A PRELIMINARY ECOLOGICAL STUDY OF THE ALPINE¹
FLORA OF POPOCATEPETL AND IZTACCIHUATL²

by

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As part of a program to develop a thorough taxonomic, phytogeographic, and ecological understanding of the alpine flora of Mexico, an ecological study on Popocatepetl and Iztaccihuatl was initiated in the summer of 1959. Through this type of investigation it is expected that more precise information can be obtained on species distribution patterns and community structure than is possible by ordinary plant collecting techniques.

In spite of frequent visits by collectors to many of the alpine areas in Mexico, the only serious attention given the alpine flora before the present project was by the early authors Hemsley (1887), Heilprin (1892), and Purpus (1907). Knowledge of the alpine flora has been limited by the scarcity of critical and comparative field data. My studies have thus far included about eight months of field work in Mexico. An outline of field work accomplished in 1958 (Beaman 1959) and some data on chromosome numbers in the alpine species (Stoutamire and Beaman, 1960) have already been published. Much more study will be necessary before complete taxonomic and phytogeographic treatments of the alpine flora are possible. This paper is the first report on an ecological analysis of the alpine and subalpine meadow vegetation.

It has been convenient for several reasons to concentrate the ecological studies of the alpine flora on Popocatepetl and Iztaccihuatl. They are the most easily accessible of all the high Mexican volcanoes; it is possible to drive to timberline on both of them, and a good road extends for a distance of 12 kilometers between them from an altitude of 3680 meters to almost 4000 meters. Excellent topographic maps of the area are available (see table 1), and it was therefore possible to geographically locate with considerable accuracy the stands where quadrats were examined. Finally, the available geological literature about Popocatepetl and Iztaccihuatl should aid in the interpretation of the ecological data. The glaciers of the two mountains have been examined recently by Lorenzo (1959), and White (1956a, 1956b) has been conducting intensive investigations on the Pleistocene geology of the area.

1 Although the term "alpine" originally pertained to the European Alps, it is now widely used throughout the world in designating features of high mountains such as the vegetation. Especially in North America it has frequently been used in referring to vegetation above tree line. The term "páramo" has been used in the same sense in Mexico (Miranda, 1952, p. 166), but in the western hemisphere this appellation of Spanish origin is rather firmly attached to the northern Andes the floristic affinities of the high-mountain vegetation of Mexico with either the Andes or the Rocky Mountains are not strong enough to merit preference for either term. In this study the flora above tree line on Popocatepetl and Iztaccihuatl is referred to as "alpine" rather than "páramo" because the former term is better understood and more generally applicable than the latter.

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Our knowledge of the climate in the alpine zone is limited, although the data published by Robles Ramos (1944) give some idea of the weather conditions that prevail. The climatic pattern of the alpine areas is similar to that of most of the rest of Mexico in having annual wet and dry seasons. The wet season extends from May or June to November or December, and the dry season occupies the remainder of the year. Night temperatures may drop to near or below freezing, while the days are somewhat warmer, especially when there are no clouds. The snow line in summer usually remains above 4700 meters, but in winter, snows may sometimes cover the whole alpine area.

The topsoils of the alpine meadows are mostly black loams containing considerable organic matter. Below the topsoil are stratified layers of pumice and former topsoils. This stratification has resulted from successive volcanic ejections and subsequent weathering. On Popocatepetl the soils above 4000 meters are not much weathered and consist mainly of fine black sand or layers of sand, pumice, and gravel. A series of soil samples has been collected in the study area, and an analysis for available nutrients in a sample of topsoil from 4000 meters on Iztaccihuatl gave the following results: pH, 6.1; NO_3 , 16 lbs/acre; P, 28 lbs/acre; K, 221 lbs/acre; Ca, 160 lbs/acre; Mg, 16 lbs/acre; Mn, 2 lbs/acre; and Cl, 160 lbs/acre.

PROCEDURE

At every 100-meter altitudinal level, from 3700 meters on the north and south sides of the Paso de Cortés to 4300 meters on Popocatepetl and Iztaccihuatl, species presence and density were recorded in meter-square quadrats. Each area sampled is hereafter called a stand. The map locations of the stands are indicated in table 1, and the relative positions of the same in figure 1. The stands were located in the field with a Thommen pocket altimeter (model 3 D 1) in conjunction with the topographic maps, and are probably within 10 meters of the elevations as shown on the maps. Five quadrats were sampled in each stand. The first quadrat was located by throwing a pick into the air and establishing a corner of the quadrat where the pick landed. The other four quadrats were on a straight line at 25-meter intervals from the first ones.

All stands were in open, grass-dominated meadow except those at 3800 and 3900 meters on Popocatepetl which were in a forest of *Pinus hartwegii*. The normal tree line on Popocatepetl and Iztaccihuatl is at an altitude of about 4000 meters, but a large strip of nearly treeless meadow extends north and south between the two mountains (see figure 2). In this paper the meadow vegetation above the altitude of the normal tree line is referred to as alpine, and that at lower levels (down to the lowest point in the Paso de Cortés) is called subalpine. Although some alpine species are found up to an altitude of more than 4500 meters, stands were not examined at altitudes higher than 4300 meters because this is about the maximum altitude of well-defined alpine meadow.

The determinations of species recorded in the quadrats are based on herbarium specimens collected in the study area. These specimens are deposited in the Herba-

rium of Michigan State University, and duplicates will be distributed to other herbaria. The names of species are provisional, and some changes undoubtedly will be necessary when the taxonomic studies have been completed.

RESULTS AND DISCUSSION

From the quadrat data it is evident that the stands vary greatly in species composition (see table 2). Variations occur in numbers and kinds of species present and in numbers of plants present. As the altitude increases, the number of species and the number of individual plants decrease (see table 1). For example, in the quadrats at 3700 meters on Popocatepetl there were 24 species and 1777 individual plants while at 4300 meters only four species and 84 plants were encountered. The species composition in stands at 3700 meters is almost totally different from that at 4300 meters. On Popocatepetl no one species was common to stands at 3700 and 4300 meters, and on Iztaccihuatl only two species, *Draba jorullensis* and *Gnaphalium vulcanicum*, occurred at both elevations. The distribution and frequency data of the species included in the stands are summarized in table 2.

The quadrat data have been employed in an attempt to evaluate the importance of the species on the basis of their frequency, density, and altitudinal range. The method for determining this importance is as follows: The total number of stands from 1 to 10 (no single species occurred in more than 10 stands) in which the species occurred is added to a number which represents the total number of quadrats in all stands in which the species occurred; the sum of these two figures is then added to a number representing the total number of plants in all quadrats in all stands in which the species was encountered; this final sum is the "importance index" number for the species. The numbers used to represent the total number of quadrats in which species occurred were arbitrary and ranged from one to seven. Likewise, the numbers representing the total numbers of plants of species in all quadrats in all stands were arbitrary and ranged from one to five. It was necessary to use these arbitrary numbers to weigh as equitably as possible the contributions to the "importance index" number of each of the three sources. The occurrence of the species by stands, quadrats, and individual plants and the arbitrary numbers used in determining the "importance index" are given in table 3. In table 4 the species are listed, from most important to least important, each with its "importance index" and the numbers used to obtain the index.

The "importance index" numbers in general agree with field observations of the alpine species. *Calamagrostis tolucensis*, the dominant grass in much of the alpine area, has one of the highest numbers. Likewise, *Muhlenbergia quadridentata*, which is dominant in the subalpine meadow, has a relatively high number which results from its high frequency and density at the lower elevations. Although *Draba jorullensis* and *Trisetum spicatum* are not dominant species, their ubiquity is responsible for their high index numbers.

Comparisons of the degree of similarity in species composition between stands were made with the use of community coefficients. The method of Jaccard as me-

dified by Gleason (1920) has been employed in determining the community coefficients. The formula for Gleason's modification is as follows:

$$\text{Community coefficient} = \frac{c}{a + b + c} \times 100$$

where a=the sum of the frequencies of species in stand A; b=the sum of the frequencies of species in stand B; and c = $\frac{1}{2}$ the sum of the frequencies of species common to stands A and B. Table 5 summarizes the community coefficients of adjacent stands on each of the mountains and of stands at equal altitudes on the two mountains. The community coefficients show that no two stands have the same species structure. The similarity of adjacent stands, however, is reflected by their coefficients usually being above 40 per cent. A continuum of similarity from stand to stand is evident, especially on Iztaccihuatl where all the adjacent-stand community coefficients fall within a narrow range between 44.0 and 54.5 per cent. The coefficient is very low only in the comparison of the 3700-3800 and 3900-4000 meter stands on Popocatepetl. These coefficients are low because the comparison is between meadow stands and stands in *Pinus hartwegii* forest. The forest stands are similar to each other (with a coefficient of 73.9 per cent), but contrast sharply with the meadow stands. The stands under *Pinus hartwegii* differ most conspicuously from those in the meadows in that the former have fewer species present (see table 2).

When stands at the same altitude on Popocatepetl and Iztaccihuatl are compared, the community coefficients are lower than those of adjacent stands. Probably the most important factor in lowering these coefficients is the influence of the sandy soils on Popocatepetl which support a poorer flora than the loam soils of Iztaccihuatl.

Although the community coefficients reveal a gradual change in species composition in the stands at different altitudinal levels, it is still possible to recognize certain phases of the continuum pattern in the alpine meadow vegetation. Four major phases, without sharply defined boundaries, can be distinguished in the study area. These phases are designated by the names of their dominant species. The *Calamagrostis tolucensis-Festuca tolucensis* meadow is most typical at about 4000 meters, but extends down to about 3800 meters, and on Iztaccihuatl up to the 4300-meter level. On Popocatepetl, however, it does not reach much higher than 4100 meters. There are variations in species presence and density in this meadow in different stands, but the general aspect is relatively uniform. A second phase, which has a low number of species present (see table 2), is the *Festuca livida-Arenaria bryoides* meadow on Popocatepetl at the 4200- and 4300-meter levels. The third meadow phase, dominated by *Muhlenbergia quadridentata*, occurs in the Paso de Cortés at the 3700-meter level, and extends up to slightly above 3800 meters where it blends gradually into the *Calamagrostis tolucensis-Festuca tolucensis* meadow. Many of the members of this phase are not alpine species, but are from lower elevations and

reach their upper limits in this subalpine meadow. The fourth phase is *Pinus hartwegii* forest with a meadow-like forest floor. Under the pines *Festuca tolucensis* is the dominant species. This phase occurs at the 3800- and 3900-meter levels on Popocatepetl. Under the tree canopy *Festuca tolucensis* develops a very heavy ground cover, but relatively few other species thrive in this habitat (see table 2).

As a means for determining the adequacy of sampling, species-area curves for minimal sampling area were constructed. With this method a line tangent to the curve indicates the point at which a 10 per cent increase in the area sampled resulted in a 5 per cent increase in species recorded. An adequate sample for a stand should exceed the number of quadrats where the line is tangent to the curve. In species-area curves for the alpine meadow stands, the tangent fell between two and four quadrats, suggesting that a sample of five quadrats per stand was adequate.

Although sampling might appear adequate from the species-area curves, the sampling technique had several imperfections. First, the meter-square quadrats were larger than necessary for efficient sampling of this vegetation. Second, an estimate of cover per cent rather than density in the quadrats would have been easier to obtain and more useful for analyses. Third, only five frequency classes are possible when five quadrats per stand are sampled. Fourth, the results are not adaptable to refined statistical analyses because the quadrats per stand were few in number and not randomly distributed.

In spite of these objections, however, the data contribute to the understanding of species interrelationships in the alpine flora. They clarify distribution patterns of the alpine species, and indicate the relative importance of species. Finally, the data permit a characterization of the species composition of the alpine meadows and comparisons among all phases of the meadows.

A further ecological study, in which the quantitative data can be treated statistically, was conducted in the same area in the summer of 1960. This investigation will be published later.

SUMMARY

At every 100-meter level between 3700 and 4300 meters on Popocatepetl and Iztaccihuatl, five meter-square quadrats were used for determining species presence and frequency. From the resulting data several observations about the alpine flora were made. With an increase in altitude, there was a reduction in number of species and number of individual plants present. The quadrat data clarified species distribution patterns and showed that most species have a restricted altitudinal range. Only two species extended from the 3700- meter level to the 4300-meter level. With the data obtained, it was possible to evaluate the relative importance of each of the species. Only a few species were extremely important, and a large number of species had little importance. Adjacent stands and stands at equal altitudes were compared by the community coefficient method. No two stands had the same species structure, but adjacent stands usually had a community coefficient of at least 44 per

cent. Stands in *Pinus hartwegii* forest, however, were distinctly different from those in meadows, as indicated by the low community coefficients when the two were compared. Four major phases of the alpine meadows were designated and briefly characterized. Although these phases did not have sharp boundaries, they usually could be readily recognized in the field.

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Table 1

Location of stands and number of species and individual plants encountered in 14 stands in the Iztaccihuatl—Paso de Cortés—Popocatepetl area.

Stand		Map*		Co-ordinates	No. of species	No. of plants
Iztaccihuatl, 4300 m.	Iztaccihuatl	14 Q-h (107)		538.10, 2116.25	10	98
Iztaccihuatl, 4200 m.	Iztaccihuatl	14 Q-h (107)		538.05, 2116.05	6	94
Iztaccihuatl, 4100 m.	Iztaccihuatl	14 Q-h (107)		537.95, 2115.80	13	221
Iztaccihuatl, 4000 m.	Iztaccihuatl	14 Q-h (107)		536.90, 2114.60	23	479
Iztaccihuatl, 3900 m.	Popocatepetl	14 Q-h (123)		537.10, 2114.45	25	527
Iztaccihuatl, 3800 m.	Popocatepetl	14 Q-h (123)		537.25, 2112.20	21	720
Iztaccihuatl, 3700 m.	Popocatepetl	14 Q-h (123)		536.70, 2111.10	23	523
Popocatepetl, 3700 m.	Popocatepetl	14 Q-h (123)		537.15, 2109.60	24	1777
Popocatepetl, 3800 m.	Popocatepetl	14 Q-h (123)		537.80, 2108.40	8	133
Popocatepetl, 3900 m.	Popocatepetl	14 Q-h (123)		537.70, 2107.60	9	124
Popocatepetl, 4000 m.	Popocatepetl	14 Q-h (123)		538.25, 2106.85	14	178
Popocatepetl, 4100 m.	Popocatepetl	14 Q-h (123)		538.40, 2106.05	11	137
Popocatepetl, 4200 m.	Popocatepetl	14 Q-h (123)		538.40, 2105.70	6	84
Popocatepetl, 4300 m.	Popocatepetl	14 Q-h (123)		538.70, 2105.35	4	84

*Maps of the Fotomapas del Valle México series, 14 Q-h (107 and 14 Q-h (123), scale 1:25,000, contour interval 10 meters, published by the Departamento Cartográfico Militar, Secretaría de la Defensa Nacional, México, D. F.

Table 2. Distribution and per cent frequency of species in 14 stands on Iztaccihuatl and Popocatepetl.

[illegible]

Species	Iztaccihuatl					Stand				Popocatepetl				
	4300	4200	4100	4000	3900	3800	3700	3700	3800	3900	4000	4100	4200	4300
	m	m	m	m	m	m	m	m	m	m	m	m	m	m
<i>Lithospermum distichum</i>	—	—	—	—	40	—	20	—	—	—	—	—	—	—
<i>Lupinus mexicanus</i>	—	—	—	80	100	100	80	60	20	20	—	—	—	—
<i>Lupinus montanus</i>	—	—	100	20	—	—	—	—	—	—	80	40	—	—
<i>Luzula racemosa</i>	20	—	20	100	60	—	—	40	—	—	—	20	—	—
<i>Muhlenbergia quadridentata</i>	—	—	—	—	80	100	100	100	—	—	—	—	—	—
<i>Oreobroma megarhizum</i>	20	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oreomyrrhis orizabae</i>	—	—	—	—	20	—	—	—	—	—	—	—	—	—
<i>Oxalis alpina</i>	—	—	—	—	20	—	60	100	—	—	—	—	—	—
<i>Penstemon gentianoides</i>	—	—	—	40	—	—	60	—	—	—	60	—	—	—
<i>Phacelia platycarpa</i>	—	—	20	—	—	—	20	60	20	20	20	—	—	—
<i>Plantago tolucensis</i>	—	—	—	60	60	100	80	100	—	—	—	20	—	—
<i>Poa orizabensis</i>	—	—	—	—	40	40	—	40	—	—	—	—	—	—
<i>Ranunculus donianus</i>	—	—	—	20	100	80	20	—	—	—	—	—	—	—
<i>Senecio bellidifolius</i>	—	—	—	—	—	40	100	100	—	—	—	—	—	—
<i>Senecio calcarius</i>	—	—	—	—	—	—	—	—	—	—	20	—	—	—
<i>Senecio gerberaeifolius</i>	—	40	60	40	—	—	—	—	—	—	—	—	—	—
<i>Senecio procumbens</i>	60	—	—	60	—	—	—	—	—	—	—	60	80	40
<i>Senecio roseus</i>	—	20	80	20	—	—	—	—	20	—	—	—	—	—
<i>Sisyrinchium bracteatum</i>	—	—	—	—	—	40	20	20	—	—	—	—	—	—
<i>Sisyrinchium quadrangulatum</i>	—	—	20	20	—	—	—	—	—	—	—	—	—	—
<i>Solanum demissum</i>	—	—	—	—	—	60	—	—	—	—	—	—	—	—
<i>Stachys eriantha</i>	—	—	—	40	80	60	100	40	—	—	40	—	—	—
<i>Trifolium amabile</i>	—	—	—	—	—	20	80	20	—	—	—	—	—	—
<i>Trisetum rosei</i>	—	—	—	—	—	—	80	100	—	—	—	—	—	—
<i>Trisetum spicatum</i>	80	20	20	60	80	100	—	—	—	—	20	40	60	20
<i>Vaccinium geminiflorum</i>	—	—	—	—	—	—	20	—	80	60	—	—	—	—
<i>Verbena teucriifolia</i>	—	—	—	—	—	—	40	—	—	—	—	—	—	—
<i>Viola humilis</i>	—	—	—	—	80	—	—	—	20	—	—	—	—	—

TABLE 3. Distribution of the species by stands, quadrats, and individual plants, and arbitrary numbers for weighting quadrat and individual plants data for the "importance index".

Stands*		Quadrats*		
number of species	number of stands	number of species	number of quadrats	arbitrary number for weighting
14	1	21	1-5	1
6	2	12	6-10	2
12	3	10	11-15	3
5	4	5	16-20	4
5	5	4	21-25	5
6	6	2	26-30	6
3	7	1	31-35	7
2	8			
1	9			
1	10			

Individual Plants*

number of species	number of plants	arbitrary number for weighting
10	1-5	1
11	6-20	2
14	21-50	3
12	51-200	4
8	over 200	5

* Under **Stands** read "number of species which occurred in how many stands", e. g., 14 species occurred in one stand only; 6 species occurred in 2 stands, etc. Under **Quadrats** read "number of species which occurred in how many quadrats", e. g., 21 species occurred in one to five quadrats, etc. Under **Individual Plants** read "number of species which were represented by how many individual plants", e.g., 10 species were represented by one to five plants, etc.

Table 4. Importance Indexes

	stand value	weighted quadrat value	weighted density value	importance index
<i>Draba jorullensis</i>	9	6	5	20
<i>Calamagrostis tolucensis</i>	8	7	4	19
<i>Trisetum spicatum</i>	10	5	4	19
<i>Gnaphalium vulcanicum</i>	8	6	4	18
<i>Lupinus mexicanus</i>	7	5	5	17
<i>Conyza schiedeana</i>	6	5	5	16
<i>Plantago tolucensis</i>	6	5	5	16
<i>Arenaria reptans</i>	7	4	3	14
<i>Cerastium vulcanicum</i>	5	4	5	14
<i>Festuca tolucensis</i>	6	4	4	14
<i>Stachys eriantha</i>	6	4	4	14
<i>Cirsium nivale</i>	7	3	3	13
<i>Luzula racemosa</i>	6	3	4	13
<i>Muhlenbergia quadridentata</i>	4	4	5	13
<i>Alchemilla vulcanica</i>	5	3	4	12
<i>Cerastium orithales</i>	5	3	4	12
<i>Arenaria bryoides</i>	4	3	4	11
<i>Phacelia platycarpa</i>	6	2	3	11
<i>Ranunculus donianus</i>	4	3	4	11
<i>Senecio bellidifolius</i>	3	3	5	11
<i>Senecio procumbens</i>	5	3	3	11
<i>Eryngium protaeflorum</i>	5	2	3	10
<i>Festuca livida</i>	3	3	4	10
<i>Lupinus montanus</i>	4	3	3	10
<i>Oxalis alpina</i>	3	2	5	10
<i>Senecio roseus</i>	4	2	4	10
<i>Agrostis tolucensis</i>	3	2	3	8
<i>Drymaria effusa</i> var. <i>depressa</i>	3	2	3	8
<i>Trifolium amabile</i>	3	2	3	8
<i>Vaccinium geminiflorum</i>	3	2	3	8
<i>Penstemon gentianoides</i>	3	2	2	7
<i>Poa orizabensis</i>	3	2	2	7
<i>Senecio gerberaefolius</i>	3	2	2	7
<i>Trisetum rosei</i>	2	2	3	7
<i>Carex peucophila</i>	3	1	2	6
<i>Cerastium molle</i>	1	1	3	5
<i>Eryngium carlinae</i>	1	1	3	5
<i>Geranium cruceroense</i>	2	1	2	5
<i>Lithospermum distichum</i>	2	1	2	5

	stand value	weighted quadrat value	weighted density value	importance index
<i>Oreomyrrhis orizabae</i>	1	1	3	5
<i>Sisyrinchium bracteatum</i>	3	1	1	5
<i>Viola humilis</i>	2	1	2	5
<i>Carex geophila</i>	1	1	2	4
<i>Halenia nudicaulis</i>	1	1	2	4
<i>Hieracium mexicanum</i>	2	1	1	4
<i>Juncus balticus</i> var. <i>mexicanus</i>	1	1	2	4
<i>Sisyrinchium quadrangulatum</i>	2	1	1	4
<i>Verbena teucriifolia</i>	1	1	2	4
<i>Achillea lanulosa</i>	1	1	1	3
<i>Castilleja schaffneri</i>	1	1	1	3
<i>Festuca amplissima</i>	1	1	1	3
<i>Gnaphalium sarmentosum</i>	1	1	1	3
<i>Oreobroma megarhizum</i>	1	1	1	3
<i>Senecio calcarius</i>	1	1	1	3
<i>Solanum demissum</i>	1	1	1	3

TABLE 5. Community coefficients, in per cent, of adjacent stands and of stands of equal altitudes on Popocatepetl and Iztaccihuatl.

Iztaccihuatl altitudes	Iztaccihuatl adjacent- community coefficients	equal- altitude- community coefficients	Popocatepetl adjacent- community coefficients	Popocatepetl altitudes
4300 m.		27.6		4300 m.
	54.5		77.7	
4200 m.		14.9		4200 m.
	44.0		66.1	
4100 m.		34.7		4100 m.
	47.0		35.4	
4000 m.		38.1		4000 m.
	54.5		14.6	
3900 m.		11.1		3900 m.
	46.6		73.9	
3800 m.		4.1		3800 m.
	53.3		13.1	
3700 m.		68.0		3700 m.

Figure 1. Profile of the Iztaccihuatl-Paso de Cortés-Popocatepetl area, showing relative positions of stands studied and total number of species and individual plants which occurred in each stand.

Figure 2. Photograph from 3750 meters on Iztaccihuatl, looking south through the Paso de Cortés to Popocatepetl.