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STUDIES IN THE CEMBROID PINES

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STUDIES IN THE CEMBROID PINES

CHAPTER I

INTRODUCTION

The continued existence of any living organism is dependent upon its ability to become adapted to a continually changing environment. The essence of this ability lies ultimately in the genetic constitution of the individual organism in that it determines the limits of ecological conditions under which the organism may survive. If we hope to understand the origin and development of divergent types of life from common ancestral stocks, we must seek to understand the characteristics of the hereditary material which permit such divergence.

Darwin suggested that variation is a natural characteristic of life and that it is essential to the development of the evolutionary scheme. Mendel demonstrated the potential effect of genetic recombination on the establishment of variability in morphological characteristics. Later, DeVries presented his concept of genetic mutation and its possible role in the introduction of new genetic material which could then be acted upon by natural selection.

Utilizing these concepts in association with paleontological evidence, various authors have attempted to outline the evolutionary development of the major categories of living organisms. Significantly, the one thing that most of the proposed systems have had in common is their tentative and often limited acceptance, even by their authors. However, these attempts have made important contributions to our understanding of evolution in that they have forced us to critically re-examine the soundness of many of the standard taxonomic concepts that have been drawn upon in the past. Additionally, they have presented a basis for the determination of those areas of study which must be better understood before more refined decisions concerning phylogeny may be made.

Perhaps one of the most significant areas in which understanding has been clouded by generalization is the process of speciation itself. I believe that far too often the terms "speciation" and "evolution" have been treated synonymously. In this dissertation I will employ these terms in the sense outlined below. "Speciation" is that aspect of evolution in which a particular group of organisms may give rise to two or more distinct taxa as a result of the interaction of natural selection with some form of isolation. This is essentially the process of evolutionary divergence which may or may not lead to the formation of new species. "Evolution" encompasses the process of speciation, but goes

beyond it in that it must include any change in the genetic structure of a taxon which may lead to an alteration of the characteristics of that taxon without necessarily resulting in the formation of divergent types. These genetic changes may occur through mutation or through any of several possible forms of recombination. I would like to consider the effect of these genetic alterations on the process of evolutionary divergence in greater detail.

Divergence is frequently explained as the result of the response of a group of living organisms to different sets of environmental conditions. This may be interpreted in at least two different ways. Commonly, divergence is thought to arise from the reaction of marginal populations to relatively local environmental differences. If these populations remain in contact with the main body of the species, the clinal variation typical of many widely distributed forms ensues. If these populations become partially isolated from the rest of the species, the stage is set for ecotypic differentiation and, conceivably, eventual speciation. This is the traditional sequence of events leading to species formation. However, it is just as likely that in a widely distributed species genetic divergence could occur in response to a changing environmental situation even though the selective factors were identical throughout the range of that species. In other words, it is possible that a species might become adapted to a widespread environmental change in more than one way. Finally, the rate

and extent of divergence are subject to the intensity of the selective factors involved, the types of isolating mechanisms that are active, and the extent and frequency of genetic interchange between the diverging forms.

In this dissertation I will attempt to show how interactions of some of the phenomena discussed above may have affected the evolutionary development of the Cembroid pines of southwestern North America. I will also present a taxonomic revision of the group based on the data resulting from this study.

CHAPTER II

TAXONOMY AND DISTRIBUTION

In his monograph of the genus Pinus, Shaw (1914) placed the Cembroid pines in the section Haploxylon, subsection Paracembra, group Cembroides. This classification has been generally accepted with some changes in rank although there is some doubt concerning the inclusion of Pinus nelsonii Shaw in the group (Martinez, 1945). Shaw's classification at the rank of species and below has had limited acceptance by later authors because of his tendency to place highly variable groups of organisms under a single specific epithet. For example, he recognizes only three species in the group Cembroides, Pinus cembroides Zuccarini, P. pinceana Gordon, and P. nelsonii Shaw, while other authors have included as many as seven.

The following classification will be employed in this dissertation:

Pinus cembroides Zuccarini

Pinus cembroides subsp. culminicola (Andresen & Beaman) stat. nov.

Pinus monophylla Torrey

Pinus monophylla var. *diphylla* var. nov.

Pinus monophylla subsp. *edulis* (Engelmann) stat. nov.

Pinus monophylla subsp. *quadrifolia* (Parlatore ex Sudworth) stat. nov.

Pinus x eduloides sp. nov.

Pinus x eduloides nm. *cochisensis* nm. nov.

Pinus nelsonii Shaw

Pinus pinceana Gordon

The remainder of this chapter is devoted to the description and distribution (Figure 1) of the taxa listed above and includes a brief discussion of the problem of synonomy in this group. Latin diagnoses of the new names introduced in this paper may be found in Appendix I.

KEY TO THE SPECIES

A. Ovulate cones subsessile; subglobose to ovoid; less than 6 cm. long.

  B. Needles in fascicles of 3 or 5; non-aromatic when fresh; seed coats uniformly thick..*Pinus cembroides*

  B. Needles in fascicles of 1, 2, 3, or 4; highly aromatic when fresh; seed coats variable in thickness.

    C. Needles in fascicles of 1, 2, or 4; seeds greater than 13 mm. in length; seed coats uniformly thin .....*Pinus monophylla*

    C. Needles in fascicles of 2 or 3; seeds less than 13 mm. in length; seed coats variable in thickness.....*Pinus x eduloides*

A. Ovulate cones pedunculate; ovoid to subcylindrical; greater than 6 cm. long.

D. Needles in fascicles of 3; basally connate; free margins serrulate; fascicle sheaths persistent .....*Pinus nelsonii*

D. Needles in fascicles of 3; totally distinct; margins entire; fascicle sheaths deciduous...*Pinus pinceana*

KEY TO INFRASPECIFIC TAXA

Pinus cembroides

A. Small tree with needles in fascicles of 3 .....subsp. *cembroides*

A. Shrub with needles in fascicles of 5..subsp. *culminicola*

Pinus monophylla

A. Needles in fascicles of 1 or 1 and 2 on the same tree.

B. Needles in fascicles of 1; 5 to 6 cm. long and 2 to 2.5 mm. in diameter .....subsp. *monophylla* var. *monophylla*

B. Needles in fascicles of 1 or 1 and 2 on the same tree; 3 to 4.5 cm. long and 0.8 to 1.1 mm. wide .....subsp. *monophylla* var. *diphylla*

A. Needles in fascicles of 2 or 4.

C. Needles in fascicles of 2.....subsp. *edulis*

C. Needles in fascicles of 4.....subsp. *quadrifolia*

Pinus x eduloides

A. Needles predominantly in fascicles of 2; 1.5 to 4 cm. long and 0.9 to 1.2 mm. wide.....nm. eduloides

A. Needles predominantly in fascicles of 3; 3 to 5 cm. long and 0.6 to 0.9 mm. wide.....nm. cochisensis

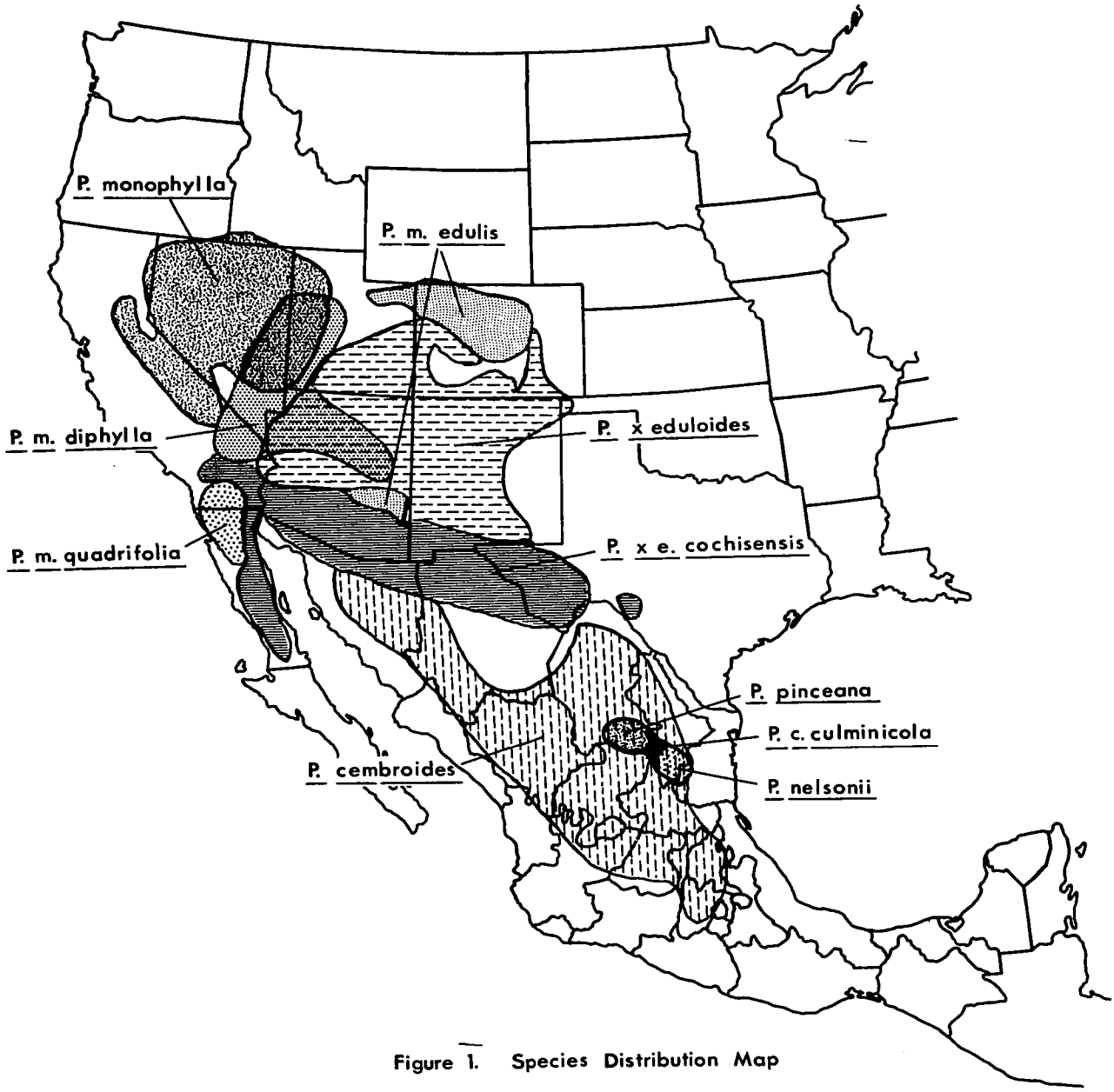


Figure 1. Species Distribution Map

Pinus cembroides Zuccarini

Small tree or shrub, 1 to 15 m. in height with short, often profusely branched trunk; needle fascicles retained on branches for a period of 1 to 3 years, rarely longer; fascicle sheaths of membranous, stramineous scales which become revolute with age; ovulate cones subglobose to ovoid, 3 to 5 cm. long, 3 to 4 cm. wide, subsessile; apophyses irregularly furrowed and centrally depressed bearing a laterally keeled, elliptical to subrhomboidal, dorsal umbo; seeds wingless, borne singly or in pairs on central and upper scales of the cone; seed length about 1.5 times its width; seed coat thick.

P. cembroides subsp. cembroides

1832 P. cembroides Zuccarini, Abh. Akad. Wiss. Muenchen, 1:392.

1838 P. llaveana Otto ex Loudon, Arb. et Frut. Brit., Species # 2267.

1838 P. llaveana Schiede, Linnaea, 12:488.

1848 P. osteosperma Engelmann, in Wislizenus, Mem. Tour N. Mexico, 89.

Small tree up to 15 m. in height; crown conical when young becoming spherical to ellipsoidal at maturity; branching pattern excurrent when young to deliquescent with age; bark irregularly fissured and reddish-brown on older portions of the stem to various shades of gray on younger shoots; needles in fascicles of 3, rarely 2, 3 to 5 cm. long, 0.5 to

1.0 mm. wide, margins entire to remotely serrulate; staminate cones variable in number of microsporophylls; microsporophylls less than 1.0 mm. broad at anthesis, reddish, coriaceous; pollen grains averaging 56 micra from wing tip to wing tip with a gap of about 15 micra between bladders; seeds about 13 mm. long and 9 mm. wide with a seed coat 1.0 mm. or more in thickness.

This subspecies ranges from central Sonora, Chihuahua, Coahuila, and Nuevo León, Mexico southeastward to the state of Puebla, Mexico and may be found from approximately 1800 to 2800 m. above sea level. Isolated individuals may occur in southern Texas, New Mexico, Arizona, and California and in Baja California.

Type locality: Mexico, near Sultepec in the state of Mexico.

P. cembroides subsp. culminicola (Andresen & Beaman) stat. nov.

1961 P. culminicola Andresen & Beaman, Jour. Arnold Arboretum, 42:437.

Shrub, 1 to 5 m. in height with dense crown; branching pattern deliquescent; bark dark brown on heavily thickened branches; needles in fascicles of 5, rarely 4 or 6, 3 to 4.9 cm. long, 1 to 1.3 mm. wide, margins remotely serrulate; seed-bearing cavity 9 mm. long and 6 mm. wide; seed unknown but probably wingless with a relatively thick coat.

This subspecies is known only from Cerro Potosí in Nuevo León, Mexico and is found from 2800 to 3600 m. above sea level.

Type locality: Mexico, near the top of Cerro Potosí in the state of Nuevo León.

Pinus monophylla Torrey

Small tree up to 15 m. in height; crown conical to ovoid, often spherical; branching pattern excurrent; bark irregularly fissured and dark brown on older portions of the stem to various shades of gray on younger shoots; needle fascicles retained on branches for a period of 5 to 11 years (average about 7 years), rarely less; fascicle sheaths of membranous, stramineous scales which become revolute with age, later deciduous; staminate cones variable in number of microsporophylls; microsporophylls greater than 1.0 mm. broad at anthesis, reddish, coriaceous, occasionally with small apical appendage; pollen grains averaging about 57 micra from wing tip to wing tip with no gap between bladders; ovulate cones subglobose to ovoid, 4 to 6 cm. long, 3 to 5 cm. wide, subsessile, highly resinous; resin strongly aromatic; apophyses striate to smooth, bearing a well-developed, laterally keeled, rhomboidal, dorsal umbo; seeds wingless, borne singly or in pairs on central and upper scales of the cone; seeds averaging 16 mm. in length and 9 mm. in width; seed coat thin (less than 0.5 mm.).

P. monophylla subsp. monophylla

1845 P. monophylla Torrey in Fremont's Rept. Expl. Exped., 319.

1847 P. fremontiana Endlicher, Syn. Conif., 183.

1848 P. llaveana (Hartweg) Hartweg, Jour. Hort. Soc. Lond. 3:226 (not seen).

1905 Caryopitys monophylla (Torrey) Rydberg, Torrey Bot. Club Bul., 32:597.

1907 P. cembroides var. monophylla Voss, Mitt. Deutsch. Dendrol. Ges., 16:95.

Needles in fascicles of 1 or 1 and 2 on the same plant.

P. monophylla subsp. monophylla var. monophylla

Needles borne singly in each fascicle, 5 to 6 cm. long and 2 to 2.5 mm. in diameter.

This variety occurs in California, Nevada, and southern Idaho between 1000 and 2000 m. above sea level. Type locality: U.S.A., near Bridgeport, Mono County, California.

P. monophylla subsp. monophylla var. diphylla var. nov.

1941 P. monophylla var. tenuis Tidestrom in Tidestrom and Kittel, Fl. Ariz. and N. Mex., 2. (without Latin diagnosis).

Needles borne singly or often singly and in pairs on the same plant, 3 to 4.5 cm. long and 0.8 to 1.1 mm. wide.

This variety occurs in Nevada, Utah, Arizona, and southern California.

Type locality: U.S.A., Zion National Park, Utah.

P. monophylla subsp. edulis (Engelmann) stat. nov.

1848 P. edulis Engelmann in Wislizenus, Mem. Tour N. Mexico, 88.

1891 P. monophylla var. edulis Jones, Zoe, 2:251.

1903 Caryopitys edulis (Engelm.) Small, Fl. Southeast U.S., 29.

1907 P. cembroides var. edulis Voss, Mitt. Deutsch. Dendrol. Ges., 16:95.

Needle leaves borne in pairs, rarely 3 per fascicle, 3 to 4.5 cm. long and 0.9 to 1.5 mm. wide.

This subspecies is most common in the mountains of northeastern Utah, central Colorado, east central Arizona, and probably west central New Mexico; however, isolated individuals may occur in other areas of the states mentioned above plus southern Wyoming and southern California between 2100 and 2800 m. above sea level.

Type locality: U.S.A., in northern New Mexico.

P. monophylla subsp. quadrifolia (Parlatore ex Sudworth) stat. nov.

1859 P. llaveana sensu Torrey, Bot. Mex. Bound. Surv., 208, pl. 53.

1862 P. parryana Engelmann, Am. Jour. Sci., ser. 2, 34:332.

1897 P. quadrifolia Parlatore ex Sudworth, U.S. Dept. Agric., Bul. 14, 17.

1907 P. cembroides var. parryana Voss, Mitt. Deutsch. Dendrol. Ges. 16:95.

Needle leaves in fascicles of 4, occasionally 3 or 5, 3 to 5 cm. long and 0.9 to 1.2 mm. wide.

This subspecies is restricted to southern California and northern Baja California and occurs between 1000 and 1900 m. above sea level.

Type locality: U.S.A., near San Diego, San Diego County, California.

Pinus x eduloides sp. nov.

Derivation:

P. monophylla subsp. edulis (Engelm.) Fogg x

P. cembroides Zuccarini.

Small tree up to 15 m. in height; trunk showing variable degrees of branching; crown conical when young becoming ovoid, spherical, or ellipsoidal at maturity; branching pattern variable, generally excurrent in young vegetative shoots and in shoots bearing ovulate cones, deliquescent in shoots bearing staminate cones; bark

irregularly fissured and dark brown to reddish-brown on older portions of the stem, gray to almost black on younger shoots; needle bearing fascicles retained on branches for a period of 2 to 7 years, often with verticillate arrangement on staminate branches; fascicle sheaths of membranous, stramineous scales which become revolute with age, eventually deciduous; needles in fascicles of 2, 3, and occasionally 4, highly variable in length and width, margins entire to remotely serrulate; staminate cones variable in number of microsporophylls; microsporophylls reddish, coriaceous, about 1.0 mm. broad at anthesis; pollen grains 50 to 60 micra from wing tip to wing tip, bladders often poorly developed with narrow gap between them; ovulate cones small, spherical to subglobose, subsessile, frequently aborting before maturity; apophyses smooth to irregularly furrowed bearing an elliptical to rhomboidal, laterally keeled, dorsal umbo, often poorly developed; seeds wingless, borne singly or in pairs on the central scales of the cone; seeds 9 to 13 mm. long and 5 to 7 mm. wide; seed coat variable in thickness.

P. x eduloides nm. eduloides nm. nov.

Needles predominantly in fascicles of 2, ranging from 1.5 to 4 cm. long and 0.9 to 1.2 mm. wide, margins entire. This variant is similar to P. monophylla ssp. edulis in appearance but much more variable and with smaller cones and seeds.

This variant occurs in southern Utah and Colorado, northern Arizona, New Mexico, Oklahoma, and extends southward into western Texas between 1500 and 2700 m. above sea level.

Type locality: U.S.A., Grand Canyon National Park, Arizona.

P. x eduloides nm. cochisensis nm. nov.

Needles predominantly in fascicles of 3, ranging from 3 to 5 cm. long and 0.6 to 0.9 mm. wide, margins entire to remotely serrulate. This variety is similar to P. cembroides in appearance but has smaller cones and seeds and when fresh exhibits the pungent aroma of the subspecies of P. monophylla which does not occur in P. cembroides.

This variety occurs in the southern portions of California, Arizona, New Mexico, and Texas and northern Mexico near the United States border between 1500 and 2700 m. above sea level.

Type locality: U.S.A., Apache National Forest, Greenlee County, Arizona.

Pinus nelsonii Shaw

1904 P. nelsonii Shaw, Gard. Chron., ser. 3, 36:122.

Small tree up to 9 m. in height with long pliant branches; bark gray; fascicle sheaths persistent and non-revolute; needles 3 per fascicle and united along a portion of their ventral surface, 4 to 9.5 cm. long, free margins

serrulate; ovulate cones cylindrical, 6 to 14 cm. long and 5 to 6 cm. in diameter, borne on stout, recurved peduncles ranging from 3 to 5 cm. in length; apophyses elliptical to quadrilateral bearing a laterally keeled, elliptical, dorsal umbo; seeds wingless, about 15 mm. long and 10 mm. wide; seed coat thick.

This species has an extremely limited range in the states of Tamaulipas, Nuevo León, Coahuila, and San Luis Potosi, Mexico between 2000 and 2500 m. above sea level.

Type locality: Mexico, near the border between the states of Nuevo León and Tamaulipas.

Pinus pinceana Gordon

1858 P. pinceana Gordon, The Pinetum, 204.

1882 P. latisquama Engelmann, Gard. Chron., ser. 2, 18:712. (Synonymous as to cone only).

Small tree up to 12 m. in height with long slender branches; bark smooth and gray; fascicle sheaths revolute and later deciduous; needles 3 per fascicle, 6 to 9 cm. long and 0.5 to 0.7 mm. wide, margins entire; ovulate cones ovoid to subcylindrical, 6 to 8 cm. long and 3 to 4 cm. in diameter, borne on peduncles averaging about 2 cm. in length; apophyses slightly furrowed bearing a poorly developed umbo; seeds wingless, about 12 mm. long and 9 mm. wide; seed coat thick.

This species occurs from southern Coahuila to northern Hidalgo in Mexico between 1900 and 2400 m. above sea level.

Type locality: Mexico, Barranca de Meztitlan in the state of Hidalgo.

The morphological plasticity of the Cembroid pines has led to the development of a complex and often confusing list of nomenclatural synonyms. I have listed most of these under the appropriate taxa in the preceding pages, but I feel that further clarification is necessary for a complete understanding of the significance of two of these combinations, Pinus llaveana and P. cembroides. The latter name was first employed by Zuccarini (1832) and was apparently based upon a specimen that had grown in southern Mexico. Pinus llaveana was first published by Loudon (1838) and credited by him to Otto and was based upon a specimen growing in the gardens of the London Horticultural Society. Later in the same year, Schiede's description of P. llaveana appeared in Linnaea in an article on the conifers of Mexico which apparently was compiled and edited by Schlechtendal. Schlechtendal, convinced that Loudon had described and illustrated his species with the wrong cone, attempted to correct this by publishing Schiede's description, which was based on a specimen growing in the Berlin Gardens. It is my opinion that both of these names are synonymous with Zuccarini's P. cembroides and have been discarded on that basis. The relatively slight differences between the three descriptions probably can be attributed to the morphological distinctions arising from the

different environmental situations under which the three plants were grown. In addition, Schiede's statement, "Die Zapfen sind klein, aus wenigen Schuppen bestehend, etwa $1\frac{1}{4}$ Z. lang, rundlich, stumpf." can be misinterpreted to the extent that the measurement is applied to the entire cone rather than one of the scales.

In 1846 Gordon, in the Journal of the London Horticultural Society, described a Mexican pine under the name P. cembroides Zuccarini and I believe that he was correct in doing so, but later, in his book The Pinetum, he discussed the same plant under the name P. cembroides Gordon and listed the combination P. cembroides Zuccarini as a synonym of P. llaveana Schiede. Apparently, the misapplication of P. cembroides by Newberry (1857) and P. llaveana by Torrey resulted either directly or indirectly from Gordon's revision of the synonymy.

The discussion above deals with some of the problems that have been encountered in the synonymy of the pinyon pines, and gives some insight into the nomenclatural confusion that has long plagued the taxonomy of this group.

CHAPTER III

ECONOMIC AND ETHNOLOGIC SIGNIFICANCE

Historically, the pinyons were probably more significant, though not necessarily more important, to the early southwestern Indians than to the present inhabitants of that area. Judging from the frequency of the pinyons in the Southwest, it is reasonable to assume that the Indians would have utilized them as fully as possible since their survival depended upon locally available resources. The most obvious feature of these pines, relative to utilization by man, is the production of large quantities of edible seeds. Most people who have lived in the vicinity of the pinyons are quite familiar with these "nuts," but the early inhabitants of the area were frequently dependent upon a regular supply of them as one of their staple foods. Some Indian tribes regularly sent some of their people in search of pinyon stands where seed production was high. These people occasionally traveled more than one-hundred miles to secure enough seeds to maintain the tribes through the winter and early spring (Gordon, 1880). Occasionally the nuts were eaten fresh, but generally they were toasted to improve

their flavor and aid in preservation during long periods of storage. Cabeza de Vaca wrote the following about the method of seed preparation he witnessed in the Texas Big Bend area in 1536, "(the seed)....while green is beaten and made into balls to be eaten," (Kitson, 1923). Gordon (1880) in his discussion of P. monophylla in The Pinetum wrote, The cones are gathered by the Indians for their principal winter and spring subsistence; either taken out and kept dry in their huts, or left in their natural storehouse, the cones in heaps under the trees, where they remain tolerably dry until wanted for use; the Indians are said to live upon them alone for months and months without any other kind of food."

Local inhabitants still eat pinyon-nuts but are no longer dependent upon them as a major food source. During 1921 over one million pounds of nuts were shipped to eastern markets from New Mexico alone (Perry, 1922), but today the state exports more peanuts than pinyons. In a railroad survey report Bigelow (1856), discussing the pinyons, stated, "In the fattening of swine, this tree would receive a share of public attention. Bears and other animals, in large numbers are known to subsist upon the fruit in those regions." Kitson (1923) reported that pinyon-nuts were used in New Mexico and some eastern stockyards to fatten cattle before shipping them to market.

Historically, and presently, pinyon wood has been used most frequently as firewood since, upon burning, the

heat released from it appears to be unequaled by any other plant in the area. In 1878 Rothrock wrote, "It furnishes capital fuel, having enough of the terebinthinate in it to make an intensely hot fire. This is the most important use to which the tree is applied." Later, Perry (1922) referred to the pinyons as "surpassing all the conifers of the Rocky Mountains in this respect." In addition to serving as firewood the pinyons have been used for fenceposts, railroad ties (Perry, 1922), and to some extent in the construction of pit houses by the Indians. Perry (1922) questions, at some length, the advisability of using pinyon for railroad ties since a single tree will rarely yield more than one tie.

Pinyons have been used for hundreds of years for purposes other than the applications discussed above. Some of these uses enter into the realms of medicine and religion and have played significant roles in the lives of the southwestern and Mexican Indians. Various parts and products of the pinyons were used in the treatment of such things as syphilis, consumption (tuberculosis?) and arrow or bullet wounds. Stevenson (1908) reports that powdered pinyon gum was in general use throughout its range as an antiseptic and Whiting (1939) states that the fresh gum was used frequently to exclude air from cuts and abrasions. Whiting's ethnobotanical study of the Hopi Indians mentions their practice of using fire as a purifying agent and also the belief that the ability to purify existed within the plants themselves. Since

juniper and pinyon were the main sources of firewood, these plants were given significant roles in certain ceremonial rites. It was for this reason that after the funeral of a member of the household, the survivors placed pinyon gum on the fire and smoked themselves and their clothes in the fumes. Another example related to this belief is that during the month of December pinyon gum was placed on the forehead when going outside the house as a precaution against sorcery (Whiting, 1939).

Many practical applications for pinyon gum were developed by the Indians. The gum was used as a waterproofing compound in the manufacture of pottery and basketry and the Hopis treated their throwing sticks (non-returning boomerangs) with the resin to prevent warping (Whiting, 1939). It was used in the manufacture of mosaic jewelry and in the preparation of a black dye. The Indians' utilization of the pinyons was almost certainly more extensive than the list presented above would indicate, but a detailed discussion of these uses is beyond the scope of this paper.

Another somewhat limited aspect of the economic value of the pinyons is in the field of horticulture. These trees are occasionally available in plant nurseries and some are sold as novelties, particularly the single-leafed P. monophylla. In cultivation the pinyons are extremely slow growing and are generally sold as plants that will form small, round, bush-like trees (Rehder, 1940).

Recently the pinyons, in association with species of Juniperus, have become a problem to many southwestern ranchers. The trees, though geographically widespread throughout southwestern North America, have existed in relatively restricted habitats between the desert scrub vegetation and Ponderosa pine forests. However, since the appearance of man in this area, particularly during the past one hundred years, the limits of habitats suitable for the establishment and development of the pinyons have changed noticeably. Perhaps the most significant factor influencing this change has been the poorly controlled introduction of grazing animals in the proximity of the juniper-pinyon association. Pinus monophylla requires abundant shade for germination and subsequent establishment of the seedlings, and this requirement could be associated with the relatively rapid regression of the pinyons in the face of overgrazing in Colorado north of the San Luis Valley. Early explorations in this area suggested a more extensive range for the pinyons than is indicated by information concerning the present distribution.

Regression is not the typical response to overgrazing throughout much of the range, for the pinyons have become aggressive in their response to grazing in many parts of New Mexico and Arizona (and probably elsewhere). Gradually the number of habitable sites for P. x eduloides in this area has increased due to habitat disturbance caused by overgrazing and genetic heterogeneity within the pinyons

themselves. Attempts have been made to prevent the expansion of juniper-pinyon into rangeland, but frequently the methods applied have created more habitat disturbances than the animals did initially, thus opening the way to faster and more extensive invasion.

Finally, I will discuss an aspect of the pinyons that has been sorely neglected until recently -- the role of the pinyons in developing and maintaining watershed areas. Perry (1922) suggested that the pinyons might play a major role in the development of water resources since they can become established where other tree species cannot grow. In areas where the pinyons presently exist surface runoff and subsequent erosion are severely limited, which would indicate that the water must penetrate the soil and, hopefully, help to replenish subterranean water resources. However, precipitation patterns are such that penetration rarely, if ever, exceeds fifteen inches. Present practices in Arizona indicate that Perry's suggestions are totally unacceptable. Douglas (1965) discusses one approach used today that involves the complete removal of the juniper-pinyon forests over large areas. Removal of the trees reduces water loss due to transpiration and increases surface runoff which can be trapped in reservoirs. The practicality of this method remains to be seen.

It may now be said that the association between man and the pinyon pines has been long and generally fruitful, but a strong doubt appears about the continuation of this relationship.

CHAPTER IV

CHARACTER ANALYSES

INTRODUCTION

The Cembroid pines are geographically widespread as shown in Figure 1 and, accordingly, we would expect to find well established gradients in many of the environmental factors, particularly in those associated with climate, throughout the range of this group. Doubtless these gradients do exist, but the distribution of the pinyons cannot be associated with any one factor, such as precipitation, temperature, soil type, etc. Emerson (1932), Daubenmire (1943), and Woodbury (1947) suggest that the main factor affecting the distribution of the pinyons is the amount of moisture which is available for growth. This concept is further supported by the work of Thornthwaite (1931) in that the pinyons occur almost exclusively within his environmental classification CB'rb. All of the studies above lend support to the idea that the pinyons are found in one of the most xeric forest types in North America. With this in mind, I will describe the variability exhibited by each of the characters analyzed and, whenever possible, attempt to suggest the adaptive significance of this variability.

The analysis of the type of variation exhibited by the pinyons is most effectively accomplished through the utilization of population techniques as outlined by Anderson (1949). Therefore, I have used this approach to study the variation patterns within the Cembroid pines, particularly, those exhibited by Pinus monophylla ssp. edulis and P. cembroides. This study was initiated during the summer of 1960 and has been continued up to the present. The data presented in this dissertation are based upon the analysis of more than 500 specimens derived from 31 populations ranging from central Colorado and Utah to central Mexico (see Figure 2 and Appendix II). In addition to these population samples, I have studied the pinyon specimens in the herbaria of the Missouri Botanical Gardens, the New York Botanical Garden, the Universities of Oklahoma and New Mexico, Grand Canyon National Park, and the Instituto de Biologia of the Universidad Nacional de Mexico. I have also utilized information obtained from observations made on more than 5,000 living specimens in the southwestern United States and Mexico (Figure 2). The population samples and field observations were made during the summers of 1960, 1962, and 1965, and the resulting information was analyzed during the intervening years. Much of the data presented in this dissertation is based on an extensive survey of the literature pertaining to the Coniferales in general and the Abietaceae in particular.



Figure 2. Map of Sample Locations

Most of the data resulting from the analyses of morphological characters have already been presented in the species descriptions contained in the second chapter. I will avoid any unnecessary repetition of these results in this chapter, but will concentrate on describing the analytical techniques employed in their determination. Additionally, I will discuss the relative stability of each of these characters under various environmental situations.

Habit

The determination of habit or growth form does not readily lend itself to objective analysis, but rather, it is most often described on the basis of subjective impression. This is particularly true when it becomes necessary to distinguish between a small tree and a large shrub. The growth habit of the pinyons has had limited use as a taxonomic characteristic, presumably because it gives the appearance of being extremely variable. Phillips (1909) gave the following account of what he interpreted as environmentally controlled variation in the growth form of the pinyons.

> A difference in development was apparent on different sites. On exposed sites the tree is globular, very scraggly when mature, and has little or no clear length. On favorable sites trees in the open have a very short clear length and a fairly regular globular or egg-shaped crown. If grown in stands, the trees have a greater clear length and a flat or vase-shaped crown. Young trees on favorable sites are conical or globular in shape and usually very regular in form.

> On the most exposed sites, shrublike trees were found which were fifty to eighty years old, and only 1.8 to 3 m. (6 to 10 feet) in height, with a crown diameter reaching a maximum of two to four times the height of the tree.

On the basis of field observations and the appearance of habit under the conditions of cultivation, I feel that growth form in the pinyons is far more stable than the above account would indicate. The shape of the crown is primarily a function of the form or type of branching pattern characteristic of each species. This character will be discussed in the next section.

In his study on alpine and subalpine races of conifers and willows, Clausen (1965) states:

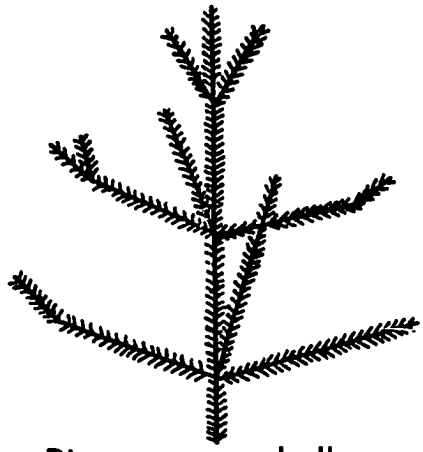
> Ability to develop elfinwood depends upon the germ plasm of the particular species, as shown by the species to species variation in the occurrence of elfinwoods. If the species has been able to develop an alpine race, such a race is a low bush or mat and extensive intercrossing and selection occurs within the upper range of the tree zone. Judging from the nature of natural hybrid swarms the segregation must be a complex multigenic one.

This is similar to the situation which seems to prevail in the pinyons even though only one subspecies, P. cembroides ssp. culminicola, occurs at timberline. The extensive variation discussed by Phillips may be accounted for on the basis that he included populations of both P. monophylla ssp. edulis and P. x eduloides in his description.

Branching Pattern

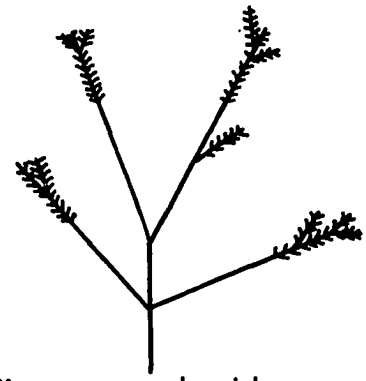
The branching pattern of the vegetative portion of a plant is closely related to the development of growth form. However, unlike habit, the branching pattern may be measured objectively in terms of the number of branches at a node, the angle of branching, the length of secondary branchlets, arrangement of varying internode lengths, arrangement and distribution of foliar structures, and a variety of other characteristics. These characters may be presented for analysis in one of two forms, statistically or pictorially. The statistical approach is undoubtedly the more objective relative to the interpretation of data, but is frequently less effective in that each character must be studied separately or at best in association with only one other. The pictorial presentation of branching pattern data permits the analyst to study several characters simultaneously and this is often significant in situations involving the complexities of hybrid recombination.

The pictorial presentation of branching pattern data utilizes diagrammatic representations of individual branches drawn to scale. The value of this technique has been suggested by Hall (1952) and Anderson, but has had only limited application to date. The patterns illustrated in Figure 3 are based upon the appearance of the terminal 30 to 45 cm. of secondary branches of the species indicated. A secondary branch is defined as a branch which arises directly from the primary axis or main stem.



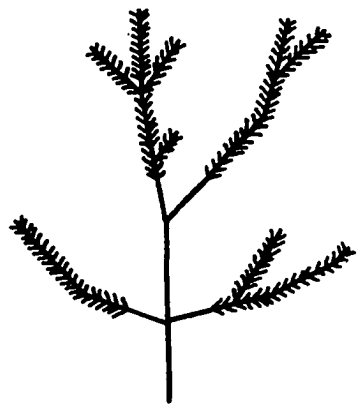
Pinus monophylla

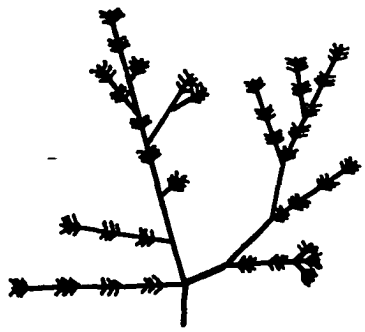
Excurrent



Pinus cembroides

Deliquescent





Pinus x eduloides

Ovulate — Staminate

Figure 3. Branching Patterns

Individuals of Pinus monophylla consistently exhibit the excurrent form of branching pattern except when some type of physical damage has been inflicted upon the apical meristem. Normally, the branching pattern of P. cembroides is excurrent in young individuals, but with the attainment of sexual maturity the deliquescent form prevails. The branching patterm of P. x eduloides is quite variable and the form prevailing in any given individual appears to depend upon the interaction of several distinct factors. Generally, in young individuals the excurrent pattern predominates, but mature trees may be entirely excurrent, entirely deliquescent, or show varying degrees of intermediacy between the two. This intermediacy may be expressed in a number of ways within a single population. Some trees may be truly intermediate throughout whereas others may exhibit a form of sexual dimorphism in which branches bearing staminate cones are deliquescent and those bearing ovulate cones are excurrent.

There is little doubt that the mechanism(s) involved in the determination of branching pattern is (are) under genetic rather than environmental control, but the nature of this control is, at best, poorly understood. I have noticed that there is a relatively strong correlation between branching pattern and the period of fascicle retention, but it is impossible to state at this time whether this relationship is causative or pleiotropic.

Fascicle Retention

I have already mentioned in Chapter II and illustrated in Figure 3 that each species retains the needle fascicles for different periods of time and that these periods are characteristic for each taxon. The number of years that fascicles persist on a given branch is readily determined by counting the internodes along a single axis which bears fascicles. Each node separating these internodes is marked by a slight constriction of the branch and a crowded cluster of primary leaf scars.

This character is quite consistent within a given tree and within populations of non-hybrid taxa, but the variability within populations of P. x eduloides may be fairly extensive. Similar to branching pattern, this character seems to be controlled primarily by the genetic constitution of the organisms. This is attested to by the fact that adjacent individuals of P. x eduloides may differ strikingly in their retention of fascicles although environmental conditions appear to be essentially identical.

If we can accept the concept that water availability is one of the most critical factors in the environment of the pinyons, we might expect the selection of morphological characters capable of limiting water loss by transpiration. Obviously, fascicle retention can directly affect the amount of leaf surface available for this process. I feel that this character in association with needle number and size may

contribute to the maintenance of an adequate water supply in these pines.

Needle Number

The utilization of the number of needles per fascicle as a key characteristic in the classification of the Cembroid pines has often led to a great deal of confusion. Characteristically, a definite number of needles per fascicle predominates within each taxon of the pinyons, but under certain circumstances this number may be altered. In Chapter II I have described the predominant needle number for each taxon and will not discuss it further here, but I would like to consider, in some detail, the factors that may contribute to the variability of this character.

Needle number variation can be expressed in two ways on any given tree. Fascicles containing different numbers of needles may be randomly intermixed along the entire length of each branch on the tree or they may be distributed in definite patterns. As an example of the latter situation, the specimens collected in a population of P. cembroides near Galeana, Nuevo León, Mexico exhibit a high frequency of two-needled fascicles among those leaves that were produced during the 1963 growing season. With the exception of that year, all of the needles on these specimens occur in fascicles of three which is typical for P. cembroides. This suggests that the environment may have some effect on the determination of needle number. Haller (1965) supports this idea by the following statement:

> There is a strong tendency in Pinus ponderosa and P. jeffreyi for 2-needle fascicles to increase their frequency at the expense of 3-needle fascicles in many situations where the moisture supply is comparatively limited: on young trees (as opposed to mature), during periods of low precipitation, at low elevations, on dry slopes, and in more extensive semi-arid regions, particularly east of the Continental Divide from Colorado northward.

Further evidence in support of this line of reasoning was given by Masters (1888) in his study on the nature of the single-leaf of P. monophylla. He suggested that under environmental stress, one of the two leaf primordia in each fascicle would abort, thus giving rise to monophylly. In view of these facts, it seems that the environment can play a direct role in the determination of needle number, but this effect cannot fully explain the intermixing of fascicles with different numbers of needles in the growth of a single season. Keng and Little (1961) reported that "hybrids from species differing in needle number generally are intermediate between the parents." I believe that both genetic and environmental factors have been active in the pinyons and that their interaction has been responsible for many of the taxonomic problems in this group.

Needle Length and Width

The values for needle length and width presented in Chapter II are based on measurements of approximately 5000 fascicles from 500 different specimens. Needle length was determined by removing the leaves from 10 fascicles on each

specimen and measuring them directly with a plastic millimeter ruler; width measurements are based on the diameter of each fascicle at a point 2 mm. above the insertion of the needles

Both of these characters may be influenced by environmental fluctuations and when considered separately are extremely unreliable as taxonomic criteria. However, when these values are expressed as the ratio of length/width they can be quite effective for the determination of the different taxa. I have shown in an earlier study (Fogg, 1962) that leaf length is a function of cell length and width is primarily a function of cell number.

Ovulate Cones

Information concerning the variation exhibited by the ovulate cones is fairly limited because of the lack of mature material at the times when population samples were made. The descriptions of cone characteristics in Chapter II are based mainly on herbarium specimens. I have reason to believe that the overall size of cones and possibly the number of cone scales may be influenced to some degree by environmental conditions. However, the structure of the apophyses and the umbos seems to be relatively stable under a variety of conditions and is valuable as a taxonomic character. These structures are quite distinct in Pinus nelsonii and P. pinceana and I refer the reader to the works of Shaw (1914) and Martinez (1945) for their further characterization. The

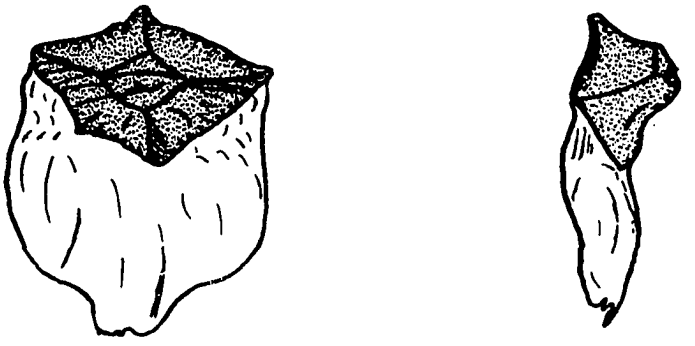
cone scales of P. monophylla, P. cembroides, and P. x eduloides are similar and often difficult to distinguish. Differences do exist among these species, but quantitative description of these differences is extremely difficult. Therefore, I have shown these distinctions diagrammatically in Figure 4. As in many other characters, P. x eduloides appears to be intermediate between P. cembroides and P. monophylla.

Seed and Seed Coat Thickness

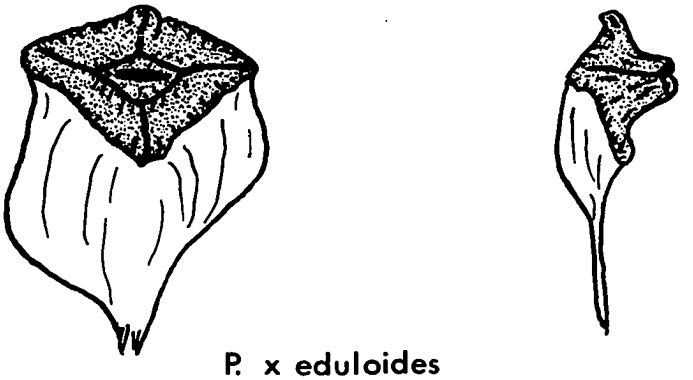
The same limitations apply to the analysis of seed shape and size and seed coat thickness as were mentioned in the preceding section, but these structures seem to afford valuable taxonomic characters and should be considered. Again, the best method of description seems to be by illustration and I have done this in Figure 5. The paired arcs above each seed represent the thickness of the seed coat drawn to the same scale as the seeds. As can be seen in the figure, the pinyons may be divided into two distinct groups on the basis of seed coat thickness alone. The seed coats are either thin as in P. monophylla or thick as in P. cembroides. This characteristic appears to be extremely stable under varying environmental situations and is quite reliable as a key characteristic.

Chemical Composition

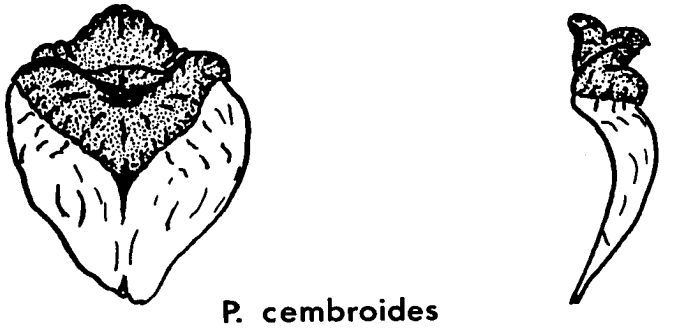
Figure 6 illustrates the results of preliminary chromatographic analyses of extracts from one-year-old leaves



P. monophylla



P. x eduloides



P. cembroides

Figure 4. Cone Scales

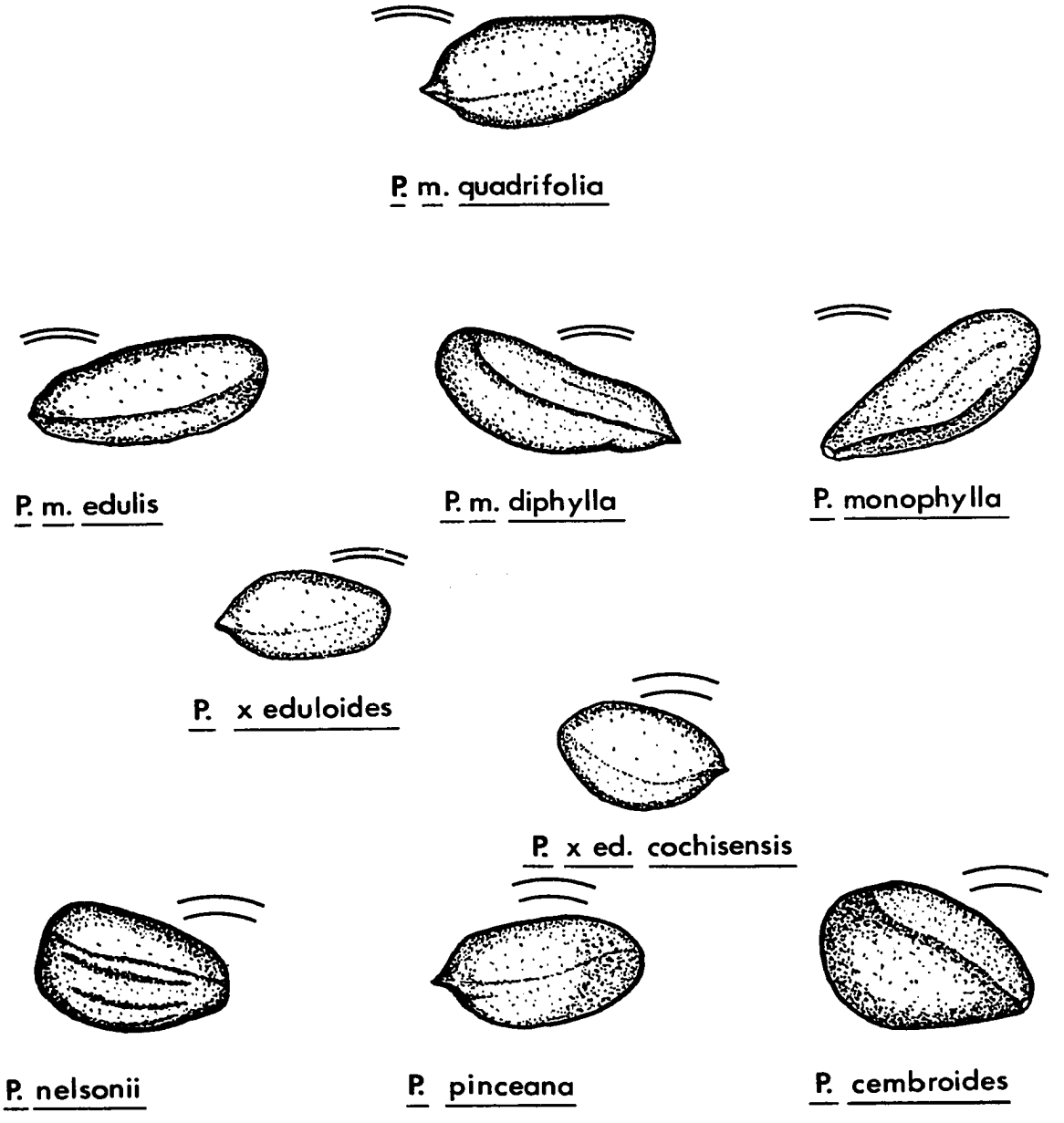
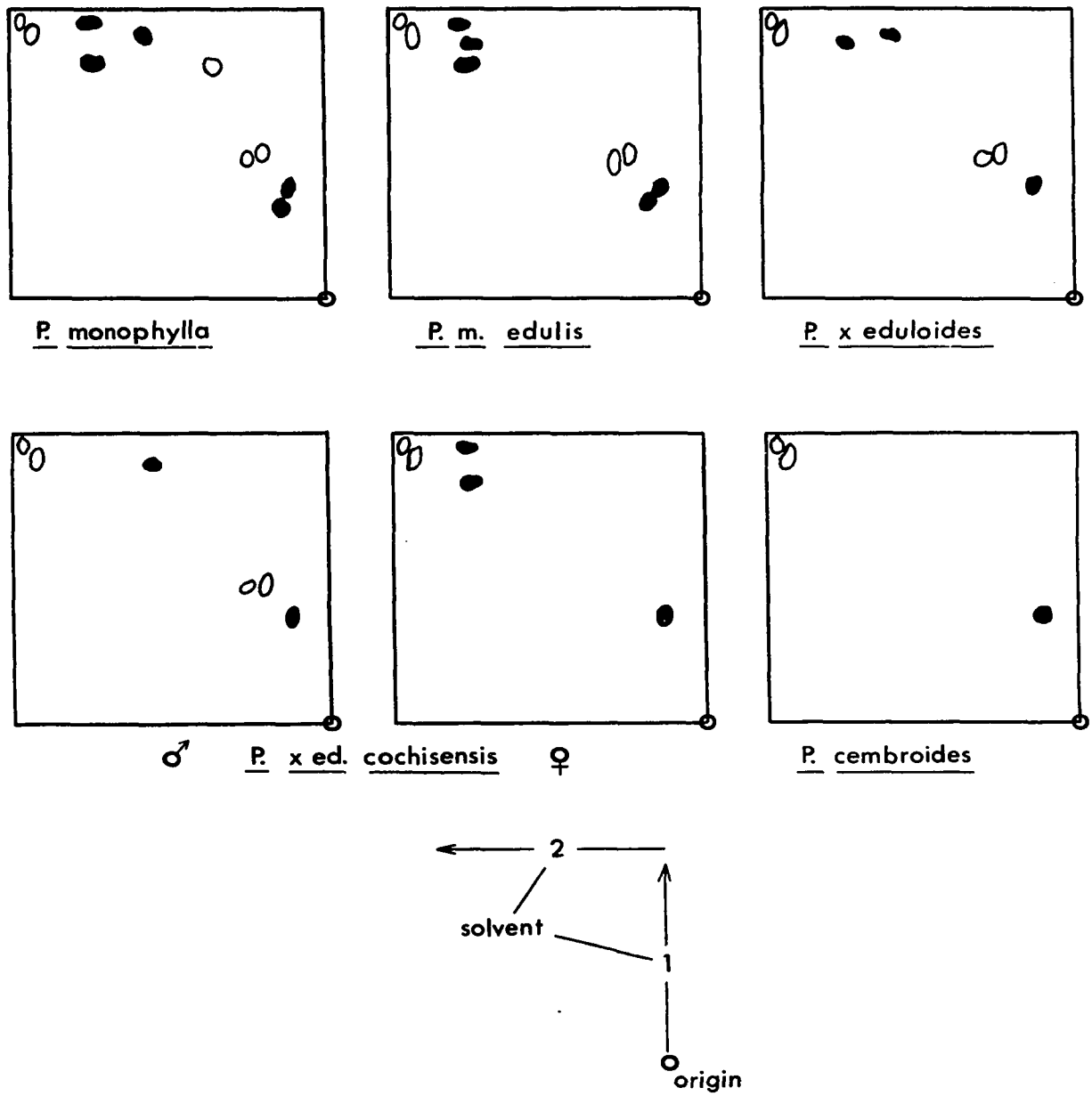


Figure 5. Seeds and Seed Coat Thickness



Solvent 1 - 70 iso Propanol: 10 Butanol: 20 H_2O

Solvent 2 - 100 iso Propanol: 5 NH_4OH: 10 H_2O

Figure 6. Chromatographs

of the taxa indicated. The analytical procedures for these chromatographs are as follow: fresh needles in absolute methanol were placed in a Waring Blender for 30 seconds, extracted by boiling for four hours, filtered hot and allowed to cool overnight. Aliquots of 0.10 ml. were spotted on Eastman Thin Layer Chromogram sheets (silica gel) with fluorescent indicator and developed in the solvents indicated in Figure 6. The resulting patterns were determined under long and short wave ultraviolet light. In the figure the dark spots indicate absorption and the light spots indicate fluorescence. Three specimens were analyzed for each taxon studied and only P. x eduloides showed extensive intrapopulational variation. Since this was a preliminary analysis to determine the existence of pattern differences, I have not attempted the chemical determination of the different compounds present; although I plan to do so in the future.

Pinus monophylla and P. x eduloides differ from the other pinyons in that they exhibit a distinct, slightly pungent odor. Mirov (1961) attributes this odor to the presence of ethyl caprylate in the resin of these pines. The presence or absence of this odor in fresh material can be helpful in some taxonomic determinations.

The environmental stability of the chemical composition of different parts of these trees is currently unknown, but Mirov (1961) remarks that the "... composition of turpentine is a genetically fixed character."

CHAPTER V

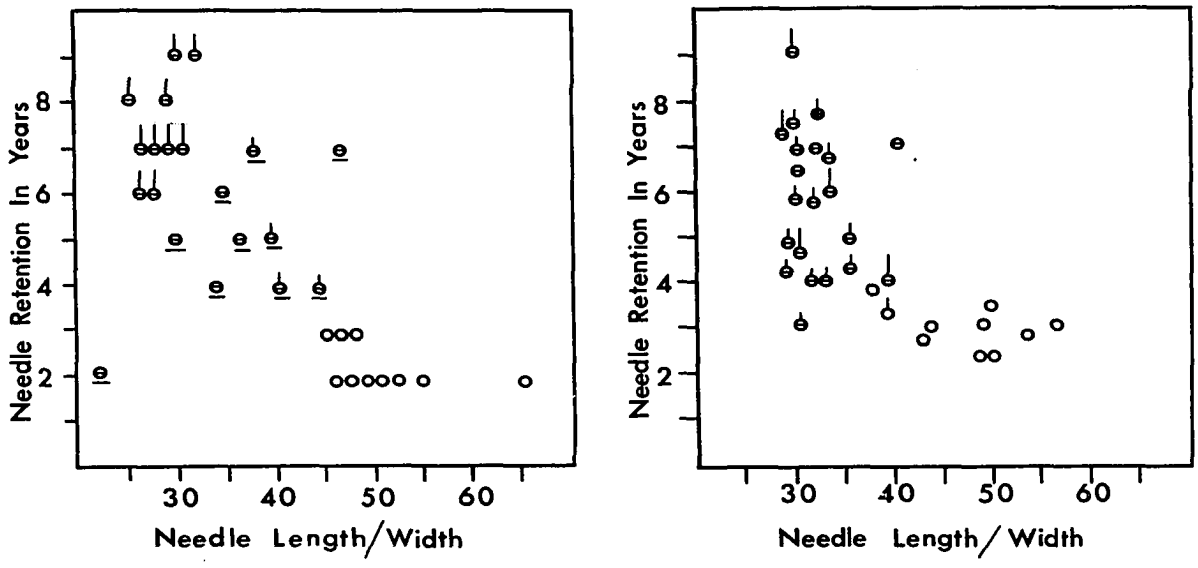
DISCUSSION

The Cembroid pines are geographically widespread but the occurrence of each species or subspecies within relatively narrow altitudinal limits often results in the formation of localized rather than continuous populations. This type of distribution can dramatically affect the nature and extent of morphological and physiological variation occurring between different populations. The size of the effective breeding population influences the relative intensities with which natural selection and random fixation interact. Wright (1931) and others have demonstrated a positive correlation between the size of the breeding population and the influence of natural selection in that population. Conversely, there is a negative correlation between population size and the extent of random fixation of genetic characteristics. Utilizing this concept, it should be possible to determine the origin of the variation patterns exhibited by the pinyon pines.

I will present several hypotheses concerning the possible sequence of evolutionary events in these pines and attempt to demonstrate their relative strength or weakness in

light of the data that have been presented. In view of the fact that currently many of the naturally occurring pinyon populations are relatively small, we might expect some degree of population variation resulting from the random fixation of genetic alleles. If this has happened it can easily be demonstrated by using a scatter diagram with each point representing the mean values of morphological characteristics within a single population. If random fixation is significant we would expect the graph to exhibit a random recombination of the characters analyzed. This graph has been made and the results are illustrated in Figure 7b. It is quite obvious from this scatter diagram that character recombination in the pinyons is not random, but instead, is clinal. This does not completely eliminate the possibility that random fixation has occurred, but does suggest that its influence has been limited. These populations, and many others, support the idea that the pinyons have been subjected to the pressures of natural selection at some time in the past; thereby implying the existence of reasonably large breeding populations. With this in mind, we must seek another explanation of the variation patterns of the pinyons.

Assuming the existence of large or even continuous populations at some time during the past, we might expect the initiation of marginal divergence under the influence of environmental gradients, in other words, ecotypic differentiation. If this has occurred, the existence of these



A. Each point represents one individual.
o = from hybrid swarm.

B. Each point represents one population.

Symbols

Branching Pattern: ô = excurrent, ô = intermediate, o = deliquescent

Needle Number: ● = 1, e = 2, o = 3

Figure 7. Scatter Diagrams

gradients should be reflected by clinal variation in the morphological and physiological characteristics of the organisms. The occurrence of several morphological clines within the pinyons is quite evident. For example, in going from north to south we may observe the following: the period of needle retention becomes progressively shorter, the needles become longer and narrower, habit becomes increasingly more deliquescent, and the seed coats become thicker. Needle number appears to increase along a northwest to southeast axis and the umbo becomes more pronounced along an east to west axis. Other morphological characters exhibit similar tendencies, but it must be emphasized that these patterns are simply tendencies and not absolute gradients. On the basis of this type of variation, particularly in regard to needle number, Shaw (1914) and others have recognized only three species of Cembroid pines; Pinus cembroides, with four varieties; P. nelsonii; and P. pinceana.

As indicated above, the clinal variation found in the morphological characters is not absolute and, furthermore, parallel gradients do not appear to exist when ecological characteristics are analyzed. There is little doubt in my own mind that divergence in the pinyons was initiated by marginal differentiation in response to environmental gradients with subsequent reinforcement by geographic isolation. This hypothesis only explains the origin of divergence within the group; it does not account for the variation patterns which

characterize present-day populations. The following argument explains the reasoning behind the last statement.

If natural selection has been the primary factor in the development of a group of organisms, its role should be characterized by a limitation of intra-populational variation. In other words, strong homogeneity within populations would indicate that an adaptive equilibrium has been established between the organisms and their environment, probably, as a result of natural selection. The existence of homogeneous populations within the pinyons is illustrated by the two sets of points that are not underlined in Figure 7a. These populations, and others like them, suggest that selective forces have been active in the development of these pines. However, the heterogeneity illustrated by the underlined population in this figure, typical of the variation found in many populations of Cembroid pines, would not be expected if ecotype formation was the only evolutionary force acting on this group. Because of this, I feel that we can reasonably exclude ecotypic variations as the sole evolutionary process leading to the variability extant in the pinyons. Briefly, neither the concept of ecotypic variation nor the random fixation of genetic alleles can account for the variation patterns exhibited by the Cembroid pines.

Since we are unable to explain the variability of the pinyons on the basis of mutation or genetic recombination within existing populations, we must consider the possibility

of genetic exchange between different populations. This line of reasoning has suggested the existence of hybrid recombination within the group, particularly that form of hybridization known as introgression. According to Stebbins (1950),

> If hybridization and subsequent introgression are taking place between species A and B, then the variation pattern of species A should be increased in the direction of species B in and near the regions where A and B are found together and where their habitats have been disturbed in relatively recent times. Furthermore, the variant, introgressive individuals of species A should not possess different characteristics of species B recombined at random with those of species A. Each individual should vary in the direction of species B in several of the characteristics distinguishing the two species, although obviously any particular characteristic would be expressed to different degrees in different individuals.

Most of the criteria outlined by Stebbins are evident in the variation exhibited by the pinyons. The graphs in Figure 7 are based upon populations of Pinus monophylla ssp. edulis (upper left), P. cembroides (lower right), and populations that have apparently resulted from hybridization between these two taxa. The morphological variation contained within each population is readily explained on the basis of hybrid recombination. However, I do not feel that extensive introgression is currently taking place within this group, but, rather, that it has occurred at an earlier time in the development of these pines. The current lack of active introgression is supported by the allopatric distribution of the taxa involved (Figure 1) and by the isolated nature of the populations concerned.

The lack of similar recombination patterns in the ecological characteristics of the pinyons would seem to defy

interpretation on the basis of any of the phenomena discussed above. Commonly, morphological clines are paralleled by ecological gradients, regardless of the mechanisms responsible for the variation. This is quite obvious in those situations involving ecotypic variation and it is usually apparent in those groups of organisms that have been affected by introgression. The pinyons are unusual, at least when compared with previously studied groups of plants, in that the ecological requirements of the different species do not appear to be significantly different. Certainly, ecological differences do exist, but the climatic factors associated with precipitation effectiveness are remarkably homogeneous throughout the range of the pinyons. The predominant climatic change in southwestern North America seems to have been toward an increasing degree of aridity. This is reflected in the fossil record by the increasing predominance of xerophytic plants from middle Tertiary times to the present (Axelrod, 1950). Since the Cembroid pines occurred in the Southwest during the Miocene (Axelrod, personal communication), it seems reasonable to assume that they must have responded adaptively to the greater aridity. Obviously, the mechanism of these adaptive changes must involve natural selection, but there is no reasonable basis for the assumption that the resultant adaptive complexes of morphological and physiological characters must be identical throughout the range of the organisms involved. In other words, isolated populations may

respond to similar environmental situations in different ways. If we can accept this hypothesis, then it becomes possible to understand the development of morphological clines without parallel ecological gradients.

Anderson has repeatedly emphasized the necessity of suitable habitats before introgression can become effective. Frequently the existence of these habitats is dependent upon the availability of some force capable of creating environmental disturbances. This has led Anderson (1949) to state, "As a consequence, it is only where man or catastrophic natural forces have 'hybridized the habitat' that any appreciable number of segregates survives." There is little doubt that man has effectively disturbed many habitats in southwestern North America, but the extent of introgression in the pinyons suggests that it was well established prior to the appearance of man in the area. The effect of man on the variability of the pinyons is indicated by the fact that the most extensive intra-populational variation occurs in association with extensive over-grazing by domesticated animals. Generally, these effects seem to be highly localized geographically and incapable of accounting for the occurrence of hybrid populations over a range which is several hundred miles in diameter. I believe that the following line of reasoning might shed some light on the possible origin of introgression in these plants. Paleontological evidence suggests that the initial divergence between Pinus cembroides and P. monophylla

probably occurred during the late Tertiary, although the exact time of this event is not crucial to the argument. The fact that divergence has occurred is significant in that it implies the existence of an effective isolating mechanism between the two groups. Subsequent divergence within these groups was probably well defined by the end of the Pliocene or early Pleistocene. In order for hybridization to occur, the parental taxa must be capable of gametic exchange. In other words, there must be a breakdown of the isolating mechanism. I feel that the climatic changes associated with the Pleistocene epoch may have permitted the southward migration of P. monophylla, particularly subspecies edulis, into the vicinity of P. cembroides, thereby initiating the introgressive process. Since the cessation of the last pluvial, the Southwest has become progressively more arid. This has caused a fairly rapid change in environmental factors and, correspondingly, rapidly changing habitat situations. It is quite conceivable that these changes have permitted or even selectively favored the establishment of introgressive segregates. The hybrid nature of the populations of P. x eduloides is further substantiated by their altitudinal distribution.

It is generally accepted that environmental differences resulting from lower latitudes may be compensated for by an increase in the altitude. The altitudinal distribution of P. cembroides and P. monophylla reflects this

pattern in that the more southern populations of each subspecies occur at higher elevations than the northern populations of the same subspecies. However, populations of P. x eduloides differ from the other pinyons in that the northern populations occur at higher altitudes than the southern ones. I feel that this strongly supports the idea that P. x eduloides is of hybrid derivation.

CHAPTER VI

CONCLUSION

There is little doubt in my own mind that introgressive hybridization has played a significant role in the evolutionary development of the pinyon pines, and this has undoubtedly been the source of much of the taxonomic confusion within the group. The introgressive segregates appear to be effectively isolated from the parental taxa by geographic and climatic barriers; are easily recognized by certain morphological characteristics; and may be found over an extensive area in southwestern North America. Because of these facts, I have given them full specific status as *Pinus x eduloides*.

Utilizing the information contained within this dissertation, I have attempted to develop a more natural system of classification for the Cembroid pines. I feel that the taxonomic revision presented in Chapter II reflects the probable evolutionary relationships within the group. In addition, I believe that this study has contributed to our knowledge of the conditions under which introgression may occur without the intervention of man.

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APPENDIX I

LATIN DIAGNOSES

Pinus x eduloides sp. nov.

Arbor hybrida (*Pinus cembroides* x *P. monophylla* ssp. *edulis*), pyramidata vel subrotunda, alta usque ad 15 m.; folia 1.5 - 5 cm. longa 0.6 - 1.2 mm. lata, duo vel tria in fasciculo; vaginae in brevi tempore crispae-rosulatae; strobilus parvus, 3 - 4 cm. longus, 2 - 3 cm. latus, subglobosus, subsessilis; semina sine alis, 9 - 13 mm. longa, 5 - 7 mm. lata.

Type: U.S.A., Grand Canyon National Park, Arizona near Hermit's Rest, 2040 m. altitude. *Fogg 144* (Bebb Herbarium, University of Oklahoma)

Pinus x eduloides nm. *eduloides*

Pinus x eduloides; folia 1.5 - 4 cm. longa, 0.9 - 1.2 mm. lata, plurimum duo in fasciculo.

Pinus x eduloides nm. *cochisensis* nm. nov

Pinus x eduloides; folia 3 - 5 cm. longa, 0.6 - 0.9 mm. lata, plurimum tria in fasciculo.

Type: U.S.A., Greenlee County, Arizona north of Granville, 2160 m. altitude. Fogg 96 (Bebb Herbarium, University of Oklahoma). Name derived from Cochise County, Arizona.

Pinus monophylla var. diphylla var. nov.

Pinus monophylla; folia 3 - 4.5 cm. longa, 0.8 - 1.1 mm. lata; fascicula tota in eadem arbori vel cum uno folio vel cum et uno folio et duobus foliis.

Type: U.S.A., Zion National Park, Utah in canyon west of park headquarters, 1250 m. altitude. Fogg 162 (Bebb Herbarium, University of Oklahoma).

APPENDIX II

POPULATION SAMPLE SITE DESCRIPTIONS

1. Black Canyon of the Gunnison National Monument, Colorado: July 21, 1960; rim of canyon; 2500 m. altitude.

2. Salida, Colorado: July 19, 1960; 4 miles northeast of Salida on Ute Trail; relatively steep, east facing slope; 2500 m. altitude.

3. Mesa Verde National Park, Colorado: July 28, 1960; on road to ruins near park headquarters; level mesa top with sandy soil; 2100 m. altitude.

4. Great Sand Dunes National Monument, Colorado: July 18, 1960; near ranger station; slightly southwest facing slope; 2500 m. altitude.

5. Monte Vista, Colorado: August 4, 1960; 26 miles southwest of Monte Vista near Terrace Resevoir; 2530 m. altitude.

6. Cedar City, Utah: August 16, 1965; 2 miles east of Cedar City on Utah Highway 14; south facing slope; 1890 m. altitude.

7. Cedar City Utah: August 16, 1965; 7 miles east of Cedar City on Utah Highway 14; south facing slope; 2040 m. altitude.

8. Zion National Park, Utah: August 16, 1965; in canyon west of park headquarters; 1250 m. altitude.

9. Bryce Canyon National Park, Utah: August 16, 1965; along Bryce Point rim trail; level; 2530 m. altitude.

10. Tres Piedras, New Mexico: August 5, 1960; 7 miles south of Tres Piedras on U.S. Highway 285; level; 2280 m. altitude

11. Questa, New Mexico: July 15, 1960; locations north and south of Questa; slopes level to slightly west facing; 2320-2440 m. altitude.

12. Taos, New Mexico: July 16, 1960; 1-7 miles east of Taos; slopes level to gently north facing; 2190-2350 m. altitude.

13. Bandelier National Monument, New Mexico: July 12, 1960; in area between Bandelier and Los Alamos; level; soil loose and sandy; 2040-2140 m. altitude.

14. Placitas, New Mexico: July 2, 1960; 3 miles north of Las Huertas campground in Sandia Mountains; northeast and southwest facing slopes; limestone bedrock; 2010 m. altitude.

15. Sandia Park, New Mexico: August 9, 1960; 3 miles north of U.S. Highway 66 on New Mexico Highway 44; level; 2040 altitude.

16. Chilili, New Mexico: August 9, 1960; 3 miles north of Chilili on New Mexico Highway 10; level; 2190 m. altitude.

17. Haynes Canyon, New Mexico: August 9, 1965; 1 mile south of New Mexico Highway 83 about halfway between Alamogordo and Cloudcroft; south facing slope; 2100 m. altitude.

18. Grand Canyon National Park, Arizona: August 14, 1965; south of Hermit's Rest parking lot; gentle south facing slope; 2040 m. altitude.

19. Grand Canyon National Park, Arizona: August 14, 1965; 0.5 mile south of the Abyss; level; 2100 m. altitude.

20. Flagstaff, Arizona: August 13, 1965; north of Flagstaff on Arizona Highway 180; level; 2100 m. altitude.

21. Walnut Canyon National Monument, Arizona: 1 mile north of main entrance; level; 2040 m. altitude.

22. Springerville, Arizona: August 12, 1965; 2 miles north of Springerville on U.S. Highway 666; slightly west facing slope; 2270 m. altitude.

23. White Mountains, Arizona: August 12, 1965; south of Alpine on U.S. Highway 666; level; 1900 m. altitude.

24. Granville, Arizona: August 12, 1965; along U.S. Highway 666 between Granville and H. & L. Saddle; east facing slopes; 2160 m. altitude.

25. Paradise, Arizona: August 10, 1965; 1 mile south of Paradise; level; 1830 m. altitude.

26. Coronado National Forest, Arizona: August 11, 1965; approximately 8 miles north of Paradise on road to National Monument: 1950 m. altitude.

27. Chiricahua National Monument, Arizona: August 11, 1965; Masai Point; 2100 m. altitude.

28. Ft. Davis, Texas: August 14, 1960; Mt. Locke on road to McDonald Observatory; gentle south facing slope; 1860 m. altitude.

29. Galeana, Nuevo León, Mexico: June 10, 1965; 7 miles west of Galeana; level; 2050 m. altitude.

30. Saltillo, Coahuila, Mexico: June 13, 1965; 14 miles south of Saltillo on Mexico Highway 57; gentle north facing, limestone slope; 2040 m. altitude.

31. Sombrerete, Zacatecas, Mexico: June 19, 1965; near border between Zacatecas and Durango on Mexico Highway 45; northwest facing slope; 2000 m. altitude.