetrating. A third possible function of organic accumulation would be as a source of nutrients. Possibly the same conditions favoring seed germination and seedling growth also favor the growth of microorganisms. These microorganisms in turn, would break down organic material and make nutrients available.

Organic material away from living plants was found to be inferior to organic material under living plants in aiding seed germination and seedling growth because it was of a different kind. In the area of complete destruction there was sometimes considerable organic material, which usually consisted of dead tree trunks and branches (Fig. 3). The dead wood did very little to control erosion and improve surface conditions for seed germination.

FIG. 3. Considerable organic material but no plant reproduction. South of Parícutin lava flows, in area where all vegetation was destroyed. Ash 6 to 8 ft deep. Erosion is continuing unabated. July, 1950.

REPRODUCTION IN OLD SOIL, AFTER ASH REMOVAL

Where soil was exposed, after removal of ash, plants quickly became established. Except where a good stand of pre-volcanic vegetation survived, to prevent erosion, the rate at which ash was removed from nonlevel areas had been amazingly rapid. Lowdermilk (1947) computed that by August, 1945, about a third of the ash erupted to that time had already been moved. The process of erosion still continues. Gullying is common and the sides of some old cones have had most of the ash removed. A great deal of this ash has been carried away by the Itzicuaro River which starts in the area, but much has simply been moved from high places and deposited in low ones as playa deposits.

The most complete exposure of old soil which was observed was on the old cone, Capátzun (Fig. 1). Capátzun lies 1.5 to 2 mi in a north-northeast direction from the vent of Parícutin. In 1945 Capátzun was covered with ash to depths of from 3 to 6 ft. By 1950 the summit, and the sides about two-thirds of the distance down, were quite free of ash. Most of this ash was deposited at the bottom of the cone, where it helped form a playa.

A number of trees survived on the cone in 1945. These were mostly pines, but included also were a few oaks and one or two small Crataegus and Arbutus. But there were not enough trees to reduce erosion appreciably. While no actual counts were made to compare the number of living trees in 1945 with that in 1950, it is believed that it was nearly the same, and that mortality had been low because of the early elimination of the effects of ash about the bases of the trees.

Shrubs and herbs on Capátzun in 1950 included 3 species which may have regrown from buried rhizomes or root stalks. These were Bouvardia, *Physalis subintegra* Fern., and *Phytolacca icosandra* L. Other species present included 1 fern, *Pteridium aquilinum;* 4 grasses, *Digitaria velutina*, *Panicum albomaculatum* Scribn., *Setaria lutescens* (Weigel) F. T. Hubb., and *Stipa mucronata* H.B.K.; a sedge, *Cyperus flavus* (Vahl.) Nees; and 7 other dicotyledonous species, *Asclepias neglecta*, *Geranium seymanni* Peyr., *Oxalis hernandezii* Schl., *Passiflora exsudans* Zucc., *Phacelia platycarpa* (Cav.) Spreng., *Senecio platanifolius* Benth., and *Trifolium amabile* H.B.K.

Capátzun was not the only cone on which old soil was exposed. Complete removal of ash from extensive areas of surface was not common but nearly all slopes were gullied to some extent and old soil was exposed in the sides or bottoms of the resulting gullies. Only immediately south of the volcano, where ash was 40 to 50 ft deep, had gullies failed to penetrate to old soil. Elsewhere, wherever old soil was exposed, plants were becoming established. Often the plants were the same species as those on Capátzun, but sometimes there were others. In gullies on the north slopes of Tancítaro mountain the regrowth in 1950 consisted of only two species, *Lupinus elegans*, H.B.K., and *Salix bartwegii* Benth. It is possible that all individuals of these two species may have regrown from old buried plants which remained alive.

REPRODUCTION ON PLAYAS

Playas at the edges of the flows into which water-borne materials are brought from adjacent hills were much more extensive and the deposits were deeper in 1950 than in 1945. These deposits consist of ash, old soil, and all kinds of plant parts. After the 1945 trip it was predicted (Eggler 1948) that the playas would probably soon be supporting plant life. By 1950 they were, in many places. One extensive playa located northeast of the flows was even planted to corn in 1950. The corn was growing, but not very satisfactorily. One reason was that silt continued to move into the area after every rain. This playa, like most others, has no stream outlet and hence drainage is poor. Following heavy rains the playas are shallow lakes for a few hours.

The principal kinds of plants observed on playas included *Argemone platyceras; Cirsium nivale* (H.B.K.) Sch.; *Cuphea jorullensis* H.B.K.; *Gaura sinuata* Nutt. ex. Seringh.; *Lupinus elegans; Mirabilis longiflora; Oenothera tetraptera* Cav.; *Perymenium flexuosum* Greenm.; *Phacelia platycarpa;* and *Rumex* sp. The presence of nodules on the roots of the lupine plants indicates that, in some places at least, the playa material is a soil which contains bacteria.

Coverage of the surface of the playas by plants probably did not average over five per cent but, judging by the progress made in five years' time, it is probable that in a few more years the playas will be nearly covered with vegetation.

PRIMARY SUCCESSION BEGUN ON LAVA FLOWS

Considerations up to this point have been largely about destruction of vegetation and secondary succession. All of the areas discussed have been modified by the past or present existence of other organisms. But true primary succession had also begun by 1950. A number of kinds of plants were growing on the lava flows. These included crustose lichens, one or more kinds of algae, mosses, and ferns.

According to the time when they were last actively moving, most of the exposed flows in 1950 were of four ages, dating back to 1944, 1947, 1948, and 1950. If any weathering had taken place it was so slight that it was not visually perceptible. There was some correlation between the kind and quantity of plant life on the various flows and the age of the flow, but not with amount of weathering. Actually, only the 1944 and 1947 flows had plant life on them in 1950.

Aa flows are composed of angular blocks of lava of various sizes. The flows at Parícutin generally included some of sand and gravel size, as well as larger pieces. When a flow finally came to rest the smaller particles tended to sift down between the big pieces. There are at least two types of habitat which plants might occupy on these flows. There are the exposed upper surfaces of lava blocks which usually lack fine textured material and receive the full impact of wind and sun. Rain water runs off about as fast as it falls. Growth conditions are unfavorable. A second would be the depressions between blocks which are protected against desiccating winds. Water draining from the exposed surfaces of rock above moves into them, and there is usually material of sand and gravel size to hold water. Physical conditions for plant growth are much more favorable.

Crustose lichens were the only plants evident on the exposed rock surfaces, and these generally covered only a small fraction of the surface. On the 1947 flows crustose lichens covered less than 1% of the surface; on the 1944 flows it was a little more.

In the depressions between the blocks, where water balance was much more favorable, grew algae, mosses, and ferns. The most abundant alga, and the only one identified, was *Gloeothece linearis* Nag., a blue-green. Where present, this alga grew in profusion in masses that could be collected by the handful.

The mosses present were mostly *Physocomitrium* sp. (material was immature). This was present on both the 1944 and 1947 flows, but was more abundant on the older one. Three ferns were present on the older flow, *Adiantum poiretii* Wikstr., *Cystopteris fragilis* (L.) Bernh., and *Pityrogramma tartarea*

(Cav.) Maxon. Ferns were just beginning to become established on the 1947 flow and only a few juvenile sporophytes of one species, *Adiantum poiretii,* were found.

Whether or not there is any interdependence between algae, mosses, and ferns, it is difficult to determine. It is possible that the alga, Gloeothece, fixes some nitrogen. During recent years evidence has been accumulating to indicate that probably several species of blue-green algae are able to fix atmospheric nitrogen. Fogg (1947) cites several blue-greens in the family Nostocaceae which he found could fix nitrogen, and he suggests that perhaps others can too.

Apparently the nitrogen fixing capacity of Gloeothece has not been tested. Its lush growth on the Parícutin flows indicates that it may possibly be getting some of its nitrogen from the atmosphere. If so, it might well be benefiting both mosses and ferns by making some fixed nitrogen available to them. However, not all mosses and ferns are restricted to sites which support algae, and it would appear that some nitrogen is available from other sources. Ammonium chloride is known to be present in the gases escaping from fumaroles and solfataras of Parícutin. It may be that enough ammonium chloride has been released to fertilize the lava flows sufficiently so they can support some plants which are unable to fix their own nitrogen. Around gas vents of one solfatara in the 1947 flow the number of moss plants was several times as great as in the area away from the solfatara. This suggested that conditions for growth were more favorable in the solfatara area. Water, from stream condensation, would be more abundant, and it is believed chemicals, including ammonium choride, contributed to the nutrition of the mosses.

In summary of conditions in 1950 it can be stated that algae and mosses had become well established on the aa flows of Parícutin in 3 yrs and that ferns were established in 4 yrs. It may well be that the algae contribute to the supply of fixed nitrogen for the mosses and ferns but it does not appear that the latter are altogether dependent on the algae for nitrogen. In-as-much as algae and mosses were established in the crevice and depression habitat almost as soon as crustose lichens started on the exposed rock surface, it appears that there was no interdependence between members of these two communities. It seems likely that they will continue as separate and independent communities for a long time, at least until they spread enough for the two communities to merge.

PRIMARY SUCCESSION BEGUN ON MAIN CINDER CONE

In 1950 Parícutin Volcano was still active. It was difficult even to think that plants could grow on the cone for a long time to come. Nevertheless, Mr. Kenneth Segerstrom of the United States Geological Survey, who made two ascents of the cone in February, 1957, 5 yrs after activity ceased, found lichens and two species of angiosperms growing on the rim of the crater. He has reported (personal communication) that the angiosperms grew "in moist, coarse lapilli where fumarolic vapors keep the lapilli moist and probably supply ammonium chloride sublimate." Neither kind of plant was in the reproductive stage and identification was difficult. One is almost certainly a species of *Gnaphalium* and the other is believed to be an *Eryngium.* It is interesting that these two seed plants would get started in this difficult situation before mosses and ferns.

VOLCANIC ASH ALONE DID NOT SUPPORT VASCULAR PLANTS IN 1950

That no plants were starting in pure ash from seeds or spores in 1950 may have been determined by several factors: unimpeded erosion, formation of a hard surface crust, lack of certain essential nutrients, and poor water retaining capacity of the ash. Erosion and crust formation were obvious. Nutrient deficiency is a negative condition and harder to demonstrate. To test this factor two simple experiments were carried out.

In one experiment several kinds of vegetable and flowers seeds were planted in an ash field "garden." A rather level area, with no organic mulch on it, which had been little eroded, and which was slightly higher than the surrounding area so it had not received any water-borne material, was selected along the west edge of the lava flows (Fig. 1). The seeds were obtained locally and were of unknown quality and viability. But most of them germinated and grew for a time. None of the plants reached maturity, presumably because of environmental conditions.

Seeds were planted on July 5, 1950. This is in the rainy season and should be the most favorable time for seed germination. In two weeks a significant number (20 to 40 of each kind) of garden peas, morning glories, and red beans had sprouted and grown to a height of about 1 in. above the soil surface. These were observed for 3 more weeks, until August 9. Most pea plants were still alive and about 4 in. tall but the basal leaves were dead and the plants did not look healthy. The beans did not grow as well as the peas and by August 9 all bean plants were dead or nearly dead. The morning glories never grew to be more than 1 in. tall and by August 9 almost all had died.

These plants all had color symptoms of nitrogen deficiency. A number of peas and beans were excavated and the root systems of all showed well developed lateral roots but poor vertical root development. A buried crust at a depth of 4 to 5 in. was probably responsible for the poor vertical penetration. No nodules were present on the roots of the legumes.

In another experiment ash was collected from near the base of the main cinder cone and upon returning to the laboratory of Tulane University rye was planted in 12 one-liter jars of this ash with provision for aeration. Distilled water was added as needed. The rye grew very slowly and, after 90 days, plants were only 2 to 3 in. tall. Color of surviving plants was pale green. In this experiment moisture, aeration, and temperature, were known to be satisfactory and the poor growth of rye was without a doubt due to nutrient deficiency. It is believed that this deficiency included fixed nitrogen.

It has been implied that pure volcanic ash is more deficient in nutrient, mainly fixed nitrogen, than lava, and such seems to be the case. Perhaps ash, being fine textured and more porous, has had nutrient leached out. And possibly there has been an actual accumulation of nutrients in the crevices and depressions of the aa flows where mosses and ferns are starting. There is also the possibility that the flows have, right from their start, had more ammonium chloride than the ash. Solfataras and fumaroles, probable sources of ammonium chloride, were not uncommon in the lava flows but were never in ash fields.

Possible Inhibiting Effect of Ash

In addition to the above-mentioned deficiencies of ash as a soil it sometimes seemed that ash exerted an inhibiting influence upon plants. Away from already established plants, where ash is present, even in a thin layer, plants are very slow indeed in getting started. This was well illustrated in an area 5 to 6 mi north of the Volcano, near the village of Carupo. Nearly-level fields totalling several hundreds of acres were still largely devoid of vegetation in 1950, as they were in 1945 (Fig. 4). In this field the chief plant is clover, *Trifolium amabile*. It is largely confined to old rows, probably where maize grew, and where ash is at most 0.5 in. thick. Between crop-rows ash is 3 to 5 in. deep and clover plants were nearly absent. However, some lateral spreading had begun. It had been 5 yrs since any significant ash fall when the picture was taken. Fig. 5 shows the condition in another part of the same general area where ash is a little deeper. Vegetation is almost absent.

Potential Influences of Livestock

From almost the beginning of volcanic activity, when growing of crops became impossible and forage scarce, livestock has been permitted to run at-large over most of the ash covered area. Cattle, sheep, horses, and burros are included among these animals. Up to 1950 there was not much evidence that they were influencing plant life but it seems likely that with time they will. Animal droppings, often containing seeds, as well as organic nutrients, will surely hasten the establishment of plants.

JORULLO VOLCANO

There are many hundreds of volcanoes in the series which includes Parícutin, but the only other one for which there is any historical record is Jorullo. This volcano is located about 60 mi southeast of Parícutin, just off the edge of the Central Plateau of Mexico. The volcanic material at Jorullo, consisting of cones, ash fields, and basaltic lava, lies at an elevation of from about 2,500 to 4,000 ft.

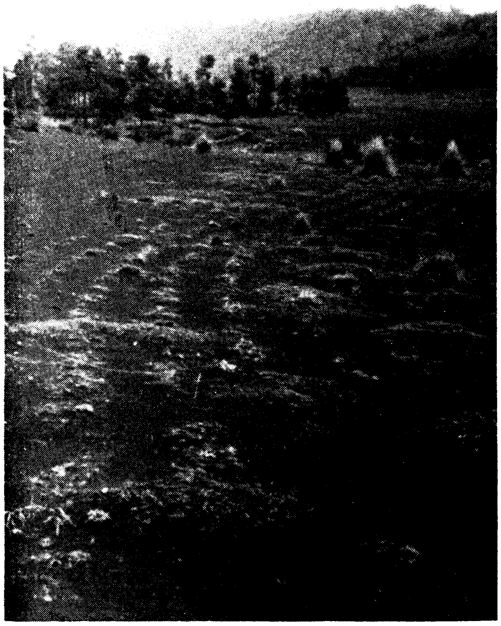

FIG. 4. An old field about 6 mi north of Parícutin Volcano. This had not been cultivated for over 7 yrs, since before volcanic activity began. The ash layer is about 0.5 in. deep in the rows and 3 to 5 in. deep between the rows. Grasses and clover are almost all pre-volcanic and are spreading very slowly. August, 1950.

FIG. 5. An old field, uncultivated since volcanic activity began. Ash is 2 in. deep in the rows and about 6 in. deep between old rows. Pre-volcanic plants are reproducing very little.

The immediate location of Jorullo Volcano is a rectangular amphitheatre, about 3 by 4 mi in extent. On the north, east, and west this is enclosed by hills rising to the Central Plateau, with its temperate climate. The south side of the rectangle opens to the warm lowlands of the Tierra Templada. One large cinder cone and three smaller ones are located at the east end of the rectangle. Most of the lava lies west of these cones.

The name Jorullo is interpreted to mean paradise, in the Tarascan Indian language, and was given to the area before the volcano erupted. The climate is still quite ideal, even though the soil is not. Temperatures are uniformly high throughout the year but precipitation is not adequate to support a tropical forest. Rainfall is about 40 in. per year, with most of it coming during the summer, May to September.

Cultivated crops grown in the region and indicative of the types of climate include bananas, maize, coconuts, lemons, oranges, and papayas.

History of Volcanic Activity

Jorullo began eruption on September 29, 1759, and continued active until about 1775, although most of the material had been extruded by the year 1766. The dates of the eruption are undoubtedly correct as recorded, but no geologist was present to note the sequence of geologic happenings. However, to anyone who has observed Parícutin in eruption the story of activity at Jorullo seems fairly obvious. Judging by the relative positions of the basaltic aa lava flows, the cinder cones, and wind and water-borne ash deposits today, the eruption of Jorullo took approximately the following course. A considerable quantity of ash, cinders, and coarser agglomerate was extruded. Then there were several periods during which lava was extruded. These were followed by, or accompanied by, the ejection of more fragmental material. Almost the last activity was the extrusion of a small lava flow from the throat of the main cone.

When activity ceased there had resulted a large cinder cone about 1,300 ft tall, and three small, subsidiary cones. One small cone, Volcancito del Norte, lies north of the main cone, and south of it are two others called Volcancito Enmedio and Volcancito del Sur. The four cones lie in a nearly straight line about 3 mi long, in a north-northeast by south-southwest direction. Four main series of lava flows are recognizable today. Each lies on the one next older but only partly buries it. The result is a series of receding terraces. The oldest flow has been largely covered with ash, and only the biggest and tallest lava fragments of this flow remain exposed. These fragments are estimated to occupy about one-fourth of the lava flow. The second flow has less ash upon it; it is about half covered. The third flow has little ash upon it, and the fourth, and youngest, has almost none. Some of the fourth flow moved up and over the west wall of the crater. This last flow breached the north rim of the large cinder cone and flowed northward for a short distance. Figure 6 shows the general arrangement of flows and cones.

Probable Habitats In 1775

When volcanic activity ceased at Jorullo the physical habitats for plants must have been quite similar to those which have been described for Parícutin. These were: ash fields, playas, lava flows, and cinder cones.

There are no records of the depth of the ash

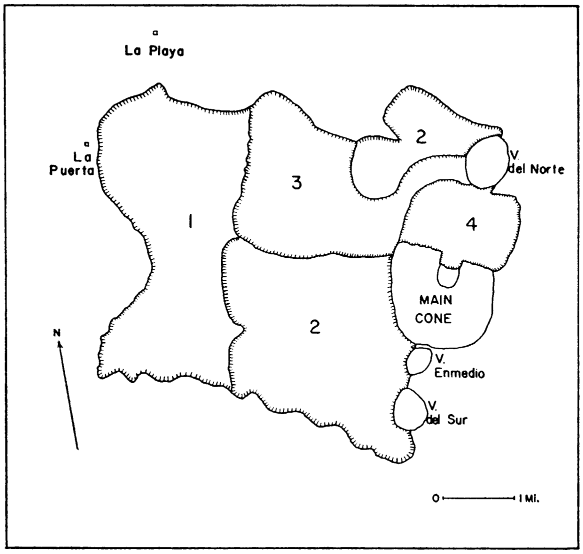

FIG. 6. Generalized map of Jorullo Volcano, with the lava flows numbered in the probable order of extrusion. Distances, and the extent of the several flows are only approximate.

mantle which may be presumed to have blanketed all the surrounding country side for several miles in all directions. Nor is there any record of the extent of the destructive effects of this ash upon plant life.

In the natural drainage pattern of the Jorullo area streams flow from the hills on the west, north, and east, down into the amphitheatre, and out from the southwest side. At the time of the eruption ash and lava blocked the streams and extensive flooding resulted, producing playas. The largest area of flooding was to the west and north of the lava area. Early reports concerning recovery of vegetation nearly all referred to plants on this playa. Today the region is called La Playa and a village by that name is situated on it.

The lava flows are basaltic, of the fragmental, aa type, similar to the lava of Parícutin. The difference in the ages of the youngest and oldest is not more than 5 yrs and has been of no long-time importance as an influence on plant invasion. The quantity of ash on the flows and hardness of the lava has been of much importance in plant invasion. The altitudinal variation from the bottom of the oldest flow to the top of the youngest, exclusive of the flow on the rim of the main crater, is about 600 ft and no observable differences in vegetation on the flows are traceable to altitudinal differences. The flows have covered an area of about 10 sq mi.

The main cone of Jorullo is similar in size to the main cone of Parícutin and, except for the flow which covers part, is similar in material. The three subsidiary cones of Jorullo vary from about 100 to 300 ft high. The four cones cover a total area of about 1.3 sq mi.

VEGETATION OF JORULLO

The author spent July 23 to August 3, 1950, at Jorullo. Most of the time was used in exploring the lava flows and cinder cones, determining what plants were present, and how the different environments have influenced the invasion of vegetation. Grazing, attempts at cultivation, and wood-cutting have undoubtedly altered the vegetation considerably in all parts except the youngest lava flows. Observations recorded by earlier visitors to Jorullo will be referred to in this discussion whenever they contribute to knowledge of vegetation during those earlier times.

In the main, vegetation in those areas with a covering of lava or deep ash is still rather sparse. Parts of some exposed flows appear from a distance to support no vegetation at all, but closer examination shows plants growing out of crevices. Some flow surfaces are populated with combinations of mosses, ferns, Selaginella, and seed plants.

Hilly areas, generally the sides of low cones, often support a savanna type vegetation, in which several kinds of leguminous trees make up most of the tree population. Disturbances, particularly overgrazing, are probably factors contributing to the savanna condition. Much of the main cone of Jorullo, exclusive of a part with a lava cap, has a mixed vegetation of low forest, shrubs, and some herbs. Because of its height and the steepness of its slope the main cinder cone has undoubtedly been disturbed much less by man and his animals than have the small cones and the ash fields. However, even here there has been timber cutting and in 1950 maize was being planted for the first time on the northeast side of the cone.

In this report the vegetation of the hills forming the walls of the Jorullo amphitheatre and that on the playa areas will be treated only briefly. That on the cones and flows will be considered in more detail. These latter habitats were sterile at formation and plant succession on them can be considered as primary in character.

Jorullo has received considerable publicity ever since a visit by Alexander von Humboldt, in 1803, who believed it illustrated the "elevation" theory of volcanism (Russell 1924). Numerous European, as well as American scientists have visited Jorullo and much has been written about it.

The most extensive report is by Hans Gadow, a British zoologist, who spent a month at Jorullo in the year 1909. Gadow (1930), not only reported his own observations, but also reviewed the literature carefully and summarized available reports, through the year 1907. He summarized reports of numerous persons, including the following, who visited Jorullo in the years indicated: Fischer and Riaño, 1789; Humboldt and Bonpland, 1803; Burkart, 1827; Schleiden, 1846; Pieschel, 1853; Laclercq, 1886; Ordoñez, 1907. Gadow cites the following sources for his information. (The present author has not had access to these publications and has relied on the summaries by Gadow.) Burkart,—?. 1836. Aufenhalt and Reisen in Mexico, in den Jahren 1825 bis 1834. Stuttgart; Humboldt, Alexander von. 1811. Essai politique sur le royaume de la Nouvelle Espagne. Paris.; Leclercq, J. 1886. Une visite au Volcan de Jorullo. Bull. Soc. Geogr. Paris. 386-402; Ordoñez, Ezequiel. 1907. Le Jorullo. Guide des excursions du X Congres geologique International. 55 pp. Mexico; Pieschel, C. 1856. Die Vulkane von Mexico. Fünfter Artikel (Jorullo) in Zeitschrift für Allgemeine Erdkunde. Bd. VI, S. 489. Berlin; Riaño, Antonio de. 1789. Superficial y nada facultativa descripción del estado en que se hallaba el volcan de Jorullo la mañana del dia de 10 de Marzo de 1789. Gazeta de Mexico, 5 de Mayo, t. III, num. 30, pp. 293-297; Schleiden, E. 1847. Fortschritte der Geographie and Naturgeschichte, von Froriep und Schomburgk. Bd. II, Lief 16.

Unfortunately all the reports, including that of Gadow, are very general on the subject of plants. None states specifically what species of plants grew on a certain cone or flow at a certain time. Humboldt reported there was no plant life on the lava flows and cinder cones in 1803 (Gadow 1930), and it must therefore be concluded that the Jorullo collections of the Humboldt expedition came from the playa and from areas outside. Gadow probably intended to give more specific information on plants that he found but he died before the mansucript was completed, and others finished it. Vernacular names for plants are used almost exclusively by Gadow. Since so much has been written about the vegetation in a very general way, and almost nothing specifically, rather complete lists of plants collected in July, 1950, are included in the present report.[3]

FIELDS AND FORESTS

Floristic composition of the plant life beyond the margin of the flows, cones, and the playa was investigated only superficially, due to lack of time. If it had been investigated more, there would have been almost no way of determining what lasting influence the ash mantle, which in some cases is still visible at the surface, has had upon the composition of the vegetation. The area now is an anthropogenic mosaic with forested, cultivated, pastured, and abandoned crop lands, the latter growing back to natural vegetation. As far as was observed, the surrounding areas, outside the amphitheatre, have recovered quite fully from the effects of volcanism.

Two possible influences of ash upon vegetation on surrounding hills may be noted. One has to do with floristic composition, and the other with soil fertility.

When Humboldt and his party visited Jorullo in 1803 they found then, as is still the case, one

[3] Acknowledgement is made to the following for identification of plants: Drs. C. V. Morton, Velma Rudd, and J. R. Swallen of the U. S. National Museum identified most of the vascular plants; Mr. A. H. G. Alston of the British Museum identified the Selaginella; Dr. L. J. Gier, William Jewell College, identified the mosses from Jorullo and also those from Parícutin.

species of palm[4] as an important component of the natural vegetation on the lower slopes rising up on three sides of the Jorullo amphitheatre (Gadow 1930). Humboldt was told locally that the palms had greatly increased in abundance during the years after the eruption. Gadow ascribed the reported increase in palms to improved conditions for germination of the seeds.

It was observed in 1950 that between La Guacana, a village about 4 mi to the southwest, and Jorullo, crop plants, mostly maize, grew bigger in soil with some ash than in soil where surface ash had been eroded away. Near La Guacana ash probably did not average more than 1 ft thick, but toward Jorullo it became progressively thicker, to about 3 ft. This ash has become incorporated into a soil which is apparently more fertile than the pre-volcanic material beneath alone.

The Playa

The playas were undoubtedly formed in a manner similar to those at Parícutin Volcano, of water-borne soil, ash, plant parts and other debris carried into temporary lakes, formed when the pre-volcanic drainage was obstructed by lava flows and ash. Hence they had a rather fertile soil from the very beginning (Fig. 6). Plants were reported as established on the playas within a very few years, as they have, more recently, at Parícutin. Humboldt (Gadow 1930) reported Salvia, palms (*Sabal pumos* considered above), and alders (*Alnus jorullensis*), growing on the playas. He also stated that on the western plain, or drier part of the playa, indigo (Indigofera) was under cultivation at that time (1803). Pieschel reported that in 1856 sugar cane was being grown on the playa (Gadow 1930).

It is evident that the playas of Jorullo have been under cultivation, at least intermittently, for about a century and a half, and it would seem to be rather futile to try to suggest now how the volcanism has influenced plant life upon them.

Lava Flows

Following the laying down of flows I and II (Fig. 6) there was a considerable eruption of ash and cinders, much of which was air-borne onto the two flows. These flows are the lowest, altitudinally, and presumably considerable water-borne ash has been deposited on them also. Two main habitats are present in flows I and II, the ash and cinder deposits which fill the depressions, and the lava peaks and ridges which remain uncovered. Conditions appear to be quite similar on the two flows so they will be discussed together. Flows III and IV will be considered separately.

[4] The palm was apparently in the Humboldt collection and was named *Corypha pumos*. Dr. Miriam Bomhard, to whom was sent the material collected in 1950, placed it in the genus *Sabal*. The material was apparently lost after Dr. Bomhard's death and was not identified to species. The name may be *Sabal pumos*.

Flows I and II in 1950

The ash fields cover about 75% of the surface of flow I and about 50% of flow II, except near the cinder cones where ash covers almost all the flow. In general, this ash supported a rather dense growth of a grass (*Bouteloua americana* (L.) Scribn.) and two sedges (*Cyperus tenerrimus* Presl. and *Fimbristylis ciliatifolia* Britton), along with other herbs and a few shrubs and trees. Bouteloua was much more abundant than the sedges and often grew in a pure stand. Less abundant, but forming almost pure stands when present, was an herb, *Tagetes patula* L. which generally grew in the shade of trees. A less common herb was *Martynia annua* L. Shrubs growing in ash included *Cordia curassanica* (Jacq.) R. & S.; *Guardiola mexicana* H. & B.; *Hamelia xorullensis* H.B.K.; and *Vitex mollis* H.B.K. Two lianas were *Cissus rhombifolia* Vahl and *Vitis tiliifolia* H. & B. Occasional trees in ash included *Enterolobium cyclocarpum* (Jacq.) Grieseb.; *Belotia insignis* Baill.; and *Verbesina greenmanii* Urban. Strangler figs, also present, as they were wherever other trees grew, will be considered in more detail later.

Lava outcrops occupied a subordinate part of the total surface of flows I and II and, in turn, plants usually occupied only a small part of the outcrop surface. Nevertheless, the number of species present was greater than in the ash fields. There were at least 7 species of trees, 3 of shrubs, 4 of ferns, plus a scattering of grass and sedges. Most of the plants grew from cracks and crevices, unless the lava was porous enough for roots to penetrate. The most abundant tree species was *Lysiloma acapulcensis* (Kunth.) Benth., followed, in order, by *Bursera jorullensis* (H.B.K.) Engler, and *Haematoxylon brasilleto* Karst. The other 4 species of trees were *Acacia cymbispina* Spr. & Riley; *A. pennatula* (C. & S.) Benth.; *Aralia humilis* Cav. and *Bursera bipinnata* (Moc. & Sesse) Engler. The individual representatives of all these species were small trees. The largest were *Lysiloma acapulcensis* which were about 1 ft in diameter, 4.5 ft from the base. Most of the other trees were 4 to 6 in. in diameter. The shrubs present included *Cordia cylindrostachya* R. & S., *Guardiola*, and *Vitex*.

Ferns on the lava outcrops of these flows were very striking, especially *Notholaena brachypus* (Kunze) J. Smith. This fern grew fully exposed and was able to send its roots into lava which other plants apparently could not. As a result, the surface of some lava outcrops was completely covered by it. Other ferns present, in smaller numbers, were *Cheilanthes angustifolia* H.B.K.; *Dryopteris glandulifera* (Liebm.) C. Chr.; and *D. karwinskyana* (Metl.) Kuntze.

A favorite type of habitat for *Notholaena* appeared to be the numerous small, dome-shaped lava mounds, which may be the hornitos (little ovens or kilns) referred to by early visitors. Humboldt reported that the hornitos were still hot in 1803 (Gadow 1930).

FIG. 7. Jorullo lava flow I. Light colored areas are grass-covered ash; trees are confined mostly to rocky out-crops. July, 1950.

FIG. 8. Jorullo. Flow I in the foreground, II behind it, and the main cone in the distance. The dark left (north) end of the cone is capped with lava, part of flow IV. July, 1950.

Figures 7 and 8 show the character of these flows with their ash fields and lava outcrops.

Reference should be made to the extensive disturbance which the ash-covered parts of these flows have had. Livestock runs at-large over the entire area that is accessible and the myriads of paths criss-crossing these flows indicate that they have been grazed intensively. Also, some of the ash fields have been cultivated. None happened to be in 1950 so it was not possible to learn how fertile the ash is as a soil for crop plants.

FLOW III IN 1950

Lava flow III is composed of rather small aa blocks, and most of the ash which fell upon it has sifted into the spaces between these. Consequently there is little or no habitat similar to the ash fields of flows I and II. Rather, it is almost all exposed lava, with every crack and crevice a potential site for vascular plants. Species of plants on flow III are largely the same as on the two older flows but density of woody plants is much greater because of more habitats suitable for trees and shrubs. Trees are all rather small, and the general aspect is that of a savanna. *Lysiloma acapulcensis* is again the most abundant tree species, followed by *Bursera jorullensis.* Figure 9 illustrates this community.

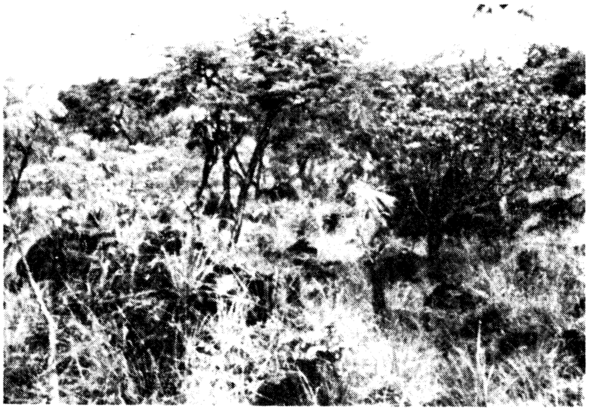

FIG. 9. A part of Jorullo flow III, with trees 10 to 14 ft. tall.

FLOW IV IN 1950

The major part of flow IV is compact, dense aa lava, in which the fragments are larger than those of flow III, and hence the crevices are farther apart. There is also less ash on this flow. Because vascular plants have been able to grow only in crevices and cracks, they are less abundant on this part of flow IV than on flow III, where crevices are more numerous. A part of the northwest side of the main cinder cone is covered with a different type of lava, one that is almost scoriaceous and much less dense and compact than most of flow IV. For this report this lava is considered to be a part of flow IV, although further investigation might indicate that it is a separate one.

The number of kinds of plants growing in the area of dense lava, described above, was small. Two kinds of trees were observed—*Cochlospermum vitifolium* (Willd.) Spring. and *Ficus petiolaris* H.B.K., with few individuals of each. One shrub, *Trema micrantha* (L.) Bl., was present and 5 species of ferns: *Adiantum braunii* Metl., *A. concinnum* H. & B., *Dryopteris glandulifera, Nephrolepis occidentalis* Kunze, and *Polypodium aureum* L.

The scoriaceous lava on the side of the main cone was little broken up, and presented a quite regular surface. There were few cracks and depressions but the lava was porous enough for roots and rhizoids of some plants to penetrate into it. More kinds of plants grew on this lava and there were more individuals per unit area than on the dense lava. The trees present, in order of abundance, were: *Pseudosmodingium perniciosum* (H.B.K.) Engler; *Lysiloma acapulcensis; Bursera sessiliflora* Engler; *B. jorullensis;* and *Cochlospermum vitifolium.* A shrub, *Perymenium verbesinoides?* was present. In no part was tree coverage over 5% of the surface, nor shrub coverage over 1%. Trees were all under 6 in. in diameter near the base.

Non-flowering plants covered much more of the surface of the scoriaceous lava than trees and shrubs. Mosses furnished up to 100% coverage in some places, ferns up to an estimated 90%, and *Selaginella pallescens* (Presl.) Spring., up to about 20%.

Mosses on this lava were all in the genus *Campylopus*, the dominant species being *C. introflexus* (Hedw.) Brid., mixed with a little *C. flexuosus* (Hedw.) Brid. Ferns present were *Adiantum braunii, Cheilanthes angustifolia, Dryopteris glandulifera, D. karwinskyana*, and *Notholaena brachypus*.

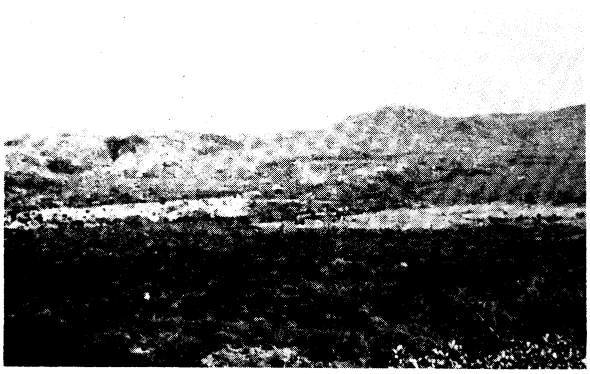

FIG. 10. View northwest, from the side of the main cone of Jorullo. Lava flows III and II; playas, the light colored, level areas; and in the distance, hills rise toward the central Mexico Plateau.

HISTORY OF VEGETATION ON LAVA FLOWS

The historical record of the invasion of the lava flows by plants is very meager and information as to what kinds of plants first invaded is almost completely lacking. The first record of plants on the flows is that of Burkart, who reported that in 1827 the flows with hornitos (the oldest flows) were being reclaimed by vegetation. After his visit of 1846 Schleiden reported that the western half of the flows (flows I and II) had vegetation. He further stated that lava on the main cinder cone (part of flow IV) was still bare (Gadow 1930).

According to the records, plants invaded the oldest flows between 1803, when Humboldt found none, and the year 1827, or between 28 and 52 years after volcanic activity had ceased. There is no record of when plants first invaded the younger flows, but it was later than on flows I and II, according to Schleiden.

In view of the much earlier invasion of flows at Parícutin, by algae, mosses, and ferns, one would think that flow III at Jorullo should have been the first to support plants. It resembles the flows of Parícutin in the nature of its crevices and in the quantity of ash present. However, according to the record, flows I and II were first to support plants. These flows have so much ash upon them that there are no very deep crevices with overhanging rocks to offer shade and protection and plants on them are largely exposed to sun and wind. There is ample ash which roots or rhizoids can penetrate.

The explanation of why flows I and II supported plants before flow III may lie in the relatively low precipitation and high evaporation rate in the region. Algae, mosses, and ferns are early able to grow on and among rocks under the comparatively cool, damp conditions of Parícutin, but apparently were not able to under the drier ones of Jorullo. Instead, at Jorullo, plants started after a much longer time, and presumably after there had been time for some weathering and disintegration of lava and ash.

Some evidence of the limitations of the Jorullo flows as habitats for plant growth was seen in the fact that trees grow biggest at the edges of the flows, for example on flow II but right next to flow III. More favorable water balance is the likely explanation of the larger size of trees in this type of location. Precipitation finds its way into cracks of a lava flow and some water moves right on through, to flow under the lava and emerge again at the edge of the flow.

CINDER CONES

MAIN CINDER CONE IN 1950

Surface material over at least 75% of the largest cone (flows cover the rest) consists of unconsolidated ejecta which vary in texture from fine ash to coarse cinders up to several inches in diameter. Fine material is adequate in most parts so roots of plants have no difficulty in penerating the substrate. Most of the surface was covered with vegetation in 1950, the dominant plants being small trees, in a number of different species. There were also some shrubs, and a number of kinds of non-woody plants. Surface material has been fixed in place wherever there is a cover of plants, but where the angle of slope is especially steep cinder slides are common and vegetation has failed to become established.

Surface material in the slide areas still retains its original black or red color but elsewhere, under a cover of vegetation, the surface tends to take on a gray color, to a depth of 2 to 3 in. This gray color is apparently due to more rapid weathering under the vegetation.

There is no striking altitudinal zonation of vegetation on the cone except that pine is confined to its upper third.

Thirteen species of trees were found on the cone in 1950. Two were most abundant and widely distributed. The first of these was *Lysiloma acapulcensis*, which was also the most abundant tree on the flows. On the cone, trees of this species grew larger, some up to about 24 in. in diameter near the ground. Also common and widespread was a small tree, *Verbesina greenmanii*.

Three other small trees, widespread but not common, were *Vitex mollis, Byrsonima crassifolia* (L.) DC., and *Pseudosmodingium perniciosum*. The last named was more abundant near the base than higher up.

Four species of trees were restricted to the upper part of the cone. Most important of these was *Pinus michoacana* Martinez, of which there were perhaps 100 trees. None was over about 18 in. in diameter near the ground and no seedlings nor very small trees were found. A second species of pine was represented by only a few individuals of *Pinus teocote* S. & C. *Pinus teocote*, but not *P. michoacana*, was growing near Parícutin. A few individuals of *Lysiloma divaricata* (Jacq.) Macbr. were confined to the upper part of the cone. Two trees of *Clethra lanata* Mart. & Gal., each about 10 in. in diameter near the ground, were growing in the bottom of the shallow crater.

Four other species of trees represented by only occasional, small individuals include *Desmanthodium fruticosum* Greenm. and *Gyrocarpus americanus* Jacq.; *Ficus lopathifolia* (Liebm.) Miq., growing as a strangler on other trees; and *Sabal pumos*, with only one or two individuals present.

The most abundant shrub on the large cinder cone was *Guardiola mexicana*. This was quite common on the lava flows also. Next in abundance was *Trema micrantha*. A third shrub, much less common and not seen on the lava flows, was *Rauwolfia heterophylla* Roem. & Schult.

Cyperus tenerrimus was common on the main cone, as was *Commelina elegans* H.B.K.

Eight species of ferns were found on this cone. The greatest concentration of ferns was near the summit, but they grew in limited numbers over the whole cone. The eight are *Adiantum shepherdii* Hook, *Aneimia pastinacaria* Moritz., *Cheilanthes angustifolia*, *Conigramme americana* Maxon., *Dryopteris karwinskyana*, *Pellaea seemanii* Hook?, *P. skinneri* Hook?, and *Polypodium aureum*.

OTHER CONES IN 1950

The single cone north of main Jorullo, and the two south of it, give evidence of more disturbance by man and his animals than does the big cone. This is to be expected since they are low and easily accessible. Volcancito del Sur was being overrun by dozens of goats in the summer of 1950 and there was not an edible leaf nor herbaceaus plant left within reach of the animals. Enmedio looked as though parts of it had been cultivated some time in the past.

Some species of plants not found elsewhere were seen on these cones. The only plants of guava (*Psidium guajava* L.), in the whole volcanic area, were growing on Enmedio. A vine, *Cissus rhombifolia* Vahl, and two herbaceous species, *Bletia fulgens* Reichb., and *Castilleja communis* Benth., were on Enmedio. The most abundant tree was *Bursera sessiliflora*.

A small tree, *Poeppigia procera* Presl, was found on Volcancito del Sur, and not elsewhere. By far the most abundant tree on del Sur was *Pseudosmodingium perniciosum*, probably because goats had destroyed almost everything else but did not eat this plant.

HISTORY OF VEGETATION ON CINDER CONES

The first recorded date for plant life on the main cone of Jorullo is 1789, 14 yrs after volcanic activity ceased. In that year a party, including Governor Antonio de Riaño of Michóacán and a German mining expert, Franz Fischer, climbed the cone in the month of March. Gadow (1930) translated part of Riaño's report; some of it is quoted here. "The whole hill of the volcano is bare and has only here and there some small trees, locally called Ortiga silvestre. . . . The hill is further covered with some patches of so-called Zacate. . . ." Zacate is a grass. Riaño commented on how easily the small trees and clumps of grass were uprooted and he evidently was as much interested in plants as aids to climbing as in the fact that plants were able to grow on volcanic cinders and ash. He could very well have overlooked any less conspicuous plants which might have been present.

Schleiden, after climbing the main cone in 1846, wrote (transl. by Gadow in 1930), ". . . the sandy slope of the main cone and the malpais show already considerable growth. Some kind of Mimosa, not very high, and Guayava trees, . . . , are the most important; a pine near the summit seems to me the most interesting of the members of this vegetation." It is not possible to tell if Schleiden found both "Mimosa" and Guayava on the malpais and cinder cone, or only on the latter.

Pieschel visited Jorullo in January, 1855, and climbed the main cone from the east side. His party found vegetation sufficient in amount so that they ". . . were much assisted (in climbing) by numerous little trees, shrubs, and grass." He says two kinds of shrubs, three kinds of small trees, and maguey (*Agave*) comprised most of the vegetation (Gadow 1930). Vernacular names only are used for the trees and shrubs. His reference to red-peeling bark on one kind of tree suggests it was probably *Bursera sessiliflora;* and reference to large yellow flowers on another suggests *Hamelia xorullensis*. These are still present. A thorny shrub he refers to probably was one of the numerous leguminous species still growing in this region. Pieschel points out that the ground was still warm and soft, just below the rim of the crater. Volcancito del Norte he described as a conical hill of ashes, and made no reference to plants on it.

In an account of a visit to Jorullo in 1883, Leclercq refers particularly to guayabas (guavas) on top of the main cone (Gadow 1930).

Gadow concluded, from his survey of historical records, that plants had practically regained the ground lost by volcanism in 90 years, by about 1865. That statement cannot be accepted literally, for obviously vegetation was sparse then, as it is even now, on much of the lava surface, nor were the cinder cones completely covered with vegetation. There is not complete coverage today. There is indication that the surface layer of the cinder cones is developing into a soil but it is not now, after almost two centuries, equal to the pre-volcanic soil. (A combination of old soil and ash is believed to be superior to either alone.) The exposed lava is still little weathered and many centuries more will elapse before it becomes soil.

Three main aspects of change in the composition of vegetation on the main cinder cone during its lifetime are recognizable. First of these is the gradual increase in the total number of individuals. This is what would be expected and the historical evidence bears it out. A second aspect of the changing vegetation is that parts of the upper cone were apparently little, or not at all, vegetated until after 1856. This conclusion is based on indirect evidence. A third aspect of change is that of change in floristic composition. The second and third aspects will be discussed.

Schleiden noted that there were about 40 gas and steam vents still active on the rim of the main crater of Jorullo when he climbed it in the year 1846. Pieschel found the ground still warm and soft just below the ring of the crater in 1855 (Gadow 1930). These two undoubtedly had reference to the same place. The south rim of the volcano was impressive in 1950 because it gave every appearance of having been a place where solfataras were active more recently than elsewhere, and it had the richest fern flora of any part of the cone. It adjoined the scoriaceous flow mentioned earlier and some Selaginella was spreading onto it from the flow. It is believed that plants did not invade the south rim area successfully until after the substrate had cooled, after 1855. Then ferns and Selaginella invaded in numbers. Seed plants are still almost completely absent.

The third aspect of change in plant life on the main cone has to do with apparent reduction in the numbers of certain species. Guava, or guayaba (*Psidium*) was reported present on the main cone by Schleiden, 1846, Leclercq 1886, and Ordoñez 1907 (Gadow 1930). Gadow did not report it and none was found on the main cone in 1950. How many plants there may have been on the cone at one time or why they disappeared is not known. Perhaps they were crowded out as other and larger woody plants increased; or, possibly they were dug up by some nearby farmer who tranplanted them to a more convenient site.

The number of pine trees on the cone decreased considerably between 1909 and 1950. Gadow (1930) referred to hundreds of pine trees, which he saw in 1909. The estimated number in 1950 was not much over a hundred. Almost complete absence of young trees indicated that pine is not reproducing enough to maintain itself. The trees present were scattered and angiosperms filled in the places between them. Pine seedlings at Parícutin (Eggler 1948) have more chance for survival in open areas and do not compete well with angiosperm trees and shrubs. What happened to the trees at Jorullo which disappeared between 1909 and 1950 can only be conjectured. Some probably died of natural causes, but very likely most were cut for timber.

Oak is another tree reported by Gadow (1930) on the main cone but not found in 1950. He referred to encina and roble, both of which may mean oak (Spanish), but gave no species. Oak would be expected to reproduce satisfactorily under the conditions on the cone. Failure to survive would suggest that there were only a few trees and that these were cut by local residents.

FAMILIES OF PLANTS REPRESENTED AT JORULLO

Three families, Leguminosae, Moraceae, and Burseraceae, supply a majority of the most conspicuous plants, the trees, which have invaded volcanic deposits at Jorullo. There are 7 species of leguminous trees in 4 genera, and 2 species of shrubs. Capacity to carry on a symbiotic existence with nitrogen fixing bacteria would certainly favor the growth of legumes in soil with a low nitrogen content. However, non-legumes apparently were established just as early as legumes and it must be concluded that there was some available nitrogen in the ash when both groups first invaded. The family with the second largest number of tree species present is Moraceae, with 6 species, all in the genus *Ficus*. The number of individuals of Ficus is probably less than a tenth the number of legumes present. Most of the fig plants observed were stranglers. It is believed all the species present can grow as stranglers and most of the individuals were. A few, still small, were found growing in rock crevices. No obvious preference for a particular kind of tree to grow on, to strangle, was apparent. The third family has 3 species, all in the genus Bursera.

The Compositae and Pinaceae each contribute two species of trees. There are also two species of shrubs and two of herbs supplied by the Compositae. Ten families each contribute one species of tree—Anacardiaceae, Araliaceae, Clethraceae, Cochlospermaceae, Hernandiaceae, Malpighiaceae, Palmaceae, Rubiaceae, Tiliaceae, and Verbenaceae. The Vitaceae are represented by two species of woody vines.

Two species of shrubs present are in the family Boraginaceae. Apocynaceae, Myrtaceae, Sapindaceae, and Ulmaceae contribute one each. Two shrubby plants growing as parasites on leguminous trees are *Phoradendron piperoides* (H.B.K.) Tral., and *Psittacanthus calyculatus* (DC.) G. Don., both in the Loranthaceae.

Six families of Angiosperms are represented by herbs only. Cyperaceae has two species present, and the other five families have one species each: Commelinaceae, Gramineae, Myrtynaceae, Orchidaceae, and Scrophulariaceae. The paucity of kinds of grasses is remarkable. Overgrazing may be responsible for keeping the grass population down.

Thirteen species of ferns—eleven in the family Polypodiaceae and one in the Schizaeaceae—are present. One species in the family Selaginaceae, and two species of mosses in the family Dicranaceae, complete the list of plant families found in 1950.

SUCCESSION ON VOLCANIC MATERIALS

After the somewhat detailed discussion of Parícutin and Jorullo we may now return to the four questions which were posed in the first part of this paper. Partial answers to the questions have been given in the discussion of the two Mexican volcanoes. That information will be summarized. In addition, pertinent facts about several other volcanoes will be used. There are many more questions which need to be asked and answered, but these four are those which seem to head the list.

1. How quickly does vegetation become established?

Establishment of at least a few plants has taken place within a very few years on all accumulations of volcanic material for which there is any kind of authoritative record. But these pioneers may be limited to only the most favorable sites, especially in regard to moisture, and coverage of the whole deposit so it approaches something like the pre-volcanic condition may require centuries, even under the most favorable climatic conditions.

Lichens, algae, and mosses were present on aa lava flows from Parícutin Volcano after only 3 yrs; ferns came in 1 yr later. Pioneer seed plants were found on the rim of the main cinder cone 5 yrs after activity ceased. However, the plants of the flows occupied only a very small part of the total flow area, and after 7.5 yrs no plants whatever were growing on the sides of the large cinder cone, nor in fields of deep ash.

At Jorullo small trees and shrubs appeared on the cinder cones in 14 yrs, and vascular plants were reported to have started on the lava flows somewhere between 28 and 52 yrs after activity ceased.

On the ash fields of Katmai, in Alaska, a carpet of liverworts was established in 18 yrs (Griggs 1933). The climate in this part of Alaska is quite moist. Precipitation is approximately 60 in./yr; skies are usually cloudy and humidity is high.

Sköttsberg (1941) described plant life on young lava flows on the island of Hawaii. On pahoehoe flows, located in a part of the island where precipitation was about 24 in./yr, ferns and seedlings of flowering plants were beginning in cracks and pits after 6 yrs. After 18 yrs they were more numerous. Where precipitation was 40 in./yr the invasion pattern was similar. On aa lava flows vascular plants were slower in getting started, but a lichen, Stereocaulon, was abundant enough to change the color of the surface of the flow.

The island of Krakatao has been the subject of several reports, since its mighly eruption in 1883. But it has become a very controversial issue. Backer (1929) has contended that the record from this island is biologically valueless because it was never established that all life was destroyed at the time of the eruption. But even if all life was not destroyed certainly new volcanic deposits were sterile and something can be learned from noting invasion onto them. Ernst (1908) reported that pumice and volcanic ash supported growths of blue-green algae by 1886, that is, in 3 yrs. He also reported the presence of ferns and seed plants in the same length of time but the record is not clear if these were on pure ash or on material with old soil mixed in. Precipitation on Krakatao is about 100 in./yr.

Robyns (1932) reported that in lava flows from Rumoka, in the Belgian Congo, ferns and over twenty kinds of seed plants had started to grow in crevices in from 13 to 18 yrs. This is in an area with low precipitation, about 15 in./yr.

These instances show time for pioneers to invade but indicate nothing about total time needed for complete coverage by vegetation. The quantity of vegetation on the main cinder cone of Jorullo approaches that on old surrounding hills, but does not quite equal it in density and size. It has had 175 yrs to reach its present status. Presumably if precipitation were greater weathering would be more rapid and soil would be deeper and vegetation taller and denser. In the Craters of the Moon area, Eggler (1941) found that level ash fields and south-facing slopes of cinder cones are often very sparsely vegetated, even after many centuries. North-facing slopes often support post-climax forest. Precipitation is about 10 in./yr.

Where lava flows are situated so that no waterborne sediments can be deposited upon them, but only wind-carried materials and the products of weathering contribute to soil formation, several centuries are apparently required to attain pre-volcanic conditions. At Jorullo the youngest, and altitudinally highest, flows have very sparse plant growth. At Craters of the Moon (Eggler 1941) both pahoehoe and aa flows may have very little plant life upon them, and that little is confined to crevices on pahoehoe, and behind protective blocks of lava an aa. On Krakatao, with its ample rainfall, it has been reported (Ernst 1908) that lava flows dating back to an eruption of 1680 were only slightly weathered and were covered with very sparse vegetation just prior to the eruption of 1883. Slightly over 200 yrs was insufficient time for lava to weather to a soil.

2. From how far away may disseminules be carried?

All volcanic eruptions of historic record which are known to this writer have been rather small, in terms of area; all life has been destroyed in a space of not more than a few square miles. Hence, the distance from pre-eruption life has usually not been more than a few miles. At both Parícutin and Jorullo disseminules were available at distances not exceeding 4 to 5 mi. No distances were given for Katmai, as far as is known, but presumably they were no greater than for the two Mexican volcanoes. The possible exception has been Krakatao. If all life was destroyed on the island, and it is doubtful if that actually happened, disseminules could have come by air, by water currents, and by birds. The nearest island not destroyed by the eruption, Sibesia, is between 11 and 12 mi away.

3 What kinds of plants pioneer?

There appears to be no one taxonomic nor ecologic group which is best fitted to pioneer on volcanic deposits. Particular types may succeed better than others under certain conditions, as in particular situations on particular flows or cinder areas. But these differ with the area.

At Paricutin, pioneers present on aa flows consisted of lichens, algae, mosses, and ferns. Flowering plants and lichens were just getting started on the crater rim. At Jorullo pioneers were seed plants, mosses, ferns, and club-mosses. At Katmai (Griggs 1933) liverworts grew on ash in pure stands, and were followed by mosses and willows. At Craters of the Moon seed plants were the chief pioneers, but there were a few ferns in crevices and some lichens on rock surfaces (Eggler 1941). Blue-green algae were pioneers on pumice and ash of Krakatao, and were joined by diatoms and bacteria (Ernst 1908). On aa flows of Hawaii, lichens were very common, with seed plants being less important. On pahoehoe flows seed plants were more important than lichens (Sköttsberg 1941).

4. Are the pioneers capable of fixing nitrogen?

There appear to be three possible sources of fixed nitrogen for pioneer plants growing on volcanic materials. In some instances the lava or ash itself may contain fixed nitrogen, notably in the form of ammonium chloride. Whether this could be a part of the rock as it cooled from a magma, or is always concentrated from gases escaping from solfatara or fumarole is not known. A second source of fixed nitrogen is from debris carried by wind, water, or other agent. Finally, the pioneer plants may fix their own nitrogen.

It is probable that many blue-green algae can fix nitrogen, and their presence as pioneers on the flows at Paricutin, and on pumice and ash at Krakatao, suggests that their success may be due to this property. Griggs & Ready (1934) were able to grow liverworts collected from the ash fields of Katmai on a medium so low in combined nitrogen that it would not support ordinary plants. This strongly suggests that the liverworts had the ability to fix nitrogen. The success of so many legumes, as earlier reported, on the lava flows of Jorullo may be due, in part, to a symbiotic relationship with root nodule bacteria.

However, only a small part of the total area of the places considered has been populated by these possible fixers of nitrogen, and it must be concluded that either, or both, of the other two sources of nitrogen has been of greater importance in the nutrition of pioneer plants.

SUMMARY

Lava and ash from Parícutin Volcano, Mexico, which was active between 1943 and 1952, destroyed all plant life in an area of approximately 20 sq mi, and part of it on a larger area of about 100 sq mi. Up to the summer of 1945, at the time of a first visit, the effects of volcanic activity were all destructive. In 1950, when the author made a second visit, it was found that both the area of complete destruction, and that of partial destruction, had increased in size. But during the intervening 5 yrs new vegetation had started to invade the lava and ash deposits.

Plants were becoming established in several types of situations. Beneath trees, shrubs, and herbs, which had survived in ash, seedlings of numerous kinds of plants were getting started; away from the influences of living plants there were no seedlings. Old soil, exposed where ash deposits were eroded away, quickly became populated with a cover of herbs and shrubs. Playas, located generally at the edges of the lava flows, supported many plants.

In addition to secondary succession, primary succession had also begun by 1950. Crustose lichens were growing on the surfaces of lava blocks of aa flows; and at least 1 species of blue-green alga, 1 moss, and 3 ferns, were growing in depressions in flows 3 to 7 yrs old.

In 1957 two kinds of vascular plants, Gnaphalium and Eryngium, were growing on the rim of the cinder cone. Fumarolic gases kept the lapilli, in which they were growing, moist and probably supplied ammonium chloride.

It is thought that ammonium chloride, which escapes from solfataras and fumaroles, in the flows as well as in the cone, is an important source of nitrogen for plants. There is also a strong possibility that blue-green algae may fix some nitrogen.

No primary succession was taking place in ash-covered fields around Parícutin, in 1950. Nitrogen deficiency is believed to be one limiting factor. Several kinds of garden seeds were planted. The results were poor, and all the plants showed strong nitrogen deficiency symptoms, as did also rye grown in ash in pyrex containers.

Failure of natural vegetation to return to old, abandoned fields, where ash was from 1 to 4 or 5 in. deep, indicated that the ash layer has had an inhibiting effect.

Jorullo Volcano, which was active from 1759 to 1775, had an eruptive history quite similar to that of Parícutin. Rainfall is less at Jorullo, and it has a semitropical climate, instead of temperate. From the historical record, and observations in 1950, it has been possible to work out a general story of invasion of vegetation onto the volcanic deposits from Jorullo.

In 1803, when the Humboldt party visited the volcano, the playas were populated with Salvias, palms (*Sabal*), and alders. Hillsides rising from the Jorullo basin had more palms on them than there were before volcanism occurred. The layer of ash on old soil seemed to favor the palms. Vegetation invaded the two oldest lava flows, which have considerable ash upon them, between 1803 and 1827. The two youngest flows, with little ash, were vegetated more slowly.

In 1950 the plant growth occupying the ash-field areas on the two oldest flows included 4 kinds of herbs, 4 of shrubs, 2 lianas, and scattered trees. The lava outcrops of these flows supported many more kinds of trees and shrubs, plus 4 kinds of ferns. In 1950 the general aspect of the two youngest flows was that of a savanna. Trees were small and scattered, and ferns and other small plants grew from crevices. In places, where the lava was porous, mosses, ferns, and Selaginella, formed dense growths on the surface.

The first recorded date (1789) when plants were observed on the main cone of Jorulla was 14 yrs after activity ceased. Small trees and a grass were noted. By 1846 there were mimosas, guayavas, and a pine tree; in 1855 two kinds of shrubs and three of trees were noted. In 1950 the vegetation on the main cone included 13 species of trees, 3 of shrubs, and 8 of ferns. One or more kinds of oaks, and guava (*Psidium*), which were reported present earlier in the century, were missing in 1950.

In seeking answers to certain basic questions having to do with invasion of vegetation onto volcanic material, it is possible to obtain help from the histories of other volcanoes, as well as Jorullo and Parícutin. The questions posed are four in number.

How quickly does vegetation become established? At Parícutin lichens, algae, and mosses were invading flows in 3 yrs; ferns came a year later. Angiosperms were on the cinder cone in 5 yrs. At Jorullo trees and shrubs were on the main cone in 14 yrs, and vascular plants were on lava flows in from 28 to 52 yrs. At Katmai liverworts formed a carpet of growth in 18 yrs. On Hawaiian flows ferns and flowering plants were appearing after 6 yrs. On Krakatao blue-green algae were present on ash after 3 yrs. Lava flows from Rumoka supported ferns and several kinds of seed plants in from 13 to 18 yrs. Even under optimum conditions, with high rainfall and temperatures, lava is only slightly weathered after 200 yrs; under arid conditions lava flows have not become soil, even after thousands of years.

How far are disseminules transported? At Parícutin and Jorullo sources of disseminules were known to be available at distances not to exceed 4 to 5 mi. A source of disseminules at Krakatao was an island 12 mi. away.

What kinds of plants pioneer? Local conditions determine which kinds of plants can succeed as pioneers, and algae, mosses, lichens, liverworts, ferns, shrubs, or trees may serve as pioneers under certain circumstances.

Are pioneers capable of fixing nitrogen? Probably some can. There is a strong possibility that blue-green algae and liverworts can fix nitrogen, when they are pioneers on sterile volcanic material. At Jorulla the family Leguminosae supplied the largest number of kinds and individuals of woody plants. A symbiotic relationship with nitrogen-fixing bacteria would be a distinct advantage for plants growing in lava or ash.

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