FIELDIANA: BOTANY

A Continuation of the

BOTANICAL SERIES

of

FIELD MUSEUM OF NATURAL HISTORY

VOLUME 31

FIELD MUSEUM OF NATURAL HISTORY
CHICAGO, U. S. A.

TABLE OF CONTENTS

FLORA, TEHUACAN VALLEY

C. EARLE SMITH, JR.

FIELDIANA: BOTANY
VOLUME 31, NUMBER 4
Published by
CHICAGO NATURAL HISTORY MUSEUM
FEBRUARY 26, 1965

FLORA, TEHUACÁN VALLEY

C. EARLE SMITH, JR.
Associate Curator, Vascular Plants

FIELDIANA: BOTANY
VOLUME 31, NUMBER 4
Published by
CHICAGO NATURAL HISTORY MUSEUM
FEBRUARY 26, 1965

Library of Congress Catalog Card Number: 65–18866

PRINTED IN THE UNITED STATES OF AMERICA
BY CHICAGO NATURAL HISTORY MUSEUM PRESS

CONTENTS

LIST OF ILLUSTRATIONS

TABLES

Flora, Tehuacán Valley

Geography and topography

The Tehuacán valley lies about 150 km. southeast of Mexico, D.F., in the southeastern corner of Puebla. It extends into the northern edge of Oaxaca. The Mexico–Veracruz highway follows the gentle slope of the valley from Tlacotepec in the northwest to Puerto del Aire at the top of the Sierra Madre Oriental on the northeast. The valley is about 170 km. long by 40 km. wide. It is bounded on the northeast by the ridges of the Sierra Madre Oriental, or Sierra de Zongolica, which separate the states of Vera Cruz and Puebla. To the southwest, the valley is rimmed by the lower masses of the Sierra de Zapotitlán. The northernmost areas of the valley are higher in elevation, the land falling away in a series of giant steps to the south. The area is drained by the Río Salado and Río Grande, which join to form part of the Papaloapan drainage.

The collections on which this paper is based were made while I was co-operating in a study of botanical fragments recovered in connection with archeological investigation of caves in the valley area. The plant collections reported here will serve as vouchers against which the recovered material will be identified. The archeological and the botanical work are being carried out under the auspices of the Proyecto Arqueológico-Botánico "Tehuacán" of the R. S. Peabody Foundation with grant funds made available by the National Science Foundation and the Rockefeller Foundation. Richard S. MacNeish of the National Museum of Canada, Human History Branch, is Director of the Tehuacán project.

Climate

The climate of the Tehuacán valley is largely controlled by the mass of the Sierra de Zongolica rising to the northeast between the valley and the Gulf of Mexico. The valley floor, lying at about 1500 m. elevation at Tehuacán, drops off to about 650 m. elevation at Tecomovaca, Oaxaca, but the mountains along the side of the

valley rise to elevations in excess of 3000 m. The mountains effectively remove much of the moisture from the trade winds blowing in from the sea. The average annual rainfall in the Tehuacán area is 478 mm. (see fig. 43); monthly averages range from 2 mm. in January to 119 mm. in September with the greatest portion of the precipitation occurring from June to September (Contreras, 1942). This climate is classed as dry.

FIG. 26. Tehuacán valley seen from the village of Apala in the region of oak-pine forest, where it is relatively level with a few low hills. Beyond can be seen the rugged masses of the Sierra de Zapotitlán along the western side of the valley.

At the opposite end of the valley at Cuicatlán, Oaxaca, the rainfall is less. Cuicatlán has an annual average rainfall of only 301 mm., with the heaviest precipitation in June and the lightest in January and February, when the rainfall is so slight that it is normally not measurable. Here the climate is classed as very dry. No other records are available for the Tehuacán valley, but it is evident that the precipitation pattern over the valley is far from uniform. Many local areas receive considerably less rainfall than the annual average

recorded at Tehuacán. This contrasts markedly with stations in Vera Cruz, like Orizaba, which reports an annual average rainfall of 2116 mm.

Description of the vegetation[1]

The vegetation of the valley below the 1800 m. level can best be described as thorn-scrub and cactus. Undisturbed vegetation above this elevation is oak-pine forest. Where the ridge is sufficiently high and exposed so that it is almost constantly wet, a true montane rainforest develops.

An excellent description of the vegetation of the Papaloapan drainage area, of which the Tehuacán valley forms a part, is given by Faustino Miranda (1948) and provides an extended background for the hypotheses presented later in this paper.

Montane rainforest

The vegetation of the montane rainforest at the top of the Sierra de Zongolica is a continuous cover, with crown heights of 15 to 20 m. Seen from above, it looks remarkably smooth with few overtopping trees, unlike the canopy of lowland rainforest. Within the forest, the boles of the trees of the upper story are free of limbs for 6 to 10 m. Except where the forest cover is broken by steep barrancas, the understory is limited to scattered individual trees. As the margin of the forest along the barrancas is approached, an understory of medium-sized tree species appears and the forest floor is closely covered with a shrub cover. The vegetation in the barrancas is an almost impassable tangle of large shrubs, small trees and tree ferns. In the high-canopy forest, lianas climb into the tree tops and epiphytic vegetation is plentiful on the upper parts of the boles and along the branches.

Collections in the rainforest were limited since rainforest vegetation does not appear among the plant fragments recovered during the archeological operations in the valley. Of the canopy trees, only *Prunus barbata* Koehne was collected, as there was insufficient time to fell trees or use climbing apparatus. The occasional understory trees include *Clethra mexicana* DC. with its crown nearly covered with white flowers, *Ternstroemia tepezapote* S. & C., the most abundant small tree, with glossy dark green foliage, and *Rapanea jurgensii* Mez., with twigs closely covered with purple fruit. In the barrancas,

[1] See also: Smith, *Agriculture in the Tehuacan Valley*, Fieldiana: Botany, Vol. 31, No. 3.

FIG. 27. Beneath the canopy, the soil surface is never closely covered with herbaceous species but the open canopy allows copious development of straggling shrubs, many of which are spiny.

two kinds of tree ferns, *Alsophila bicrenata* (Liebman) Fourn. and *A. schiediana* Presl, which may grow to be 3 m. tall, spread their light green umbrellas of feathery fronds. The long fronds of *Hypolepis repens* (L.) Presl appeared from the top to be tree ferns, but they develop no trunk and the fronds rise directly from a horizontal rhizome at the surface of the soil. In the barranca, *Bouvardia macilenta* Blake, which is capped with light yellow flowers, grows to 2 m. in height. Occasionally, *Centropogon grandidentatus* (Schlecht.) Zahlbr. straggles among the other shrubs, where its few orange flowers are conspicuous. Two other conspicuous straggling plants among the shrubs were *Cestrum fasciculatum* (Schlecht.) Miers, whose large,

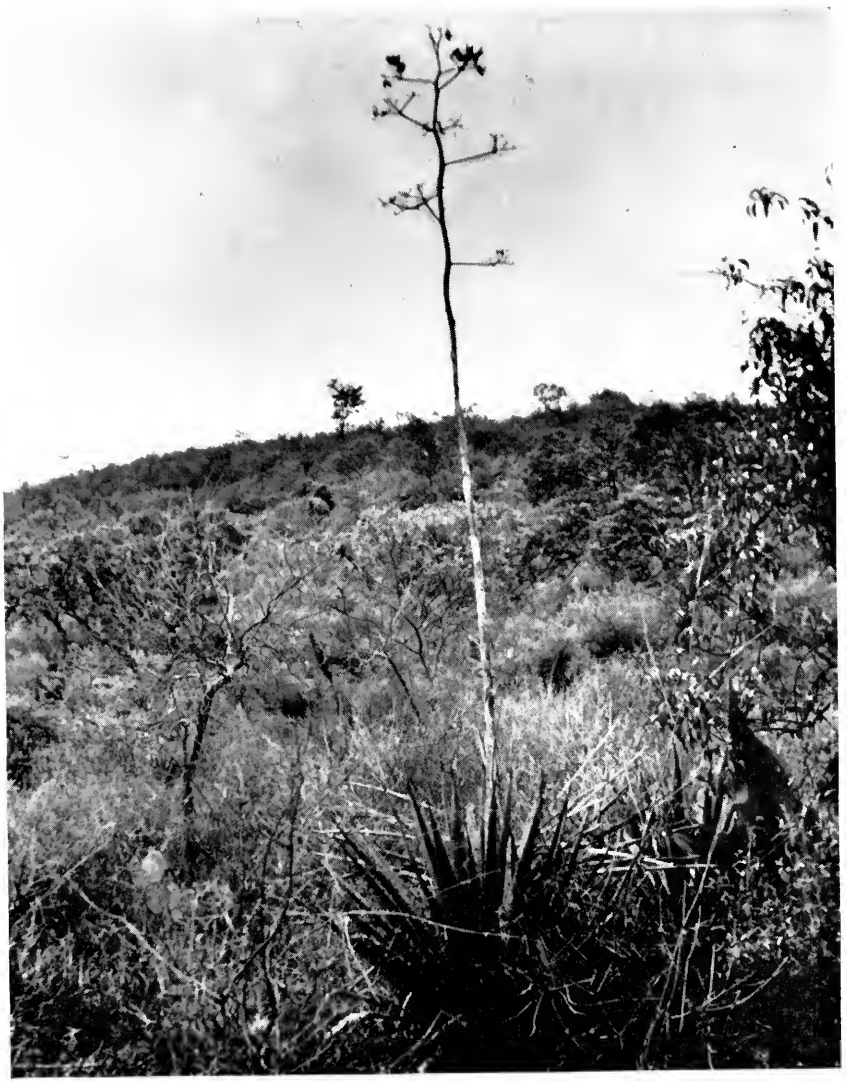

FIG. 28. In drier areas the trees are scattered and the shrub vegetation forms a nearly continuous cover. In the foreground is lechuguilla (*Agave karwinskii* Zucc.) from which a fiber is obtained. To the right can be seen the leaves of *Ipomoea walcottiana* Rose.

light red flowers are strangely different from those of the commonly cultivated Cestrums, and *Phytolacca rugosa* Br. & Bouche, which straggles lazily to a length of 5 m. or more. Where the forest is opened along the road, *Mikania cordifolia* (L. f.) Willd. is festooned with white flowers, and *Tibouchina schiediana* (L. & C.) Cogn. with its bright magenta flowers provides contrast. In these open borders, *Miconia* spp. were fruiting heavily. At one place, a stand of *Fuchsia microphylla* HBK. with its small, bright green leaves and tiny, hanging, shining red flowers made a spectacular contrast. Frequently these exposed shrubs are intertwined with vines among which are an *Exogonium* sp. and *Phaseolus coccineus* L. with scarlet flowers. Under the high canopy, the stand of shrubby *Ardisia liebmannii* Oerst. persists only near the margin. Occasionally scattered plants of *Asplenium sessilifolium* Desv. grow in the soil and the somber darkness is sometimes startingly broken by the bright red plants of *Monotropa coccinea* Zucc. Near the margin, *Passiflora adenopoda* DC. hangs its cream and purple flowers among the shrubs and up into the trees. The only identifiable liana recovered was *Smilax aristolochiaefolia* Mill. The remainder either broke before their tops pulled out of the canopy or were too firmly fastened to come down. Mixed among the epiphytes on the boles of the trees were *Polypodium lowei* C. Chr., *Peperomia deppeana* S. & C., *Peperomia reflexa* (L. f.) A. Dietr., *Isochilus linearis* (Jacq.) R. Br., with its small, purple flowers and grasslike foliage, and the very rare *Odontoglossum ehrenbergii* Link, Kl. & Otto, with its pink or white flowers splashed with chocolate brown.

Oak-pine forest

The oak-pine forest at the lower elevations on the western slopes of the Sierra (down to about 1800 m.) is far different in appearance from the rainforest above. Near the upper edge where some of the species of the rainforest intermingle with those of the oak-pine forest, the rainfall is still sufficiently high to maintain a heavy epiphyte population. The canopy is more broken and the increased light allows a much greater development of shrubbery through which one must push. Farther down in the zone of less rainfall, the under canopy of medium-sized trees is entirely eliminated, while the shrub growth is more of an annoyance. Here the forest may be nearly pure stands of either oak or pine or mixtures in any proportion. Local variation appears to be closely linked to subsurface drainage, as little difference in the soil is evident. When a closed cover of

FIG. 29. Beneath the canopy of oak-pine forest, the rough bark of the oak trees is frequently covered by epiphytic lichens, but the leaf litter, herbaceous plants and scattered shrubs are reminiscent of temperate North American hardwood forests. Where the soil is less well drained, as in this forest, oak trees predominate; pine is mixed with oak in better drained areas and becomes a dominant in nearly pure stands on well-drained slopes and knolls.

oak is found, the forest looks like temperate zone forests in little-disturbed moist valley areas of New York or Pennsylvania. The rough bark of the trees supports a fine epiphytic population in the canopy, however. The ground cover is of low shrubs of the family Ericaceae or herbs of many genera familiar in temperate zone woods. When the pine is predominant, the canopy is more open and the ground cover is thicker, with a lower percentage of Ericaceae, but grasses and sedges are more marked among the herbaceous plants. Here the maximum height of the canopy probably seldom exceeds 20 m. and heights of 12 to 18 m. are more common.

Canopy trees in this forest are much easier to collect. Around and above Apala near Coxcatlán, the most common oaks are *Quercus brachystachya* Benth. and *Q. obtusata* H. & B. The pines include *Pinus hartwegii* Lindl. and *P. pseudostrobus* Lindl. var. *apulcensis* Mart. In some places, the ericaceous tree *Arbutus xalapensis* HBK. is conspicuous, with smooth, cinnamon-colored bark and clusters of orange to red fruit.

In openings and around the forest margin, ericaceous shrubs are common. Among the shrubs in the openings are *Vaccinium confertum* HBK., with shining black fruit, *Pernettya mexicana* Camp and *Arctostaphylos conzattii* Fern. On the forest floor, *Gaultheria parvifolia* Small and *Arctostaphylos pungens* HBK. occur where the canopy is relatively open. Sometimes *Geranium schiedianium* Schlecht., bearing magenta flowers, is conspicuous. *Erigeron karwinskyanus* DC. is one of the most common composites in the area, forming shrubs up to 0.75 m. tall. Around the edges of occasional abandoned milpas *Muhlenbergia versicolor* Swallen and *Stipa ichu* (R. & P.) Kunth form a nearly continuous cover broken only occasionally by the deep pink flowers of *Oenothera multicaulis* R. & P. and the scarlet flowers of *Bouvardia ternifolia* (Cav.) Schlecht.

The forest cover may be nearly solid pine or oak trees depending upon local conditions. Where man or grazing animals have caused little disturbance, the species composition of the associations is probably undisturbed. Thus, in the more open woods with a moist oak litter, *Pinguicula* sp., with brilliant royal purple flowers, is abundant; where the floor is drier and the litter is lacking, thickets of *Lyonia squamulosa* M. & G. will occur and the bare soil areas may have local carpets of *Sedum muscoideum* Rose or *Arenaria lycopodioides* Willd., the former with yellow flowers and the latter with white. When the oak canopy is heavy and the forest moist, the herbaceous plants may vary from *Dahlia scapigera* (A. Dietr.) L. & O. var. *australis* Sherff,

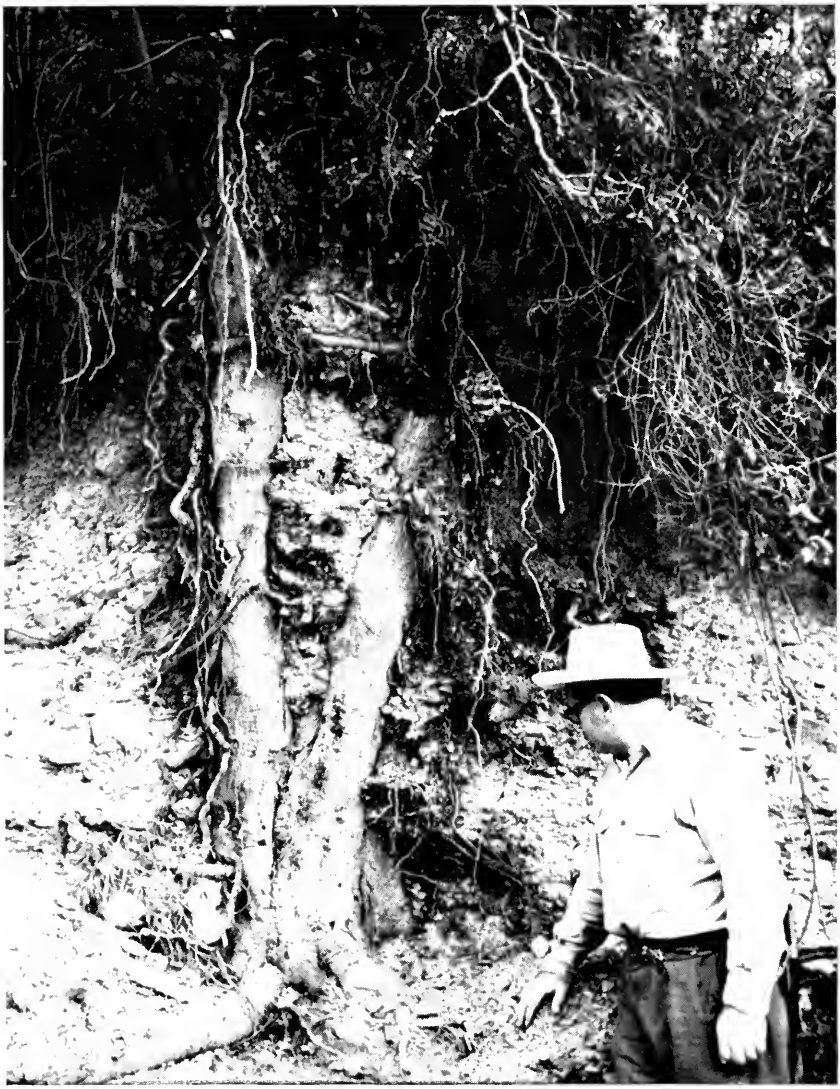

FIG. 30. The stream beds throughout the Tehuacán valley are normally dry, even in the rainy season, but there is ample evidence that occasional storms fill the streams to overflowing. This tree on the edge of an arroya near Coxcatlán began as a seedling on a ground level near the man's right hand. Subsequent flooding deposited nearly five feet of alluvial material around the trunk of the tree and many adventitious roots formed. Still later, another surge of water cut the bank away, again exposing the trunk and base of the tree.

Aneilema karwinskyana (R. & S.) Woods., *Peperomia campylotropa* Hill and *Echeveria racemosa* Schl., which are tropical in connotation, to *Asclepias circinalis* (Dcne.) Woods., *Viola hookeriana* HBK., *Oxalis alpina* Rose, *Didymaea mexicana* Hook. f. and *Ranunculus petiolaris* HBK., all of which lend a temperate forest aspect to the woods. This impression is soon dispelled on looking upward, as the trees are festooned in some areas with vining *Struthanthus deppeanus* (C. & S.) Blume or the graceful hanging, yellowish-green stems of *Phoradendron longifolium* Eichl., while the limbs are frequently crowded with epiphytic *Tillandsia* spp., *Epidendrum vitellinum* Lindl., with bright orange flowers, *Echeveria guatemalensis* Rose, *Peperomia berlandieri* Trel. and *Polypodium martensii* Mett. On the exposed rocky ridges, the oaks may be dwarfed and closely grown together with ericaceous shrubs, all of whose branches are thickly covered with lichens, including hanging strands of *Usnea*.

Thorn-scrub cactus vegetation

Below the oak-pine forest, at about 1800 m. elevation, the change in the vegetational cover is dramatic. Here the rainfall is obviously less, for the forest cover is nearly always open. The maximum height of the canopy is about 6 to 8 m. and is much less in many places. The shape of the trees differs markedly, also. Here the crowns of the trees tend to be umbrella shaped, with contorted branches and many short branchlets. The rough bark of the trees of the montane forest is replaced by the smooth boles or peeling bark usually associated with vegetation in arid areas. The candelabra forms of giant cacti are scattered through the trees and are so abundant locally as to form nearly pure stands of one or two species. Openings are occupied by spreading colonies of prickly pear cacti or the overgrown shrubby mala mujer (*Jatropha urens* L.). Open stretches of bare soil are relieved here and there by colonies of *Mammillaria* or barrel cacti with only open scattered patches of broad-leaved shrubs. Much of the vegetation bears spines or thorns, or the short shoots are stout and pointed. The leaves on many of the plants are compound and the leaflets small; the simple leaves of many are microphylls.

Local variations in the composition of the vegetation seem to depend both on edaphic factors and on available moisture. Large areas in the Tehuacán valley are obviously highly alkaline as the base rock is limestone which outcrops on the hillsides and forms a pebble and cobble mixture with the soil. More restricted sites are saline because of local saline springs or because of the continuing use of the partially

FIG. 31. The vegetational cover for most of the Tehuacán valley is thorn-scrub and cacti which most nearly approaches a forest in the vicinity of Coxcatlán. Here many species of trees of the Leguminosae, Burseraceae, Anacardiaceae, and other families are intermixed with columnar cacti. In places, the cacti may form nearly pure stands. The trees are usually short with umbrella-shaped crowns and smooth bark.

saline mineral waters of the valley for irrigation. In the major portion of the valley area from Tlacotepec in the northwest, to Chazumba, Oaxaca, on the west, to Tecomovaca, Oaxaca, in the south, the vegetational cover is uniform although the species composition may vary in percentage. These changes in the vegetational cover seem to relate to local drainage patterns and the amount of water available to the plants.

The valley vegetation extends for long distances into the mountainsides in the barrancas to the east where it finally meets the moist-area vegetation coming down from the mountains. This extension has been accentuated by the diversion of the normal water drainage in the barrancas into a multiplicity of irrigation channels. Far into the mountains the change to mesophytic vegetation is dramatic even

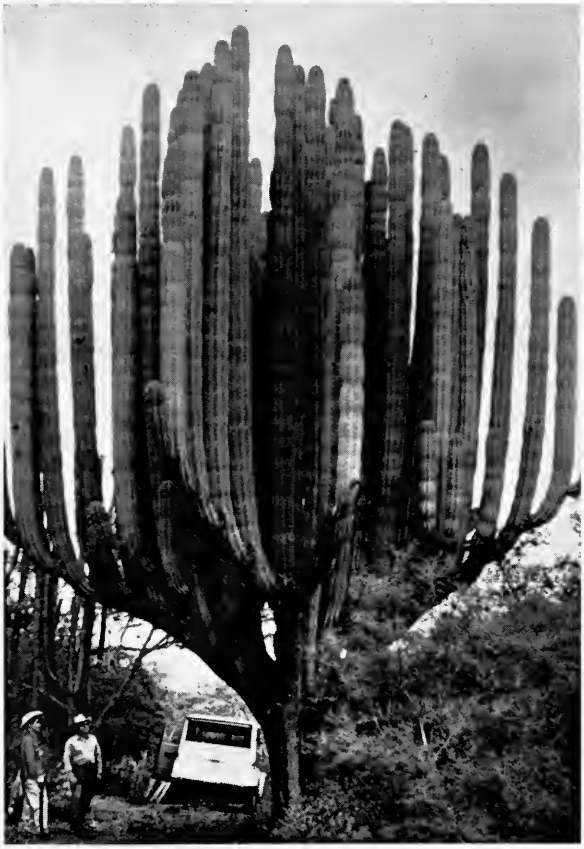

FIG. 32. One of the largest columnar cacti is *Lemaireocereus weberi* Britt. & Rose, whose branches grow like the arms of a candelabra.

though it is severely restricted by the intensive cultivation of the mountainside above the barranca.

In the remnants of what must once have been a more extensive moist forest along the barrancas are found *Erythrina americana* Mill., with bright red seeds persisting in the open tan pods, *Inga paterno* Harms, which has an edible white flesh around the seeds, *Parathesis* aff. *chiapensis?* nearly solidly covered with creamy-white berries, *Ficus cotinifolia* HBK., the source of a local bark paper, *Solanum verbascifolium* L., the leaves of which are used to scour pots, *Bocconia arborea* Wats. and *Pterostemon mexicanus* Schauer., which was heavily laden with clusters of pink flowers. Shrubs in the open areas include *Calliandra capillata* Benth. and *Anisacanthus gonzalezii* Greenm.

with colorful red flowers. The vine *Canavalia villosa* Benth. twines over the shrubs. In the small patches of forest, *Tillandsia* spp. are frequent epiphytes and *Adenocalymna alboviolaceum* Loes. climbs over the tree tops. Herbs are uncommon, but *Rivinia humilis* L. is conspicuous. In a moist area along the stream *Equisetum giganteum* L. forms a tangled mass.

The vegetational cover of the Tehuacán valley has been removed many times and then allowed to recover gradually as the farmers have moved their fields over the gently sloping hills and across the plains. Evidence is good that the population of the valley before historical times may have been considerably larger than at present. Evidences of former large villages and the remains of terraces, check dams and irrigation works, where the vegetational cover now appears to be stable and very old, indicate that even these areas were once cultivated. In spite of the dry climate, recovery of the thorn-scrub cactus vegetation from disturbance must be rapid. It is certainly much faster than is the recovery of mixed hardwood forests in the eastern United States where evidence of disturbance persists for long periods.

The markedly uniform composition of the vegetation over the whole area is accentuated by the forms of the individual species. The large cereus-type cacti all lend a similar appearance even though many different species are found in the forests. Trees of the Leguminosae, Anacardiaceae and Burseraceae tend to have similar bark and crown shape although the details of the foliage, flowers and fruits readily distinguish them. The masses of shrubs have a similar straggly, sparsely-foliaged appearance but many different plants are involved. Only when the plants are in full bloom is the tremendous variety of the vegetation displayed.

Common trees in the valley are *Acacia subangulata* Rose, *Cassia pringlei* Rose ("tecuahuile" whose foliage and bright yellow flowers are fed upon by dark striped caterpillars which are called by the same name and are locally considered a delicacy when fried in deep fat), *Acacia villosa* (Sw.) Willd., *Mimosa luisana* Brandg., *Acacia cymbispina* Sprague and Riley, and *Acacia sericea* M. & S., all of the Leguminosae. *Zizyphus pedunculata* (Brandg.) Standl., with its green and red marble-like fruits, locally called "cholulo," is used for soap. *Actinocheita filicina* (DC.) Barkley and *Juliana adstringens* Schlecht. are similar in appearance but the latter is readily distinguished by its winged fruit. *Celtis pallida* Torr. provides a contrast with simple foliage and much branched extremities. *Bursera sub-*

FIG. 33. The trunk of *Fouquieria formosa* HBK. is covered with a thin, smooth greenish-yellow bark which peels in sheets. Bark of this texture is common to many trees or the valley.

moniliforme Engl. is the largest of all of the burseras. *Morkillia mexicana* (Moc. & Sessé) Rose & Paint. is particularly evident when bearing its large magenta flowers. Equally distinctive is *Thouinidium insigne* (Brandg.) Standl. with inflated, winged, tan fruit hanging in clusters. The occasional specimens of *Tecoma stans* (L.) HBK. or *Theretia peruviana* (Pers.) Merr., with bright yellow flowers, are conspicuous. *Hintonia standleyana* Bull. is sometimes 8 m. tall and nearly covered with large white flowers. Perhaps the largest tree

of the whole formation is the "pochote," *Ceiba parvifolia* Rose, whose trunk and limbs are covered with corky, thick spines when it is young. Among the most unusual appearing trees are *Jatropha neopauciflora* Pax, with very thick twigs and bursera-like fruit, and *Manihot pauciflora* Brandg., with *Oxalis*-like foliage, which looks very unlike other species of *Manihot*.

The tree which characterizes the Tehuacán valley forest cover more than any other is *Fouquieria formosa* HBK., whose peeling, greenish-yellow bark is conspicuous everywhere.

Jutting up through the trees of the valley and foothills are individuals and patches of candelabra cacti. One of the most common is "jiotillo," *Escontria chiotilla* (Weber) Rose, with yellow flowers and laxly branched stems. In contrast are the straight upright stems of *Myrtillocactus geometrizans* (Mart.) Cons. with tiny, glaucous fruit along the ribs, *Lemaireocereus stellatus* (Pfeiffer) B. & R. with red flowers, and *Lemaireocereus weberi* Britt. & Rose with its huge bulk of repeatedly branched arms reaching many meters above the crowns of the surrounding trees. In some places the fuzzy tops of *Cephalocereus* sp. are conspicuous.

Few of the shrubby plants grow in compact shapes and some are tortuously intertwined and difficult to collect for botanical specimens. Among the more compact are *Bursera arida* (Rose) Standl. and *Jatropha dioica* Sessé. *Castela tortuosa* Liebm. has numerous attractive red fruits. Perhaps the most common and conspicuous straggling shrub is *Cordia stellata* Greenm. with tight balls of white flowers which later mature into bright red fruits, but the morphological complexity of the flowers of *Ayenia fruticosa* Rose, another of the very common shrubs, makes it far more interesting to botanists. Numerous shrubby plants with inconspicuous flowers such as *Iresine rotundifolia* Standl., *Croton morifolius* Willd. var. *obtusifolius* Mull.-Arg., *Cordia brevispicata* M. & G., and *Croton fragilis* var. *sericeous* Mull.-Arg. intermingle with *Echinopterys lappula* Juss., *Haplophyton cinereum* (A. Rich.) Woods., *Perymenium ovatum* Brandg., *Parthenium tomentosum* DC., and *Hibiscus brasiliensis* L. all of which have relatively showy flowers. Included here should be *Agave macroacantha* Zucc., which forms colonies of glaucous rosettes on the hillsides, *Agave rubescens* Salm-Dyck., which grows as a sessile rosette, *Agave washingtoniensis* Baker & Rose? and *Agave karwinskii* Zucc., a stalked agave locally called "lechuguilla." Thickets of the edible *tunas*, *Opuntia pilifera* Weber and *Opuntia hyptiacantha* Weber, and the scattered "mala mujer," *Jatropha urens* L., make walking hazardous

FIG. 34. The tallest tree of the area is *pochote* (*Ceiba parvifolia* Rose) which has distinctive corky spines on the trunk when it is young. The fruit has been collected by the local population since before the Conquest both for the fiber around the seeds and for the seeds themselves which are eaten.

for the unwary. The parasitic shrub, *Psittacanthus calyculatus* (DC.) Don, with clusters of bright orange flowers, is not uncommon on the branches of various trees. Occasionally *Lamourouxia nelsoni* Rob. & Greenm. is plentiful and very conspicuous because of its bright red flowers with purple mouths. Over and among the shrubs, *Cardiospermum halicacabum* L. frequently throws a webby tangle of stems. The vines *Marsdenia zimapanica* Hemsl. and *Gonolobus fraternus* Schlecht. are not uncommon. By far the most common plant in the shrub vegetation is *Lantana camara* L., whose scattered plants always seem to be in bloom.

The herbaceous plant representation is surprisingly varied although there is much open ground and the herbaceous vegetation is nowhere very thick. *Hechtia* sp. sometimes forms extensive colonies on the hillsides. The composite family is represented by *Sanvitalia fruticosa* Hemsl., *Tridax procumbens* L. and *Pectis canescens* HBK. *Argemone mexicana* L. and *Solanum amazonicum* Ker. are abundant in disturbed soil along the dry watercourses and the latter is especially abundant along trails and roads. Among the conspicuous weedy herbs is *Nicotiana glauca* Grah. which may grow as tall as 3 m. In this dry habitat, several fragile looking plants, including *Oxalis neaei* DC., *O. berlandieri* Torr., *Talinum paniculatum* (Jacq.) Gaertn., *Commelina erecta* L. and *C. dianthefolia* Del., are well represented. The smaller cacti which form small cushions with bright red fruit are *Mammillaria napina* Purpus and *M. carnea* Zucc. In the dry areas, *Selaginella lepidophylla* Spring. remains tightly rolled until rainfall provides sufficient moisture for the stems to relax and expose the rich green tops. In the rock crevices of the banks and hillsides, *Notholaena candida* Hook. and *Cheilanthes microphylla* Sw. form clumps. Finally, epiphytic on the trees and candelabra cacti, *Tillandsia recurvata* L. and another species of *Tillandsia* are not rare. Whether *Opuntia decumbens* Salm-Dyck. should be included in the herbs or the shrubs is difficult to decide, since the tuna de viboras is low and succulently herbaceous, but possesses the same stout stem and root structure which characterize upright opuntias.

Lime-soil facies

The most distinctive vegetation within this general pattern in the Tehuacán valley is the plant association on the areas of shallow soil over limestone. To the north near Azumbilla is a small area of this type, but immediately to the west of Tehuacán at El Riego are nearly cliff-like limestone hills the top of which is known as La Mesa. To

FIG. 35. In the background can be seen the level northern reaches of the Tehuacán valley. The foreground area is the top of a limestone formation from which the vegetation was cleared for cultivation; the fields have been abandoned but remain open.

the southwest along the road through Zapotitlán and for intervals as far as the limits of the area at Chazumba, Oaxaca, there are other limestone outcrops both large and small. Among the least disturbed of these is the mesa near the settlement of Teloxtoc.

All the limestone areas appear to be so well drained that the tree cover common to the major part of the valley is eliminated. Instead, a shrubby, conspicuously spiny, vegetational cover is developed. Agaves, cacti, yuccas and hechtias grow in greater abundance. Somehow, flowers on the vegetation seem to be larger and more colorful. This impression may be false and stem from the low height of the shrubs which allows one to see almost anything blooming. Open areas of soil and rock are prevalent, especially if a pocket heated more intensely by reflection from surrounding rock walls occurs. To the western edge of the area, the only palm seen, *Brahea dulcis* (HBK.) Mart., grows on lime soil; this palm is the source of fibers used locally to weave hats.

Trees in the limestone area are few and frequently scattered in distribution, perhaps due to persistent clearing. Any flat area with

FIG. 36. Another variation in the vegetation of the Tehuacán valley is conditioned by the outcropping of lime rock. This limestone mesa top near Teloxtoc is still relatively undisturbed but other areas of this type are under cultivation. The strange *Beaucarnea gracilis* Lem. trees of the Liliaceae form an open forest interspersed with barrel cacti (*Echinocactus grandis* Rose) and many species of small shrubs.

lime soil usually has been intensively cultivated. The top of La Mesa near Tehuacán is deeply scarred with furrows and the marks of field boundaries are everywhere. Only an occasional *Fouquieria formosa* HBK. stands above the shrubs. One specimen of *Beaucarnea* indicates that this tree may have once been more plentiful, while occasional clumps of *Yucca periculosa* Baker provide variety across the horizon. In the quebradas cut into the mesa behind El Riego, several tree species occur. *Tecoma stans* (L.) HBK., with bright yellow flowers, *Ptelea trifoliata* L., which, when cut, smells like skunk, *Malpighia galeottiana* Juss., a nanché with pricking hairs and edible fruit, and *Hesperothamnus purpusi* (Harms) Rydb., with bright magenta flowers, are all small trees seldom exceeding 4 m. in height.

The shrubs on the limestone are many and varied. The large cacti, *Echinocactus grandis* Rose, which grows to 1.5 m. tall and half that in diameter, and *Ferrocactus robustus* (L. & O.) B. & R., which

FIG. 37. Among the most interesting cacti of the lime soil area is *Ferrocactus robustus* (L. & O.) B. & R., which forms large mounds. In the foreground are the gray-green, leafless stems of a plant of *Pedilanthus cymbifera* Schlecht.

forms massive mounds many feet across, are by far the most conspicuous forms. Nearly as different are the plants of *Pedilanthus cymbifera* Schlecht., with red, slipper-like flowers on gray-green, leafless stems, and "candelillo," *Euphorbia antisyphilitica* Zucc., the basis of an industry which supplied wax for candles, hence the common name. *Hintonia standleyana* Bull. is an occasional shrub here. Among the shrubs bearing colorful flowers are *Calliandra hirsuta* (Don) Benth., with bright red stamens, *Salvia thymoides* Benth., with bright blue flowers, *Zexmenia pringlei* Greenm., whose rays and disk are deep yellow, *Dalea tuberculina* (Rydb.) Herm., with royal purple blossoms, *Hibiscus elegans* Standl. and *Cassia macdougliana* Rose, both with yellow flowers, and *Berendtiella laevigata* (Rob. & Greenm.) Thieret, with reddish-orange, trumpet-like flowers. Less conspicuous shrubs include *Croton incanus* HBK., *C. ciliato-glandu-*

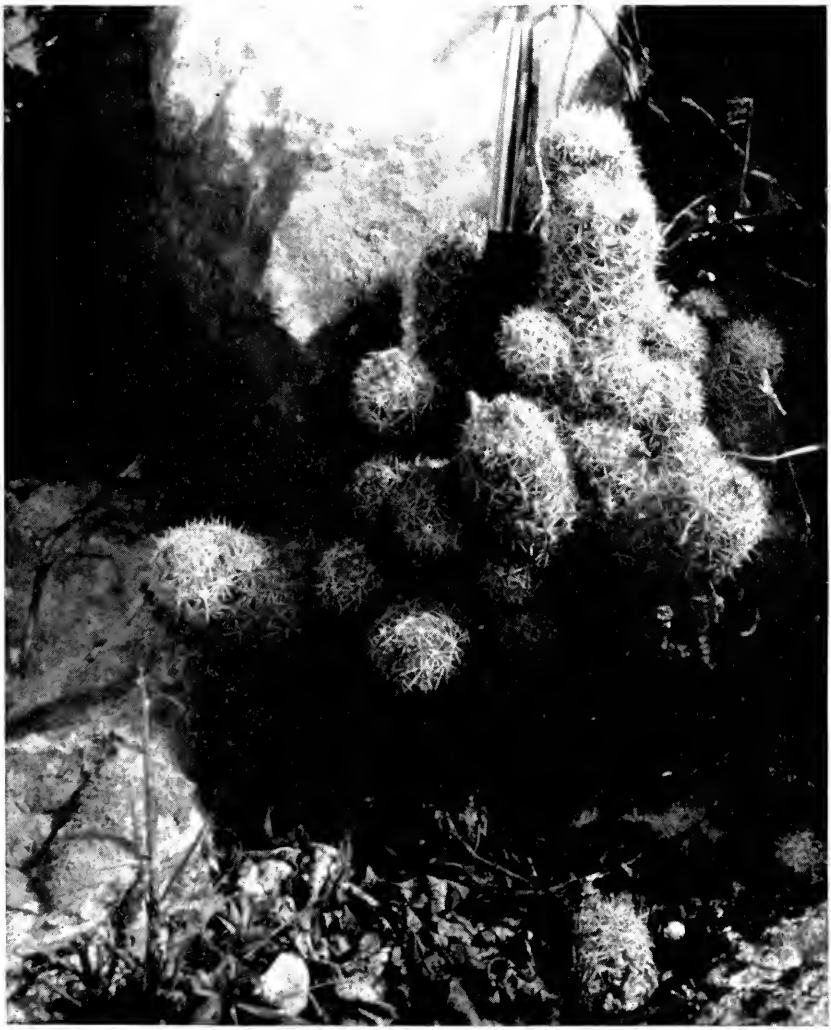

FIG. 38. Colonies of *Mammillaria collina* Purpus are frequent among the shrubs. A greater variety of cacti seem to be present on the lime soil areas rather than in other parts of Tehuacán valley.

losus Ort. and *Lasiocarpus salicifolius* Liebm., of the Malpighiaceae but bearing fruit much like *Heliocarpus.*

Herbaceous plants are scattered and never form a very thick cover over the surface of the soil. Part of this sparsity may be due to the inroads of grazing animals which are allowed to feed through all areas of the countryside not actively being cultivated. In sandy

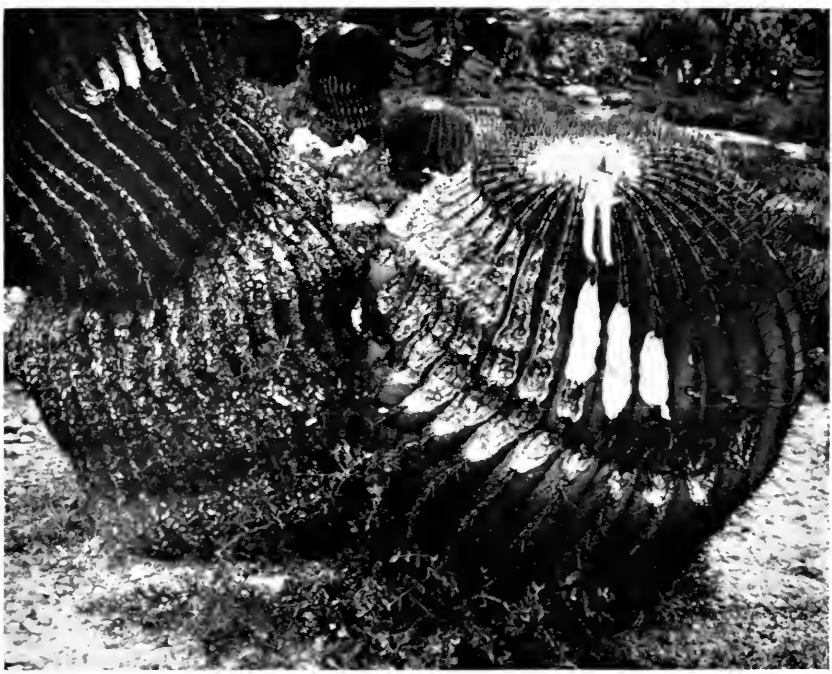

FIG. 39. Even the stiff, sharp spines of *Echinocactus grandis* Rose fail to provide protection against the goats which eat everything not poisonous or too spiny.

areas, *Apodanthera galeottii* Cogn. sends its runners outward in several directions from the root. Among the species of *Anthericum* found on the limestone areas are *A. leptophyllum* Bak., *A. torreyi* Bak. and *A. durangense* Greenm. *Polygala alba* Nutt. var. *tenuifolia* (Pursh) Blake, *P. obscura* Benth., *Bouteloua triaena* (Trin.) Scribn., *Zephyranthes* aff. *longifolia* Hemsl., *Kallstroemia parviflora* Nort., *Asclepias linaria* Cav., *Lycianthes ciliolatum* (M. & G.) Bitt. and *Hoffmanseggia pueblana* (Britt.) Standl. grow scattered among the shrubs on the lime-soil area. Perhaps *Verbena canescens* HBK. is the most commonly encountered herbarceous plant.

In the vicinity of Teloxtoc, the vegetation on the top of a limestone mesa appears to be much less disturbed than on La Mesa near Tehuacán. In some areas here, *Fouquieria formosa* HBK. forms the tree cover in an unbroken but scattered stand. In other areas, *Beaucarnea gracilis* Lem. forms forests of trees sometimes 6 m. tall with curious bulbous trunks and tufts of long linear leaves on the ends of branches. *Echinocactus grandis* Rose is a common feature of the landscape among the trees and shrubs. Surface water is nonexistent in the locality and the goats chew into the ribs of the barrel cacti in spite of the spines.

Saline-soil facies

The other vegetational change from the general pattern through most of the valley is caused by highly saline soils around the areas of saline springs and, in some parts of the valley, by highly charged mineral waters which have been used for irrigation over long periods, as mentioned earlier (p. 116). The former kind of area is well illustrated by the conical hill known as Petlanco to the west of the Rio Salado at Pueblo Nuevo south of Axuxco. Its outline and some of the rock outcropping on its surface indicate that Petlanco is the remains of a volcanic cone. At many places on and near the summit of the hill, salt springs flow and fill small pools which evaporate to leave layers of salt. Over the years, large salt domes have been built up on the hillside. The numerous remains of salt pans and channels around the base of the hill show that the springs once had sufficient volume to flow into streams which were diverted and evaporated by the Indian population so that the salt could be gathered. On some of the surrounding plains the soil is so highly saline that large areas are completely bare. Most of the hillside is covered with a mantle of vegetation not unlike that generally found throughout the valley.

Trees on or near Petlanco include *Leucaena puberulenta* Benth., *Jatropha dioica* Sessé, which is short and spreading, *Zizyphus pedunculata* (Brandg.) Standl., *Juliana adstringens* Schlecht. (cuatchalalan of the Indians), *Pithecolobium acatlense* Benth. and, near the top, a few individuals of *Fouquieria purpusii* Brandg. which is a curious small tree with a bright green trunk enlarged toward the base like *Idria* of Baja California. *Agave kerchovei* Lem. and *A. macroacantha* Zucc. are common on the hillside.

The shrub cover is not dissimilar from that in other nearby areas. No real change in the species composition of this group of plants could be seen. On the level plain not far from the base of the hill,

FIG. 40. Stretches of open soil visible from the top of Petlanco attest to the salinity which has accumulated from the saline water springs.

the principal shrubs in one patch are *Euphorbia antisyphilitica* Zucc. and *E. xantii* A. Gray.

Around the salt seeps, the herbaceous plants are restricted to a few species. *Juncus* aff. *robustus* S. Wats. forms large tussocks. *Euphorbia revoluta* Engelm., *Distichlis stricta* (Torr.) Rydb., *Gomphrena pringlei* Coult. & Fish., *Trianthema portulacastrum* L., *Cathestecum erectum* Vasey & Hack and *Jacquemontia smithii* Rob. & Greenm. are more prevalent here than in other parts of the Tehuacán valley. The crevices of the rocks near the summit of the hill are thickly filled with plants of *Notholaena sinuata* (Sw.) Kaul. In the full sun, where the rock surface is hot to the touch, *Echeveria minutiflora* Rose is a frequent succulent.

A prime example of the second kind of saline soil condition, as described on page 129, is located near the city of San Gabriel Chilac on Hacienda San Andrés. Over large stretches on the plain below the foot of the escarpment known as Cerro San Andrés, the soil has the fine texture of alkali flats and is nearly white. While tree and

shrub vegetation and some herbaceous plants grow here, large patches of soil are bare. The trees are small and *Opuntia* spp. are common.

The face of the escarpment is literally criss-crossed with the remains of old irrigation water channels used to lead the mineral waters from the springs in the valley above to the fields near Chilac. Irrigation water is still brought by this route. Mineral deposits along the channels had apparently built up so that the amount of flow was restricted, or the pattern of the fields in the valley below changed so that water had to be diverted to different areas leading to the abandonment of many channels over a long period of time. Leakage from these channels undoubtedly led to a gradual build-up of salt in the soil. There is also some sign that there were spring seeps from the rock strata on part of the escarpment face; these may well have been springs heavily charged with salts. In this area tree cover

FIG. 41. At the height of the rainy season, the Río Salado at the ford at Venta Salada is a small stream due to diversion into irrigation systems.

FIG. 42. A thunderhead over the mountains to the east provides water for the barranca streams leading into Tehuacán valley.

FIG. 43. Random rain clouds like those shown here enter the Tehuacán valley from the west but generally furnish little precipitation. Over the top of the Sierra de Zongolica to the east can be seen the banks of clouds, from the Gulf of Mexico side, trapped against the mountains. Major precipitation in the valley results when hurricanes force clouds over the valley in summer.

is scattered but shrub growth is fairly heavy. Herbaceous plants are scattered over the ground surface among the shrubs, but the area seems to be overgrazed. The moist borders of the irrigation channel currently in use furnished specimens of several species difficult to collect elsewhere since the goats and sheep prevent them from maturing flowers. Among these were *Eustoma exaltatum* (L.) Griseb., with large lavender flowers, *Chloris virgata* Sw., *Pringleochloa stolonifera* Scribn., *Muhlenbergia tenuifolia* (HBK.) Kunth and *Bacopa monnieri* (L.) Wettst. The last named species was restricted to a moist depression.

Relationships of the Tehuacán flora

The 650 specimens on which the description of the vegetation is based were collected from all areas discussed. Since the main purpose of the collection was to provide vouchers against which archeological plant remains could be compared, most collections (427 numbers) were made in the thorn-scrub and cactus vegetation of the valley below the 1800 m. level. When collecting the specimens, I had no intention of describing the flora of the area, but material in identifiable condition was gathered generally. When identifications were checked against the collections at the Chicago Natural History Museum, it became apparent that a number of species in this flora are restricted to the Tehuacán valley area. Several had been collected only a few times even though they are not rare in the areas in which they grow. Subsequently, the identifications of some of the less clearly delimited species were checked against the collections at the U. S. National Herbarium. At that time, the ranges of the species as shown by specimens in the herbarium were recorded.

From the 427 numbers collected in the dry Tehuacán valley area it was possible to select 253 species whose identities appear to be unquestionable, and are native plants in the area. All duplicates, adventives, foreign weeds and specimens with questionable identifications were eliminated. Since the purpose of the collection was to gather as many valley plants as possible, bias against the most common, weedy plants was eliminated. The collection was not made with a statistical study in mind thus eliminating any bias toward the selection of unusual or rare species. (I was so ignorant of the flora of the area that I would not have recognized a rare species at the time the collections were prepared.) Rightly or wrongly, because of the ease with which spores may be disseminated, all non-seed plant species were eliminated from this study although *Selaginella* and several fern genera are important in the flora of the Tehuacán area.

The only limiting element in the collection is its restriction to the rainy season in July and August. For this reason, a number of the species of the valley flora may not have been collected. On the other hand, specimens of cacti, agaves and other succulents were prepared with flowers and fruit as they were found so that a general cross section of the flowering plants has been obtained. Nothing was ignored because it was difficult to prepare or notoriously difficult to identify. On this basis, the following summary of endemism has been compiled.

Only 127 species of plants from the Tehuacán valley area could be classed as widely distributed. Some of these are found far south of Mexico; others have ranges extending northward into the United States. The bulk of the widely distributed species are restricted to Mexico, but their distribution is so general that it is not possible to establish that they have affinities in any particular direction from the Tehuacán valley. These generally distributed species comprise 50.1% of the sample. They represent 47 different families of seed plants. Of these, 25 families, forming 19.6% of the total widely distributed species, are represented by only 1 species each. On the other hand, the family Leguminosae is represented by 13 species, or 10.2% of the widely distributed species. In decreasing order of importance and number of widely ranging species Euphorbiaceae, Compositae, Gramineae, Convolvulaceae, Verbenaceae, Solanaceae and Scrophulariaceae follow the pattern generally expected in Mexico. These are all groups with many species found in the dry areas of North America. However, the succulent species of the Cactaceae, Crassulaceae and Amarylidaceae (the first with one widely distributed species, or 0.4% of the species considered here) show a remarkable restriction in range although they are admirably suited to the dry areas of Mexico. Is this a true endemism or is it the final effect of too fine a division of species? While the latter may be true among the plants now in cultivation, those species known only from the wild seem to be amply distinct from one another and are probably truly very restricted in range.

The remaining 52 species with a distribution outside of the Tehuacán valley area could be assigned to groups denoting the areas with which they show affinities. The largest group of species, 35 species or 13.8% of the whole sample, has ranges extending into the northern states of Mexico; several species range into San Luis Potosí. Many have been collected from the northern tier of Mexican states, particularly Chihuahua. Of this group, seven species (20%

of the group, or 2.8% of the total sample) belong to the Leguminosae. Among the plants with northern affinities are five species (14.3% of the group, or 2.0% of the sample) of Cactaceae. This is to be expected for a North American desert flora. The remaining families with large representation to the north are the Compositae (three species, 8.6% of the group, or 1.2% of the sample), Loranthaceae (two species, 5.7% of the group, or 0.8% of the sample) and the Liliaceae (two species). Northern distribution was shown by one species in each of five additional families.

The next largest group of species were those having distributions on the Pacific side of Mexico. This group of 11 species makes up 4.3% of the total sample and includes six species of Leguminosae (54.5% of the group or 2.4% of the sample), two of Euphorbiaceae and Anacardiaceae and one of Asclepiadaceae. These plants comply with a distribution pattern indicated by a map showing the annual number of days with rain. It is expected that species within the low rainfall area should show a restricted distribution and it is unusual that so few plants in this sample follow the pattern. A few species in the widely distributed group should have been placed with the species restricted largely to the Pacific coast states of Mexico.

A group of six species shows affinities to the south of the Tehuacán valley area. The Leguminosae is represented by three species (50% of the group or 1.2% of the sample). The other three plants are one species each of the Moraceae, Rubiaceae and Amaranthaceae; they are not represented in the Table.

The group of species endemic to the Tehuacán valley area is made up of 74 species belonging to 28 families. This is 29.1% of the species in the total sample. While the families with large numbers of Mexican species are well represented among the endemics in the Tehuacán valley, the Cactaceae with 12 endemic species in the area (16.2% of the group, or 4.7% of the sample) shows the highest percentage of endemism. Of all the families represented in the total sample, the Amarylidaceae with five endemic species (6.8% of the group, 2.0% of the sample) of a total of six species has by far the highest rate of endemism. The endemic species belong to the genus Agave.[1] It is to be expected that the Leguminosae (11 species, 14.9%

[1] Howard Gentry has written (in litt.): "*Agave rubescens*, I think, will prove to include *A. pacifica* and other names from northern Sinaloa, south to Michoacán and east to Puebla and Oaxaca. *A. karwinskyi* is also native about Mitla in Oaxaca. As species now stand, fide Berger, there are about 10 spontaneous in the Tehuacán Valley." Therefore, the percentage of endemism in this group is somewhat higher than my collections indicate.

of the group, 4.3% of the sample), Euphorbiaceae (four species, 5.4% of the group, 1.6% of the sample) and the Compositae (seven species, 9.5% of the group, 2.8% of the sample) would include high numbers of endemic species. A few families show unexpected percentages of endemism. The Labiatae with four endemic species (5.4% of the group, 1.6% of the sample) and the Malpighiaceae with three endemic species (4.1% of the group, 1.2% of the sample) have a high rate of endemism in Tehuacán valley in proportion to their representation in the Mexican flora as a whole. It is not surprising to find three endemic species of Crassulaceae as this is a highly developed family in Mexico including several genera of succulent plants largely restricted to the desert areas of the country. The Scrophulariaceae, Boraginaceae, Liliaceae, Burseraceae and Sterculiaceae each have two endemic species in the area. The remainder of the families has one endemic species each in the Tehuacán valley.

For the most part, the flora of the Tehuacán valley is similar to the flora of other portions of Mexico with a similar climate as witnessed by the 127 species (50.1% of the sample) known to be widely distributed. For purposes of comparison with the endemism, the 52 species tabulated in the categories of northern, southern, and Pacific coastal distributions can be included with the widely distributed species adding to a total of 179 species (70.9% of the sample). A glance at Table 1 immediately indicates that these species fall within the family pattern familiar throughout much of the less well-watered portion of western North America. The Leguminosae is represented by the greatest number of species (29 species, 10.5% of the sample), followed by the Euphorbiaceae (13 species, 5.2% of the sample), Compositae (12 species, 4.8% of the sample), Gramineae (10 species, 4.0% of the sample) and other families in decreasing numbers of species. Miranda (1948) noted, "La flora de la cuenca alta del Papaloapan muestra en su parte árida dos classes evidentes de relaciones: una con la flora de la cuenca del Balsas y otro con las barrancas áridas de las cuencas superiores de los ríos Moctezuma, Santa María y Verde en la zona hidalguense-queretano-potosina, con extensiones hacia el N. hasta el sur de Texas."

There may be a bias toward tall, woody, poisonous and very spiny plants in these totals since the Tehuacán valley is now heavily grazed by sheep and goats. This must be ignored since population pressure will continue to increase here and the flocks will undoubtedly grow in rough proportion to the demand for animal products. There is little hope that the flora will be allowed to return to its ungrazed state.

A. J. Sharp (1953) analyzed the Mexican flora on the basis of the families of plants reported in Standley's *Trees and Shrubs of Mexico* and found that only five of about 140 families of woody plants were nearly endemic to Mexico. No family was entirely restricted to the country. By far the greater number of families of woody plants are tropical or subtropical in affinities with the next largest number showing relationships with temperate zone floras. On the basis of Sharp's analysis, no substantial amount of endemism is indicated.

The endemic species of the Tehuacán area make up a surprisingly large portion of the species included in the sample. Seventy-four species (29.1% of the sample) are found only in the area, while some are restricted to special habitats and are very local. J. Rzedowski (1962), in an independent study based on the genera of woody plants recorded by Standley, found that 28% of the genera in zones of semiarid climate in Mexico is endemic. Many of the species of the Tehuacán area range widely through the thorn-scrub and cactus vegetation where they are a conspicuous and important element in the plant formation. These include the species of Leguminosae, Compositae, Cactaceae, Crassulaceae and Labiatae. *Pedilanthus cymbifera* Schlecht., *Jaquemontia smithii* Rob. & Greenm. and *Echeveria subsessilis* Rose are abundant herbaceous plants in their habitats; *Cordia stellata* Greenm., *Sanvitalia fruticosa* Hemsl., *Agave rubescens* Salm-Dyck., *Lasiocarpus ovalifolius* Ndz., *Salvia aspera* M. & G., *Ayenia fruticosa* Rose and *Ferrocactus robustus* (L. & O.) Britt. & Rose are all conspicuous members of the shrub community whereas *Leucaena pueblana* Britt. & Rose. *Yucca periculosa* Bak., *Beaucarnea gracilis* Lem. and *Escontria chiotilla* (Weber) Rose are common arborescent species in the valley. However, some of the endemics appear to be very local. *Grabowskia geniculatum* (Fern.) C. L. Hitchc. and *Fouquieria purpusii* Brandg. were seen only on Petlanco. The former is inconspicuous and may have been overlooked at other stations, but the latter is a very conspicuous small tree which would have been difficult to disregard under the most adverse conditions.

Many species listed are amply distinct from their relatives. Little doubt can be had that the development of these entities has proceeded over a long period of time. *Jaquemontia smithii* is an upright, woody, shrub with flowers very much like *Evolvulus* which cannot be said to be closely related to the majority of *Jaquemontia* species with a herbaceous-vine habit. A few, like *Beaucarnea* and *Escontria*, belong to highly modified groups of plants in which the Tehuacán area species show ample distinctions beyond the variations seen in other

members of the family or subfamily. Some endemic species of the flora differ startingly from their nearest relatives. *Acanthothamnus aphyllus* (Schlecht.) Standl. (Celastraceae) is much like the spiny-twigged species of the Rhamnaceae. *Setchellanthus caeruleus* Brandg. (a monotypic genus of the Capparidaceae) is difficult to see in the field as the pubescent pods and closely appressed small leaves are very inconspicuous. It has little resemblance to other capparids in the Tehuacán flora. *Manihot pauciflora* Brandg. is a small tree scattered through the area. The foliage is about the size and configuration of a medium-sized *Oxalis* leaf and looks nothing like the foliage common to many species of the genus.

A few species of the endemic flora are obviously closely related to the other species of the genus to which they belong. *Echeveria minutiflora* Rose, sometimes placed in another genus, is obviously a member of the group of echeverias bearing a spike or raceme. On its host, *Struthanthus inornus* (Rob. & Greenm.) Standl. forms a beautiful shrub with hanging branches, but the details of the flowers, fruit and foliage show its relationship with the other species of the genus. Although it generally has single-seeded fruit more nearly resembling fruit of the Burseraceae, *Jatropha neopauciflora* Pax is obviously closely allied to *J. spathulata* Muell.-Arg. Similarly, the species of *Juncus* found around the salt springs of Petlanco is very near *Juncus robustus* Wats. of Baja California.

For a geographic area contiguous with a gigantic continental land mass, the Tehuacán valley harbors a surprising amount of endemism. The masses of the Sierra Madre Oriental are a portion of the ridges running northward into the United States and southward, with the break at the Isthmus of Tehuantepec, into Central America. These have undoubtedly served as an avenue for plant and animal distribution for many ages. To the south of the Tehuacán area lies an area of dry mountains and valleys which could serve as the entryway for many plants requiring xeric habitats. Logically, the flora should be similar to the floras of dry areas to the northwest and to the south.

Endemism in Tehuacán valley begins to approximate the rates of endemism found in insular floras. For instance, the Canary Islands are reported to have 45% endemic species in their flora. On the other hand, islands well isolated from neighboring land masses may have much higher percentages of endemics; Hawaii is reported to have 82% endemic species in its flora. Similarly, the flora of the tops of mountain masses tends to harbor an increased number of endemic species. The larger the habitable area and the greater its

degree of isolation from similar areas with comparable floras, the greater the percentage of endemism found. The Tehuacán valley barely fills any of the criteria necessary for the development of a high percentage of endemism in its flora as it is neither elevated nor distantly separated from land area with similar habitats.

The key to the development of a high rate of endemism in the flora of the Tehuacán area probably lies in the age of the region. Cain (1944, p. 218) following Szymkiewicz says, ". . . endemism in a mountain system on a continental mass should be in proportion to its relative age (i.e., the time it has been available for occupancy by flowering plants). . . ." Though this statement is made in specific reference to mountainous areas, it is readily applicable to any area which has attained a degree of isolation by any means. The Tehuacán valley area has attained a degree of isolation in that it is a dry valley bounded by masses of mountains with elevations in excess of 1800 m., the approximate lower limit of the oak-pine forest in this part of Mexico. At the present time, the isolation is far from complete as the same thorn-scrub and cactus vegetation extends southward in Oaxaca to the Pacific coastal area and then northwestward to the deserts of northern Mexico. The relatively great age of the Tehuacán valley area coupled with a greater degree of isolation in the past are the causes for the high rate of endemism.

One of the criteria of endemism cited by many students is the availability of varied habitats which have allowed sufficiently wide genetic variations to become established among the progeny of a species. As in any mountainous area, the Tehuacán valley region offers marked variations in topography and, consequently, microclimates, as well as a variety of geological formations from which the soil has been derived. It has already been pointed out, that the variations in habitat are reflected only in minor differences in the species composition of the plant communities. Because of the increased subsurface drainage, limestone areas lack arboreal species for the most part and the number of species of Cactaceae and shrubs is increased. A portion of this change in species formation can be attributed to the change in soil pH since the majority of species found in the limestone areas are also found throughout the valley flora. Only a very few species are restricted to the saline-soil areas. These have been noted and they are not, for the most part, species which can be identified as endemics. For example, only three endemic species were found on Petlanco, the hill with many natural salt springs; this is 4% of the total species judged to be endemic to the Tehuacán area.

A long-term stability in the climatic regimen might have been responsible for an increased rate of endemism in the flora of the Tehuacán valley. Since the biggest influence on the climate of the valley seems to be the Gulf of Mexico to the north and east, the elevation of the masses of the Sierra de Zongolica has played a major role in the control of rainfall. Probably there has been no major change in rainfall pattern or distribution since the mountain mass became elevated during the Laramide Revolution at the close of the Cretaceous (Schuchert and Dunbar, 1949). Since the close of this orogenic disturbance there have been a number of major climatic disturbances during the Pleistocene which may have increased the rainfall at higher elevations, thereby more effectively isolating the flora of the Tehuacán area. How acutely these may have affected the climate on the valley floor is not known. However, there is now evidence that the late Pleistocene fluctuations which caused marked changes in climatic patterns in the north of Mexico and the southwestern United States had little influence on the climate of the Tehuacán valley. Vegetal remains dating from about 11,000 B.C. and forming a nearly continuous series to historical times show almost no change in morphological character or species composition (personal observation). Probably there has been no marked difference in the rainfall pattern since the Tertiary. Rzedowski (1962), discussing Pleistocene fluctuations, states, "Por otro parte, el haberse demonstrado que la extensión de zonas de clima seco en los Estados Unidos variaba en los diferentes períodos y que en general debe haber sido menor que en la época actual, no implica que el mismo regimen de cambios incluía a todo México, y menos aún que en esta país no hayan existido regiones con climas francamente árido a lo largo del Terciario. Por el contrario, los datos fitogeográficos parecen inclinarse más bien en favor del hecho de una existencia prolongada de climas áridos en México, necesaria para el desarrollo de una flora tan individualizada y diversificada como la que se observa actualmente."

Under a uniform rainfall regimen, competition among the species of the flora must have been particularly strong. There is insufficient variation in habitat to have allowed the establishment of genetic variants under conditions which would exclude the parental forms. So far as can be determined, there has always been a reservoir of parental germ plasm in contiguous dry areas; isolation has been far from complete so that the accumulation of variations must have progressed over a very long time indeed. The only possible explanation of more complete isolation might have been the pluvial effects of the

Pleistocene which could have surrounded the Tehuacán area with a ring of better-watered hills particularly to the west and south.

Summary

The vegetation of the Tehuacán valley can be described best as thorn-scrub and cactus. It is remarkably uniform throughout the area. Locally, as on the well-drained hill slopes, one or another species may become dominant. Only where the soil is underlain by and derived from lime rock formations is there a marked distinction in the species composition of the vegetational cover. Here the arborescent forms are largely absent and species of Cactaceae and shrubs are dominant. Areas of saline soil, whether due to natural saline springs or to the use over long periods of time of the mineral spring water from the northern end of the valley, are recognizable primarily by a few halophytic species and large open soil surface. By far the largest proportion of the species of the saline soil areas are common to the rest of the valley.

Endemism in the flora of the Tehuacán valley is surprisingly high. A carefully selected sample of 253 species, from 427 numbers collected over a five-week period, whose identification appeared to be unquestionable, was checked for distribution. 29.1% of the species can be said to be endemic to the Tehuacán valley area. Only 50.1% of the species can be classed as widely distributed, while 13.8% can be said to have affinities in northern Mexico, 4.3% in the Pacific coast states of Mexico and 2.7% in the states to the south of the area.

Since the Tehuacán valley is far from isolated, being contiguous with areas having similar habitats, the high rate of endemism in the flora must be accounted for by other factors. Great age is one of the factors often cited as conducive to the accumulation of variations and the development of endemic species in a flora. Little doubt can be had that the Tehuacán region is old, but this alone is insufficient to account for the facts. Probably the age of the area is coupled with a uniform climate for a very long period because of the mass of the Sierra de Zongolica along the northeastern side of the valley. No marked change in the rainfall pattern may have occurred since the Tertiary; the vegetal remains for a period from about 11,000 B.C. to historical times recovered in cave deposits show no changes reflecting late Pleistocene climatic changes such as are known for northern Mexico and the southwestern United States.

TABLE 1.—Family and Geographic Relationships of 253 Species of Tehuacán Area Plants

(Families represented by only one species not included)

FAMILY	*Widely distrib.* 127 *spp.* 50.1%		*No. Mexico* 35 *spp.* 13.8%		*Pacific Coast* 11 *spp.* 4.3%		*So. Mexico* 6 *spp.* 2.3%		*Endemic* 74 *spp.* 29.1%	
	% of 127 spp.	% of 253 spp.	% of 35 spp.	% of 253 spp.	% of 11 spp.	% of 253 spp.	% of 6 spp.	% of 253 spp.	% of 74 spp.	% of 253 spp.
Leguminosae	10.2	5.1	20.0	2.8	54.5	2.4	50.3	1.2	14.9	4.3
Euphorbiaceae	7.8	4.0	2.9	0.4	18.2	0.8	...	...	5.4	1.6
Compositae	7.0	3.6	8.6	1.2	...	...	...	...	9.5	2.8
Gramineae	7.0	3.6	2.9	0.4	...	...	...	...	...	...
Convolvulaceae	4.7	2.4	...	...	...	...	...	...	1.4	0.4
Verbenaceae	4.7	2.4	...	...	...	...	...	...	...	...
Solanaceae	4.7	2.4	2.9	0.4	...	...	...	...	1.4	0.4
Scrophulariaceae	3.9	2.0	...	...	...	...	...	...	2.7	0.8
Nyctaginaceae	3.1	1.6	...	...	...	...	...	...	...	...
Apocynaceae	3.1	1.6	...	...	...	...	...	...	...	...
Commelinaceae	3.1	1.6	2.9	0.4	...	...	...	...	...	...
Asclepiadaceae	2.4	1.2	...	...	9.1	0.4	...	...	...	...
Boraginaceae	2.4	1.2	...	...	...	...	...	...	2.7	0.8
Cactaceae	0.8	0.4	14.3	2.0	...	...	...	...	16.2	4.7
Loranthaceae	1.6	0.8	5.7	0.8	...	...	...	...	1.4	0.4
Liliaceae	1.6	0.8	5.7	0.8	...	...	...	...	2.7	0.8
Anacardiaceae	1.6	0.8	...	...	18.2	0.8	...	...	...	...
Amarylidaceae	...	...	2.9	0.4	...	...	...	...	6.8	2.0
Labiatae	0.8	0.4	2.9	0.4	...	...	...	...	5.4	1.6
Crassulaceae	...	...	...	...	...	...	...	...	4.1	1.2
Malpighiaceae	0.8	0.4	...	...	...	...	...	...	4.1	1.2
Burseraceae	1.6	0.8	...	...	...	...	...	...	2.7	0.8
Sterculiaceae	0.8	0.4	...	...	...	...	...	...	2.7	0.8

REFERENCES

Cain, S. A.

1944. Foundations of plant geography. Bibliog. xiv. 556 pp. New York.

Contreras, Alfonso

1942. Mapa de las provincias climatologicas de la Republica Mexicana. [Mexico] Sec. de Agricultura y Fomento, Dir. de Geografia, Meteorologia y Hydrologia, Instit. Geografico.

Miranda, F.

1942. Estudios sobre la vegetación de México III. Notas generales sobre la vegetación del s. o. del estado de Puebla, especialmente de la zona de Itzocan de Matamoros Anal. Inst. Biol. Mex. **13**, pp. 417–459.

1948. Datos sobre la vegetacion en la cuenca alta del Papaloapan. Anal. Inst. Biol. Mex. **19**, pp. 333–364.

Rzedowski, J.

1962. Contribuciones a la fitogeografiá floristica e historica de Mexico. I. Algunas consideraciones acerca del elemento edémico en la flora Mexicana. Bol. Soc. Bot. Mex. **27**, pp. 52–65.

Schuchert, C. and C. O. Dunbar

1949. Historical geology. xii, pp. 567. New York.

Sharp, A. J.

1953. Notes on the flora of Mexico: World distribution of the woody dicoty ledonous families and the origin of the modern vegetation. Journ. Ecol. **41**, pp. 374–380.

Publication 987