INVESTIGATIONS INTO THE ECOLOGICAL RELATIONSHIPS OF PONDEROSA PINE IN SOUTHEAST ARIZONA

by

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A Dissertation Submitted to the Faculty of the

BOTANY DEPARTMENT

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1963

THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Richard Archie Dodge entitled Investigations into the Ecological Relationships of Ponderosa Pine in Southeast Arizona be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy.

Raymond M. Turner — April 24, 1963
Dissertation Director — Date

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ACKNOWLEDGMENT

I wish to express my indebtedness to Dr. Raymond M. Turner for his generous encouragement and guidance through the course of this investigation. Without his inspiration and suggestions, this work would not have been initiated or completed.

I wish further to express gratitude to the members of my guidance committee, Dr. Stanley W. Buol, Dr. Edwin B. Kurtz, Jr., Dr. Charles H. Lowe, Jr., and Dr. Robert H. Maier for the numerous suggestions, encouragement and interest shown during this study. Special thanks is extended to Dr. Harold C. Fritts for assistance with parts of the studies and for analyzing data from portions of the work.

Gratitude is given to the Department of Botany, Department of Agricultural Chemistry and Soils, and the Laboratory of Tree Ring Research of the University of Arizona for assistance from interested personnel and for making essential equipment and facilities available. Appreciation is extended to the personnel of the Coronado National Forest, U.S. Forest Service, for assistance and support during phases of the field research, and to the personnel of the Saguaro National Monument and Coronado National Memorial, U.S. National Park Service, for the availability of facilities and actual field assistance by members of these organizations.

Gratitude is also extended to The Arizona Academy of Science which has aided portions of this study with financial support.

Appreciation is extended to my wife, Donna Dodge, for her assistance and considerable encouragement during all phases of this research.

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ABSTRACT

Studies to determine differences between Arizona and ponderosa pine have been carried on in the mountainous areas of southeast Arizona, utilizing plotless phytosociological techniques, morphological studies, and dendrometer investigations. Samples from northern Arizona and Sonora, Mexico, have been included for comparison. Ponderosa and Arizona pine are found in these regions from approximately 7000 to above 9000 feet elevation, associated with oaks in the lower portion of the elevational range and with other conifers in the upper part of the range. Comparison of needle number per fascicle indicated that three-needle ponderosa pine is found at the upper part of the elevational range, while the five-needle Arizona pine occupies habitats below ponderosa pine. Intergradation of the two taxa is indicated by a general increase from three to five needles per fascicle occurring with decreasing elevation; this relationship is more pronounced with decreasing latitude. The number of stomates per unit length of needle was found to increase slightly from north to south. Volume and length of pistillate cones were not useful criteria in separating the taxa. Cone density, however, was found to increase with decreasing latitude, and little overlap was present in the two most distant stations.

Cone-scale prickle curvature generally tended from an upward to downward pointing direction with decreasing latitude. Dendrometer studies among groups of trees classed as three-needle ponderosa pine, five-needle Arizona pine, and mixed-needle hybrids indicated differences in time of radial expansion commencement. The trees classed as Arizona pine and hybrids between Arizona and ponderosa pine commenced radial expansion prior to ponderosa pine.

No distinct differences were observed between the two taxa, and it is concluded that Arizona pine is a variety of ponderosa pine.

INTRODUCTION

Arizona pine, reported in southeast Arizona adjacent New Mexico and Sonora, has been considered both a distinct species (e.g. Engelmann, 1878) and a variety of ponderosa pine (e.g. Shaw, 1909). Within the geographic range of Arizona pine, specimens occur which are either markedly distinct from, or intermediate to, the Rocky Mountain ponderosa pine found in northern Arizona and into the Rocky Mountains. The apparent intergradation tends to support the hypothesis that Arizona pine is a closely allied variety of ponderosa pine. The variability of Arizona pine in several mountain ranges of southeast Arizona and the degree to which ponderosa pine is present in concurrent habitats with Arizona pine is the subject of this study.

The general area of occurrence of ponderosa pine and Arizona pine in Arizona is shown in Figure 1. In the northern part of Arizona, ponderosa pine is found from near 5000 feet to 8000 feet elevation and occurs in a broad belt extending from the New Mexico border across the Mogollon Plateau to northwest of Flagstaff. In addition, large areas of ponderosa pine are found near Prescott, the Grand Canyon, the Coconino Plateau, the Kaibab Plateau, and the Hualpai Mountains to the

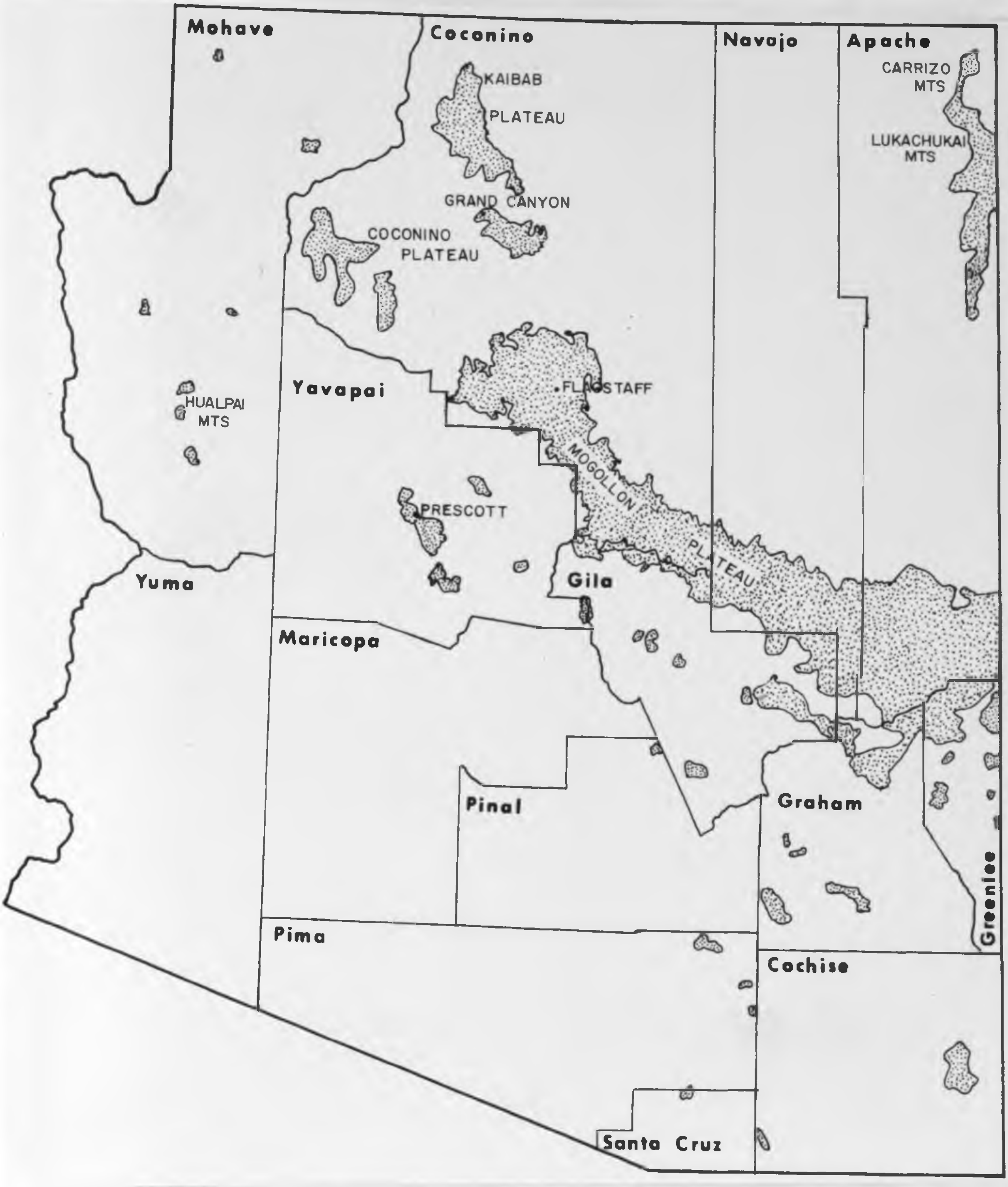

Figure 1. General distribution of ponderosa pine in Arizona (Nichol, 1952).

west, and in the northeast part of Apache County in the Carrizo and Lukachukai Mountains (Nichol, 1952).

These areas, generally the northern two-thirds of the state, are considered to support the typical Rocky Mountain variety of ponderosa pine. This taxon is also reported from high elevations in the mountain ranges of southeast Arizona. These areas, notably in the Pinaleno, Galiuro, Santa Catalina, Rincon, Chiricahua, Huachuca and Santa Rita Mountains, have been described as habitats for both ponderosa and Arizona pine.

Within the state, Arizona pine is allegedly restricted to mountain ranges in southeast Arizona that rise to an elevation of 7000 feet or more. The distribution of Arizona pine is described as including the Pinaleno, Galiuro, Santa Catalina, Rincon, Santa Rita, Huachuca and Chiricahua Mountains (Kearney and Peebles, 1951). With the exception of the Pinaleno and Chiricahua Mountains, these southern mountain ranges ordinarily rise slightly above 9000 feet, and ponderosa pine may be found to the summits of the several high peaks usually present. The lower elevational limit of the tree is generally found to be near 7000 feet; in sheltered areas it may be found below 6000 feet. Ponderosa pine extends to elevations near 10,000 feet in the Pinaleno Mountains.

Arizona pine was first collected by Rothrock in 1874 in the Santa Rita Mountains, and was described by

Engelmann as a new species, Pinus arizonica (Wheeler, 1878). Engelmann apparently attached great significance to the five-needle fascicles and the small cone size. In his description, Engelmann states:

> This seems to be a meager account to found a new species upon, in a genus so difficult as Pinus, but I find it impossible to unite it with any other of the allied species. It has the cone of P. ponderosa, especially of the form figured by Torrey as P. deflexa, and, like all forms of that species, it has the peculiarity that the fallen cones, found on the ground, are always imperfect, their lowest part remaining attached to the branch for another season. I do not know of any other pine with this singular character. But we could not well class this five leaved pine with the three leaved ponderosa. On the other hand, the form of the cone and its scales will not permit us to refer it to the Mexican P. Montezumae, though the structure of the leaf is very similar to that of this polymorphous species, which appears to include P. Hartwegii. The three parenchymatous ducts of the leaf and the strengthening cells within the sheath of the vessels are exactly as we find them in Montezumae and different from ponderosa. (Wheeler, 1878, pp. 260-261)

Other authors have similarly been impressed with the number of needles in the fascicle and the cone size of Arizona pine. Sudworth (1917) concurs with Engelmann that the five-needle fascicle and the distinct characteristics of the cone appear to be "good reasons for still maintaining Arizona pine as a species." Sudworth recognized variability in these characters which will be referred to later.

More recent investigators also recognized Arizona pine as distinct from ponderosa pine. Johnston (1943) included in his flora of northern Mexico a description of Pinus arizonica, which he states cannot be separated from the typical _P_. _arizonica_ of Arizona. Johnston pointed out, however, that the _P_. _arizonica_ of Coahuila much resembles _P_. _ponderosa_ growing in the Rocky Mountains. He noted differences in the needle number (three to five), the weak umbo on the cone scales, usual glaucescent branchlets and more southern distribution.

Martinez (1948) recognized the close affinity of _P_. _arizonica_ and _P_. _ponderosa_, but he recognized _P_. _arizonica_ as distinct. In his description of pines growing in the northern states of Mexico, Martinez found Arizona pine more often exhibiting needles in threes, very rarely four or five in the same fascicles; the smaller cone size (2 - 3¼ in.) was, nevertheless, exhibited by the specimens examined.

In addition to recognizing Arizona pine as distinct, Martinez proposed a new variety. The variety (_P_. _arizonica stormiae_ Martinez) differs from _P_. _arizonica_ on the basis of larger leaves containing fewer resin canals, and on the basis of somewhat larger cones than the taxon he recognized as _P_. _arizonica_.

Because of the great similarity between Arizona and ponderosa pine, numerous workers have assigned Arizona pine to a variety of ponderosa pine. This was originally proposed by Shaw (1909) and has been accepted by later workers (Shaw, 1914; Sargent, 1922; Dallimore, 1929; Little, 1950; Kearney and Peebles, 1951). Two of these workers in earlier editions of their publications cited Arizona pine as a species

(Sargent, 1905; Kearney and Peebles, 1942), but later considered Arizona pine a variety of _P_. _ponderosa_ (Sargent, 1922; Kearney and Peebles, 1951).

Sudworth (1917) listed both _P_. _arizonica_ and _P_. _ponderosa_ in his descriptions of the pine trees of the Rocky Mountains. Since he recognized _P_. _arizonica_ and _P_. _ponderosa_ as distinct, Table 1 has been constructed from his descriptions to demonstrate the similarities and to contrast the differences between the taxa.

Kearney and Peebles (1951) characterize the yellow pines of Arizona as _P_. _ponderosa_ var. _scopulorum_ Engelm., occurring in northern and central Arizona, and _P_. _ponderosa_ var. _arizonica_ (Engelm.) Shaw, occurring in the mountains of Graham, Cochise, Santa Cruz, and Pima Counties. The common name, ponderosa pine, is used when referring to the two taxa collectively unless otherwise noted. Plant names used in this paper are from Kearney and Peebles (1960).

Three primary approaches were used to determine the evolutionary status and ecological role of the ponderosa pines in the mountain habitats of southeast Arizona: (1) field-survey transects in each mountain range where the taxa occur were made to quantify the phytosociological relationships of the populations; (2) morphological investigations were conducted to reveal differences, if present; and (3) dendrometer studies were conducted to illustrate the response of the ponderosa pine complex to the habitat in a single area.

TABLE 1. Distinguishing characteristics of Pinus arizonica and P. ponderosa, after Sudworth (1917).

Character	Species	
	P. arizonica	P. ponderosa
Height at Maturity	75 - 100 ft	125 - 140 ft
Trunk Diameter	30 - 50 in.	36 - 60 in.
Bark Thickness	2 in.	3 - 4 in.
Color	Very dark brown	Dark red-brown
Scales	Reddish brown	Russet brown
Crown	Rounded	Columnar
Leaves - Needles/fascicle	5 (occas. 2, 3 or 5)	3 (occas. 2, rare. 4 or 5)
Length	4 - 9¼ in.	4-3/4 - 11¼ in.
Basal sheath ln.	3/4 - 1 in. ½ deciduous	---------- deciduous
Resin ducts	3 per needle	2 - 5 per needle
Cone length	2 - 3¼ in.	2-3/4 - 5-3/4 in.
Scale Color - upper	Cinnamon brown	Russet brown
- lower	Deep purple-brown	Purplish
Prickle	Incurved	Reflected
Basal Scales	Remain attached to branch when cones are shed.	

METHODS

Habitat Studies

Before attempting intensive studies of ponderosa pine habitats in southeast Arizona, a general survey was made to locate regions where ponderosa pine is extant. This was accomplished initially by an aerial survey of each mountain range where the presence of ponderosa pine was expected; mountain ranges 7000 feet or higher were examined from the air to detect the presence of ponderosa pine. In most mountain ranges examined, the presence of ponderosa pine was immediately determined. However, in two cases a very careful low-level survey was required. Ponderosa pine was not detected in the Dragoon or Baboquivari Mountains, although it had been reported from these areas previously (Little, 1950; Kearney and Peebles, 1951). If ponderosa pine is present in these two locations, a study of those populations would not add materially to this study because of the small number of individuals and the restricted habitats. Figure 2 locates the mountain regions of southeast Arizona where studies were conducted.

In addition to aerial surveys, roads leading into ponderosa pine regions were extensively traveled and numerous needle and cone samples were taken from trees to reveal

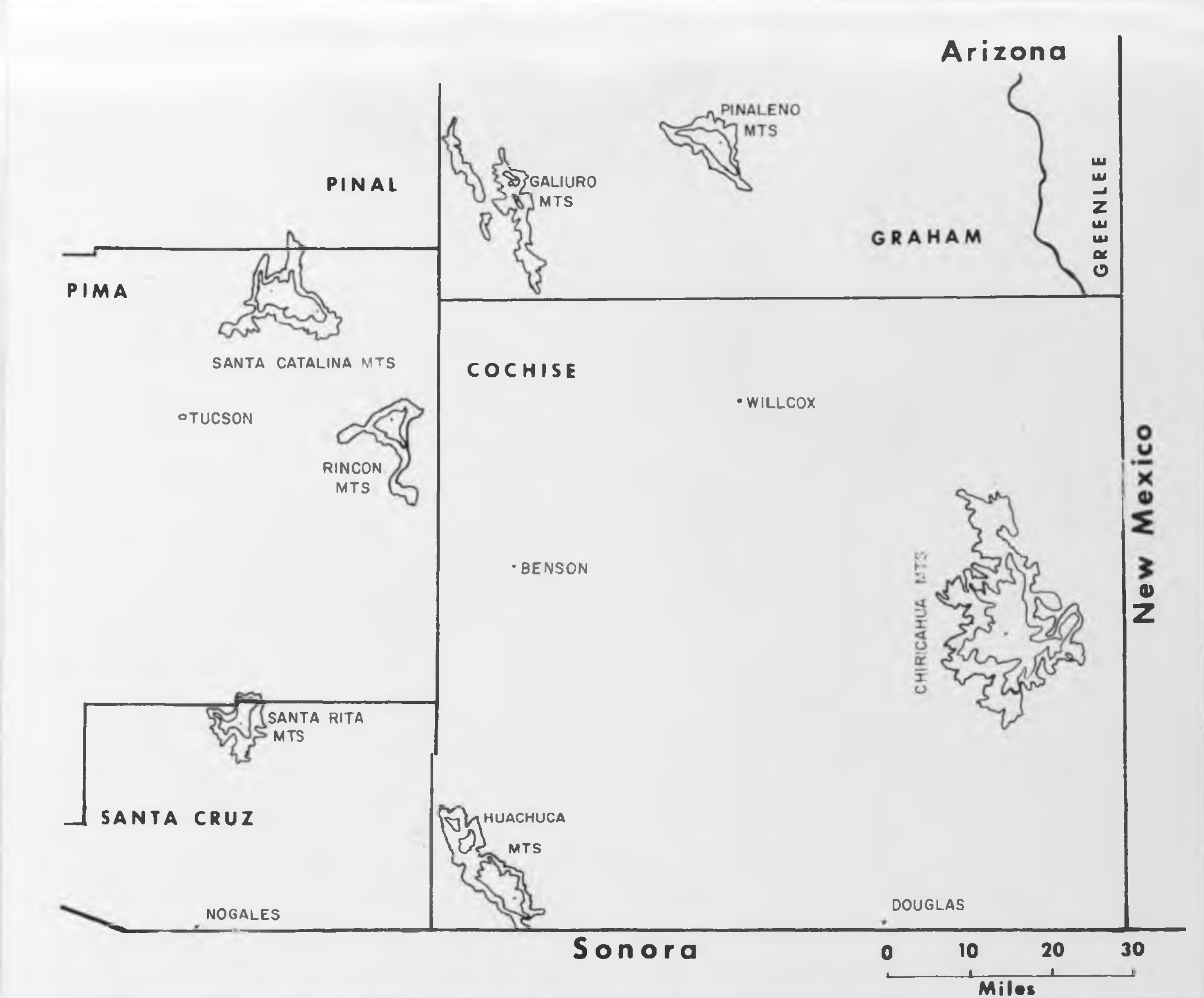

Figure 2. Location of mountainous regions of southeast Arizona in which ponderosa pine was studied. The 6000 and 7000 foot contours are shown.

differences exhibited within the populations. The elevational range of ponderosa pine was traversed by foot or horseback in the mountain areas studied in southeast Arizona.

Two types of sampling were employed. Where the extent of the forest was sufficient, phytosociological studies were made at regular contour intervals throughout the elevational range of ponderosa pine. The phytosociological investigations were conducted on exposed, south-facing slopes. South slopes were used for investigations because ponderosa pine attains its greatest elevational breadth in these positions.

In some areas, it was not fruitful to attempt plot studies because of the small number of pines present. These areas were especially evident in mountain ranges with narrow, sharp ridges, or precipitous topography on the south-facing slope, or in ranges where the highest elevation was not sufficient to support stands of ponderosa pine on the south-facing habitats. When situations were encountered that made the establishment of phytosociological sampling sites difficult or unfruitful, the elevational range of ponderosa pine was traversed for collection of needle and cone samples only.

Phytosociological Sampling Techniques

A plotless phytosociological technique was used to study the relationship between ponderosa pine habitats in southeast Arizona. In the areas where intensive sampling was carried on, a point-centered quarters quadrat method was employed. This technique has been used in the past by several investigators. Stearns (1949) reported that the quarters quadrat dates back to the middle of the last century, when it was used by federal surveyors. More recently, Curtis (1950, cited by Cottam and Curtis, 1956) adapted the point-centered quarters method for ecological studies. Other investigators have also relied upon this method to study phytosociological relationships of plant communities (Lindsey, 1956; Lindsey, et al., 1958; Phillips, 1959; Beals and Cottam, 1960).

Cottam and Curtis (1956) recognized that the use of extensive studies of many stands in related community types may be a better approach to understanding a regional vegetation than the more widely used but intensive study of a small area. Cottam and Curtis (1956) compared and contrasted four plotless techniques with a classical quadrat study in several populations and came to the conclusion that the quarters method gives the least variable results, provides more data on tree species per sampling point, and is least susceptible to subjective bias when compared to the other plotless techniques. In their opinion, the quarters method is, in most respects, superior to other distance-method techniques, and they recommended its use.

In this study of pine forests in southeast Arizona, a base line was established along an elevation contour. At intervals along the contour, a point, considered to be the center of four quarters, was established. The limits of each quarter around the point were determined by the cardinal points of the compass. Within each quarter the species nearest the point were determined, and the diameter breast high (DBH) for each tree was measured.

DBH was used to calculate the relative species dominance:

$$\text{Relative dominance} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100.$$

Relative density was calculated by:

$$\text{Relative density} = \frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \times 100.$$

If each group of four quarters is considered to be analogous to a quadrat, relative frequency determinations can also be made:

$$\text{Frequency} = \frac{\text{Number of quadrats of occurrence for the species}}{\text{Number of quadrats of occurrence for all species}} \times 100.$$

$$\text{Relative frequency} = \frac{\text{Frequency for the species}}{\text{Frequency total for all species}} \times 100.$$

The use of frequency derived from plotless determinations was developed by Cottam and Curtis (1956) and referred to by others (Lindsey, 1956; Phillips, 1959).

Relative dominance, relative frequency, and relative density were summed to provide the relative importance value for each species enumerated in the samples (Curtis and McIntosh, 1950). The maximum importance value equals 300.

This will occur when a population is composed of a single species. By using importance values, the relative contribution each species makes to the total population can be compared and contrasted with other similar populations.

In the southeast Arizona study, the quarters samples were made only in those mountains where the altitudinal range of ponderosa pine exceeded a breadth of 1500 feet. These areas were in the Santa Catalina, Rincon, Pinaleno, and Chiricahua Mountains. A System Paulin altimeter, which can be read to the nearest 10 foot interval, was used to determine the lowest elevation at which ponderosa pine appeared. The lowest extent of ponderosa pine on the exposed slopes occurred near 7000 feet in the areas studied. Succeeding samples were made up the slope at 250 foot elevation intervals until the upper limit of ponderosa pine was reached.

An Abney level was used to follow the contour at each elevation. At 10 meter intervals, a point was established for the center of four quarters. Ten points were usually established at each contour, yielding forty quarters. This value was lower in some areas because unexpected topographic features, such as an abrupt change in slope aspect or precipitous conditions, were encountered and prohibited the establishment of additional points. To minimize personal bias in selection, the first point was established 10 meters away from the trail location where elevation was determined.

Slope angle was determined with the Abney level, and the mean magnetic azimuth was estimated with a compass.

In addition to the data obtained from the quarters studies, needle samples were taken from all ponderosa pines encountered in the quarters. The number of needles in each of ten fascicles was tabulated for all ponderosa pines enumerated along the contours. Needle samples were taken directly from the tree when the branches were low enough to permit easy collection. If branches were too high, a handful of needles was picked up from the ground at the base of the counted tree, and ten fascicles were selected randomly and needles were counted. It is recognized that this practice may allow fascicles from other trees to be sampled, but this is not considered objectionable. The needle factor was designed to demonstrate the change in number of needles per fascicle with elevation, and thus, the population at a given elevation will reflect this factor throughout. The selection of needles from the ground may result in samples with greater randomness, and thus, may better characterize the number of needles per fascicle in a population than selecting the needles from the trees directly.

In addition to the needle counts from the ponderosa pines in the quarters, spur branches were collected for later observations. Staminate cones were collected in season, and pistillate cones were gathered where available in the ponderosa pine belt. The disposition of these samples will be discussed in a later section.

In areas where quarters samples were not feasible, needle and cone collections were made at frequent intervals along the trail. Altitude was recorded for each sample collected.

From every tree sampled in the traverse of the ponderosa pine zone, the number of needles per fascicle was enumerated from at least ten fascicles. The number of needles was grouped by 250 foot elevation intervals to derive a needle factor which was used to examine the change in number of needles per fascicle with elevation and to compare the needle number between mountain ranges.

Location of the Study Areas

The mountain ranges in southeast Arizona in which phytosociological investigations were conducted are positioned in an area bounded by 33° 50' and 31° 20' north latitude and 110° and 109° east longitude (USGS Base Map, Arizona, Figure 2). The general physiographic description of this area is classified as the Mountain Region (Ransome, 1923) of the Basin and Range Province (Fenneman, 1931). The abruptly rising mountain masses are of variable elevation and extent. The highest peak encountered, Mt. Graham in the Pinaleno Mountains, rises to an elevation of 10,713 feet. Chiricahua and Flys Peaks in the Chiricahua Mountains rise to nearly 9800 feet elevation. Miller Peak, in the Huachuca Mountains, and Mt. Wrightson, in the Santa Rita Mountains, reach almost 9500 feet elevation. Mt. Lemmon, in the Santa Catalina Mountains, exceeds 9100 feet. The only other sites in southeast Arizona where ponderosa pine was observed were the Rincon Mountains (Mica Mountain, 8500 feet) and the Galiuro Mountains (Kennedy and Bassett Peaks, standing at approximately 7500 feet).

Santa Catalina Mountains. The Santa Catalina Mountains comprise an area of approximately 200 square miles between latitudes 32° 20' and 32° 30' north, and 110° 30' and 111° 00' longitude east. The mountain area is drained on the northeast by the San Pedro River, on the south by Rillito Creek which drains into the Santa Cruz River, and on the northwest by numerous small drainage systems, principally Canada del Oro, which also empties into the Santa Cruz River.

The highest elevation, Mt. Lemmon, rises to 9196 feet; a series of peaks to the southeast, Mt. Bigelow (8550 feet) and Green Mountain (7890 feet), make up the backbone of the mountain range.

In general, the slopes are precipitous, as are nearly all the higher mountain ranges of this area. Geologically, the upper slopes of the Santa Catalina Mountains are composed of granite (Forrester, 1960). The soils are extremely shallow, and there are no major areas of soil accumulation. The extensive erosion and little chance for soil development results in most of the range being composed of Lithosols.

The quarters study plots were established at 250 foot contour intervals on a north to south baseline commencing at 8500 feet on Mt. Bigelow, passing through Rose Canyon, and terminating at the last stand of ponderosa pine below Lizard Rock, at 7000 feet.

Table 2 gives the elevation, magnetic azimuth of the slope and the general slope angle of the quarters series in the Santa Catalina Mountains. Ten meter intervals between quarter points were maintained throughout the study. Unless otherwise noted, ten points were established at each contour resulting in the enumeration of forty quarters at each elevation.

Because of the proximity of the Santa Catalina Mountains to Tucson (approximately 40 miles by road to the Palisades Ranger Station), a site was selected halfway between the Palisades Ranger Station and the Mt. Bigelow Lookout on the Lookout Trail for a dendrometer study of ponderosa pine. This location was selected because the road to the Ranger Station is, except for infrequent snow blockage, open to travel all year, and an area was found on the Lookout Trail at about 8200 feet where a number of three-, five- and mixed-needle trees were growing near one another. Mixed-needle trees contain fascicles with three- and four-, four- and five-, or three-, four- and five-needle fascicles on the same spur branch.

TABLE 2. Elevation, magnetic azimuth of slope studied, general slope angle and number of quarters sampled in the Santa Catalina Mountains.

Elevation (feet)	Magnetic Azimuth (degrees from magnetic north)	Slope Angle (degrees)	Number of Quarters
8500	160	20	40
8250	170	17	40
8000	215	10	40
7750	160	11	32
7500	160	30	32
7250	150	17	40
7000	160	36	40

The dendrometer study will be discussed in detail in a later section but is introduced here to identify the location of the study site.

Rincon Mountains. The Rincon Mountains are located a few miles southeast of the Santa Catalina Mountains and are connected to the Santa Catalina Mountains by a low mountain range known in part as the Tanque Verde Mountains. The area of the Rincons slightly exceeds 100 square miles and is positioned between 32° 03' and 32° 18' north latitude and 110° 26' and 110° 38' east longitude. Geologically, the mountains are formed primarily of gneiss (Forrester, 1960).

Mica Mountain (8550 feet) occupies a position of prominence on the north end of the range; Rincon Peak (8482 feet) is located approximately seven miles to the south; between these is found Happy Valley Saddle, a pass of approximately 7000 feet elevation. To the north and east of Mica Mountain, steep slopes fall away rapidly. To the west, a series of ridges with well-developed ponderosa pine stands extend downward to meet the Tanque Verde Mountains. The slope to the south is more gentle and supports a broad stand of ponderosa pine at upper elevations.

The quarters on the Rincon Mountains were started at Mica Mountain and followed the slope directly south from there for the 8500 and 8250 foot contour intervals. At elevations lower than this, considerable disturbance was encountered because of the numerous and frequent fires which occurred here. As a result, the 8000 foot quarters were taken in an area near Manning Camp, southwest of Mica Mountain. The 7750 foot contour was made on the trail from Spud Rock Cabin to Manning Camp, also southwest of Mica Mountain. The 7500 and 7250 foot contours were taken on the Manning Camp-Green Shack Trail and also had southwesterly exposures.

Elevation, slope magnetic azimuth and slope angle are given in Table 3 for the Rincon quarters stations.

It will be noted that at the 8000, 7500 and 7250 foot contour-quarters, only five points were established. Additional samples were not taken at the lower two elevations because of the narrowness of the ridge and the resulting abrupt changes in slope direction. The 8000 foot contour was interrupted by construction and disturbance at Manning Camp, and the value of additional samples under these conditions was questioned. Since no ponderosa pines were observed on the slopes below the 7250 foot contour, no quarters were made at 7000 feet.

Galiuro Mountains. The Galiuro Mountains are about 20 miles northeast of the Santa Catalina Mountains across the San Pedro River Valley. This range is extremely rugged and precipitous. Since no roads penetrate the entire area of the range, the forested areas were inaccessible except by trail. The range extends 32 miles in a northwest to southeast direction. On the westerly slopes it drains into the San Pedro

TABLE 3. Elevation, magnetic azimuth of slope studied, general slope angle and number of quarters sampled in the Rincon Mountains.

Elevation (feet)	Magnetic Azimuth (degrees from magnetic north)	Slope Angle (degrees)	Number of Quarters
8500	140	19	40
8250	140	19	40
8000	160	7	20
7750	240	17	40
7500	160	10	20
7250	200	19	20

River, while the easterly slopes drain into Arivaipa Creek. Geologically, the range is composed of rhyolite rocks, with andesite rocks predominant at the northern end of the range (Forrester, 1958). The northwest end of the mountain range is located at 32° 49' north latitude and 110° 27' east longitude; the southeast end is located at 32° 23' north latitude and 110° 10' east longitude; the area of the mountain range is approximately 170 square miles.

The main physiographic features are two long, narrow ridges separated at most by 8 miles, with a much eroded and dissected center region of 5000 to 6000 foot elevations. The east ridge is the higher and is dominated by a series of peaks; from north to south these peaks are China Peak (6592 feet), Kennedy Peak (7540 feet), Sunset Peak (7094 feet) and Bassett Peak (7650 feet). Connecting the several peaks there is an almost continuous high ridge at about 7000 feet elevation. The west ridge is lower and dominated by a series of peaks between 6500 and 7000 feet. The central portion of the range is drained by Rattlesnake Canyon to the northeast, Paddy's River to the east, High and Ash Creeks to the southeast, Redfield Canyon to the southwest, and several smaller drainage systems on the west-facing slopes of the west ridge.

The Galiuro Mountains support meager ponderosa pine stands, almost all of which are restricted to scattered populations on the north slopes of the higher mountain peaks and ridges. In addition, ponderosa pine was found at lower elevations along many canyons and drainage systems.

Studies in the Galiuro Mountains were restricted to the east ridge. The trail traveled commenced at Deer Creek Cabin, continued to Kennedy Peak, followed south along the top of the east ridge to the head of Paddy's River and down this drainage system back to Deer Creek.

The area around Kennedy Peak was examined. However, in view of the small size and scattered nature of ponderosa pine on the north slopes and the absence of ponderosa pine on the south slopes, no quarters studies were made. Fascicles were collected from ponderosa pine along the trail to determine the number of needles per fascicle.

In addition to needle samples, spur branches, staminate cones, and pistillate cones were collected, for later study, at several stations along the route traveled.

Pinaleno Mountains. The Pinaleno Mountains lie 10 miles northeast and parallel to the Galiuro Mountains. The Arivaipa Creek drainage lies between these mountain ranges. The Gila River drains the northeast side of the Pinaleno Mountains. The granitic Pinalenos (Forrester, 1958) are about 150 square miles and attain the highest elevation found in southeast Arizona, as was noted earlier. Like the Galiuro Mountains, the Pinaleno Mountain range runs from the northwest (32° 50' north latitude, 110° east longitude) to the southeast (32° 35' north latitude, 109° 45' east longitude) in a long, high ridge with steep southwest and northeast facing slopes.

The quarters studies were started on the south slopes of Mt. Graham at about 10,000 feet and terminated at Snow Flat (8750 feet) because of the precipitous cliffs south of this basin. The transect baseline was continued farther east down Shake Spring Trail from the point where it leaves Swift Trail at 8500 feet. Shake Spring Trail was followed to the lower limit of ponderosa pine at approximately 7000 feet. Thus, a series of forty quarters was established at 250 foot contour intervals from an elevation of 10,000 to 7000 feet.

Table 4 summarizes the elevation, magnetic azimuth and slope angle for each contour studied.

<u>Chiricahua Mountains</u>. Fifty miles southeast of the Pinaleno Mountains are found the Chiricahua Mountains. In this mountain system, which is approximately 35 miles long and 20 miles wide, there is a central geomass with several peaks exceeding 9000 feet. Chiricahua Peak (9796 feet) and Flys Peak (9666 feet) are the highest.

This mountain range is located between 31° 30' and 32° 08' north latitude and 109° 05' and 109° 27' east longitude and is approximately 450 miles square. The range is primarily made up of rhyolite (Forrester, 1959). The west slopes are drained by the Sulfur Springs Valley and the east slope by the San Simon and San Bernardino Valleys.

TABLE 4. Elevation, magnetic azimuth of slope studied, general slope angle and number of quarters sampled in the Pinaleno Mountains.

Elevation (feet)	Magnetic Azimuth (degrees from magnetic north)	Slope Angle (degrees)	Number of Quarters
10000	220	23	40
9750	220	11	40
9500	180	12	40
9250	225	14	40
9000	270	18	40
8750	220	18	40
8500	140	11	40
8250	140	14	40
8000	150	12	40
7750	140	11	40
7500	160	5	40
7250	180	6	40
7000	160	17	40

Quarters plots were established along a trail from Rustler Park to Rucker Canyon by way of Raspberry Ridge Trail. The first quarters contour was established at 9500 feet on the south slope of Chiricahua Peak. Only five points were established here because a steep slope and a large mass of rock appeared on the east end of the contour, making further extension of the transect risky.

The next quarters were established along Raspberry Trail at 500 foot contour intervals. At elevations below 9000 feet, this ridge becomes precipitous and there was little opportunity to establish more than five quarters at each elevation. Ponderosa pine was not observed below 7500 feet on the arid south exposures. The pine was present in the deep canyons and on some sheltered north exposures. In the sheltered locations, it grows with _Pinus latifolia_.

Table 5 summarizes the elevation, magnetic azimuth and slope angle for each of the contours studied.

Huachuca Mountains. The Huachuca Mountains are located approximately 75 miles southwest of the Chiricahua Mountains. The Huachucas consist basically of a single northwest-to-southeast ridge with four prominent peaks; from north to south these are Huachuca (8410 feet), Ramsey (8751 feet), Carr (9214 feet), and Miller (9466 feet). The area of the mountain unit is approximately 125 square miles. It is composed of granite and limestone (Forrester, 1959).

TABLE 5. Elevation, magnetic azimuth of slope studied, general slope angle and number of quarters sampled in the Chiricahua Mountains.

Elevation (feet)	Magnetic Azimuth (degrees from magnetic north)	Slope Angle (degrees)	Number of Quarters
9500	200	26	20
9000	265	23	40
8500	160	18	20
8000	225	12	20

The Huachucas are located between 32° 20' and 31° 37' north latitude and 110° 15' and 110° 30' east longitude. They are drained on the north and east by the San Pedro River. On the southwest, small tributaries drain south into Mexico. The most southerly slope was studied from Montezuma Pass to Miller Peak along Miller Peak Trail. This slope rises nearly 3500 feet in three miles. Surprisingly, only one area suitable for quarters plots was located. The exposed south slope in this area is almost devoid of ponderosa pine. The major development of pine forests occurs north of Miller Peak in high-elevation regions between the several peaks.

Along Miller Peak Trail, fascicles were collected for needle number determinations from the scattered trees encountered on north slopes or protected sites. Spur branches and cones were also collected where available.

Santa Rita Mountains. The Santa Rita Mountains are located approximately 30 miles northeast of the Huachuca Mountains and 50 miles south of the Santa Catalina Mountains. This rather small range, approximately 100 square miles, has one main peak, Mt. Wrightson (9453 feet). Mt. Wrightson is located at 31° 47' north latitude and 110° 51' east longitude. It is formed of rhyolite, and the region to the west of Mt. Wrightson is granitic (Forrester, 1960).

The Santa Rita Mountains are drained on the southwest and north by tributaries of the Santa Cruz River; the east slopes ultimately drain into the San Pedro River system.

The sharp rise of Mt. Wrightson results in steep slopes which do not support large stands of ponderosa pine on the south. No quarters plots were established in this range. The needle factor analysis was made along the trail which runs southeasterly from Madera Canyon to Mt. Wrightson. Spur branch and pistillate cone samples were collected along this trail.

<u>Other Geographical Areas</u>. In addition to the ponderosa pine regions cited for southeast Arizona, several other sites were visited to obtain material for comparison. Most of these collections were made in central and northern Arizona. Additional samples were also collected in Sonora, Mexico.

The areas of central and northern Arizona in which collections were made are from the New Mexico border to the east, along the Mogollon Plateau to north of Flagstaff; from an area south of Prescott; and from an area south of the Grand Canyon on the Coconino Plateau. The Sonoran collection was from the slopes of El Tigré Mountain, a peak approximately 60 air miles south of Douglas, Arizona, located on the western slopes of the Sierra Madre Occidental. The range slightly exceeds 7000 feet, and ponderosa pine is mainly restricted to north slopes.

Morphological Observations

While performing the phytosociological investigations in the various mountain sites, a persistent effort was made to qualitatively determine the taxonomic relationship of each ponderosa pine tree observed in the quarters. Identification was most often estimated from the frequency of needles per fascicle since this character is usually the easiest to ascertain in the field. While this character may not precisely identify a specimen, it is useful for rapidly characterizing a population. Field collections of branches, pistillate cones and, when available, staminate cones were also collected from the regions studied.

Branch and needle samples were bagged, labeled and frozen until more detailed studies could be made. Pistillate cones were likewise bagged, labeled and dried until they could be studied and compared more closely. Staminate cones were collected in season and immediately placed in small vials containing FAA (formalin 5%, acetic acid 5%, ethyl alcohol 90%) until microscopic examinations were made.

Needles and Branches

Branches from ponderosa and Arizona pine were collected from all populations visited. On occasion a pruning head on a 12 foot pole was used. At other times branches were collected from the highest object available--the roof of a car, atop a horse, from an elevated topographic feature--or from ground level if branches could be reached.

In one location in the Santa Catalina Mountains, where large numbers of samples were collected, a 12-gauge shotgun was employed to collect branches from 10 to 50 feet above the ground. It was found that a magnum birdshot shell and full choke bored shotgun was extremely useful for cutting branches up to one inch in diameter at these heights.

This technique was used in several other areas where a road was nearby. This instrument was not used in all cases, especially where a long hike was required, because of the added weight of the shotgun and the quantity of shotgun shells required to gather an adequate sample.

In collecting branches, the highest that could be easily reached were taken. Since a large number of samples was collected in each population studied, the samples were likely random and all sides of the trees were represented within the population.

Because of the large number of samples collected and the limited availability of freezer storage space, needles were stripped from the branches and stored in small plastic bags. Ten fascicles were selected at random from the most recent year's growth and the average number of needles per fascicle was determined for each collection. These values, in addition to those enumerated in the phytosociological studies, were used to determine the needle factor for the various populations.

At a later time, sample needles from some of the populations were measured to the nearest millimeter. After measurement, the number of stomates in a 5 mm section were determined from loose fascicles selected at random.

In slash and loblolly pine, Mergen (1958, 1959) showed that the number of stomates per unit length was under "fairly rigid genetic control." Furthermore, he also demonstrated that hybrids were intermediate between the parent types. He concluded that the number of stomates per unit length in loblolly and slash pines was relatively independent of environmental effects, and that the distribution of stomates per unit length in the phenotype was a very close expression of the genotype (Mergen, 1958).

From his evidence, Mergen (1959) concluded that an analysis of the stomates can be used as a valid test to identify putative hybrids, and can be used to verify the hybrids from controlled crosses. Mergen was able to identify hybrids produced from the crosses of _Pinus thunbergii_ x _P. densiflora_, _P. densiflora_ x _P. nigra_, and _P. monticola_ x _P. strobus_. He recognized that this technique was not always successful since a hybrid between _P. ayacahuite_ x _P. strobus_ did not have a frequency distribution dissimilar enough to allow for separation (Mergen, 1959).

This method was tested with members of the southeast Arizona ponderosa pine complex. Collections cited earlier from a small area in the Santa Catalina Mountains were intensively tested in this manner. Three classes of trees were defined on the basis of needle number per fascicle. The three categories were considered to be: Arizona pine with primarily five needles per fascicle; ponderosa pine with three needles per fascicle; and those intermediate, with mixed-needle fascicles.

Each row of stomates on a needle was considered a sample. The needle was cut one inch from the base, was placed under a dissecting microscope with 40x magnification, and was illuminated obliquely. The stomates stand out clearly because they are sunken and are surrounded by a whitish bloom or exudate. Stomates on all rows from all three faces of each needle were enumerated. An ocular micrometer was used to delimit a 5 mm section. A hand-operated counter provided a rapid means for tallying the number of stomates in the 5 mm sections.

In addition to the area studied in the Santa Catalina Mountains, stomates from other areas were also counted so that frequency distributions from different regions could be compared.

<u>Pollen</u>

Study of pollen grains for diagnostic purposes has been advanced by paleobotanists for identification of fossil and other unknown pollen. Axelrod and Ting (1960) cited experiments in which they relied on grain dimensions for identification of unknown pollen. In saccate grains they made three measurements: the overall width, body width, and width of the bladder (Figure 3). The body diameter was compared

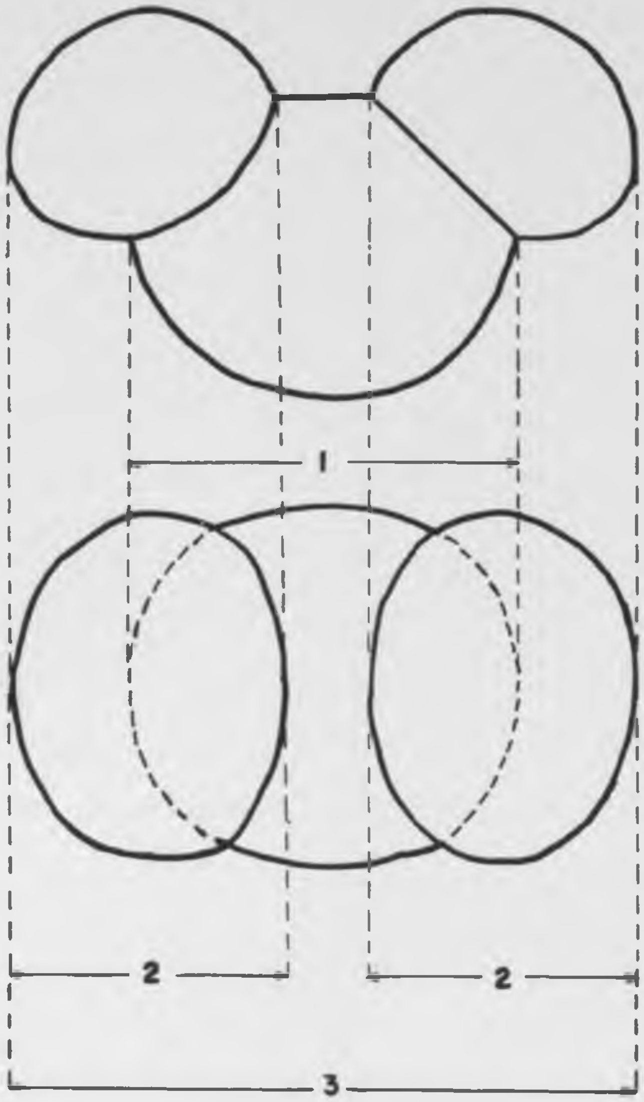

Figure 3. Pollen grain dimensions: (1) pollen grain width, (2) bladder width, and (3) total width (Axelrod and Ting, 1960).

with the bladder width to determine a ratio for the species (Axelrod and Ting, 1960). Comparing known pollen-size frequency distributions with the dimensions determined for unknown pollen grains facilitated species identification.

In this study it was reasoned that the pollen-grain distributions may show differences between ponderosa and Arizona pine. Therefore, pollen collected from the Santa Catalina study area was subjected to this test. Three classes of pollen were examined: pollen from three-needle, five-needle, and mixed-needle trees.

Near the end of April (April 29, 1961), staminate cones were first observed in the Santa Catalina Mountains at an elevation of 8100 feet. The progress of staminate cone development was observed approximately every week thereafter. Pollen shedding was first observed on July 4 in a few trees. This phenomenon was general by July 11, and by July 21 staminate cones were falling from the trees. During the period of greatest pollen shedding, staminate cones were collected from 30 different trees in the Santa Catalina study area. Ten trees were sampled from each needle class. Several staminate cones were gathered at each tree and immediately placed in small glass vials containing FAA.

In addition to the Santa Catalina study area, samples were collected in the Santa Rita, Pinaleno, and Galiuro Mountains. Additional collections were made in northern

Arizona for comparative purposes. Collections were made during the month of July in the general season of pollen shedding.

Collections could not be made from all study areas because of the short time when mature pollen was available and because of the great distances separating the mountain ranges where ponderosa pine occurs.

The pollen samples were prepared for microscopic examination by a method outlined by Wodehouse (1935) in which a glycerine jelly (composed of fuchsin, glycerine and phenol) is used as a mounting medium. An eye dropper was used to place a drop of pollen-laden preservative from the storage vials on a clean microscope slide. The preservative solution was allowed to evaporate. The pollen sample was washed with alcohol to distribute the grains over the glass slide. A drop of heated glycerine-jelly was placed over the pollen grains. A cover-slip was placed over this, and the slide was gently heated by passing it through a Bunsen-burner flame or by placing it on a warming oven until the fixing and staining solution spread under the cover-slip. Heating also permitted the cover-slip to settle over the grains and oriented them into a single layer. The slides were allowed to cool, thus setting the glycerine-jelly and holding the pollen grains rigid.

The slides were observed under a compound microscope at 430 diameters. Measurements were made with a calibrated ocular micrometer. Three measurements were made for each pollen grain in a manner similar to that used by Axelrod and Ting (1960) (Figure 3).

The slide was scanned by using a stage micrometer and the first 25 whole, properly oriented grains encountered were measured. Pollen grains oriented so as to distort the size of the bladders or grain were not used in the sample.

The pollen-grain measurements were grouped according to the needle-class designations and were subjected to statistical analysis. An additional test was accomplished by determining the ratio between the bladder width and the grain width and subjecting this value to statistical tests.

Pistillate Cones

Cone size is one of the most often cited differences between ponderosa and Arizona pine (*i.e.*, Engelmann, 1878; Sudworth, 1917; Martinez, 1948). The cone of Arizona pine is cited as being smaller than the cone of the Rocky Mountain ponderosa pine. However, Table 1 demonstrates the overlap of cone size, and the usefulness of this character is confused in cases where the two populations occur sympatrically.

Pistillate cones are often not produced by all of the trees in a given season. However, scattered trees can usually be found which produce a good cone crop in any year. Since given trees within the populations studied could not be utilized for cone samples, cones were collected when and where available. In general, sufficient cone quantities were found to adequately characterize an area. At no time were sufficient cones available in the specialized study areas to provide a collection that could be tentatively classed as *Pinus ponderosa* or *P. arizonica*. Therefore, samples were gathered where available, and comparisons were made between geographic regions studied.

In almost all cases, cones were collected from the ground. Because the lighter color of the most recent cone crop was distinct, it was certain that only the current year's crop was collected. All of the cones present at scattered cone-bearing trees were collected to diminish bias.

Cone Size. Cones were dried at approximately 60° C until they attained constant weight. The dried cones were measured for length and greatest diameter with a caliper. Since the basal rosette of the scales often remains on the branch when the cone is shed, correction was made for missing scales. The value for this correction was determined from several basal rosettes that separated from whole cones during the drying period.

The cone length was compared by geographic location in order to determine the cone-size range shown by the Arizona ponderosa pine populations studied.

Haller (1957, 1962a) used a cone-volume measurement to compare ponderosa and Jeffrey pine in California. This value was more satisfactory than length to determine cone-size differences. The approximate volume was calculated by:

$$V = (4/3\pi r^2\ H)\ (\tfrac{1}{2}).$$

This formula assumes every cone is half an oblate spheroid. Haller admitted that this is seldom true, but he thought that pine cone shapes closely approximate such a figure. In the formula, H is equal to the greatest length of the cone and r is one-half the greatest diameter.

Cone Density. The comparison of cone densities was another character used by Haller (1957, 1962a). Densities were determined by dividing the weights of dried cones by the calculated volume. This value was calculated for the cones collected in Arizona and Sonora. No statistical evaluation could be made of the calculated density values in this study because of the small sample size and the wide geographic area compared. Frequency histograms were constructed to compare and to detect, if possible, shifts of density with geographic change and to determine possible taxonomic variation.

Cone Prickle. Sudworth (1917) and Martinez (1948) described the prickle direction on the cone scale as a useful character for identification of the two-pine taxa. Sudworth (1917) referred to the cone scales of *P. arizonica* terminating in a delicate incurved prickle. Likewise, Martinez (1948) described Arizona pine-cone scales with a short, thin, midrib spine, almost always incurved (Martinez, 1948:295, ". . . espina corta y delgada, casi siempre encorvada."). This character was studied in all cones collected.

Only the largest, completely developed cone scales at the center of the cone were observed and enumerated. At least ten scales were examined and classified according to the extent and direction of umbo spine curvature.

A comparative class was established in which the cone-prickle direction was placed in one of five categories. A prickle turning inward and sharply down, forming an arc greater than 45 degrees, was placed in class one. Prickles curving downward slightly and up to 45 degrees were placed in class two; those pointing outward without curvature were designated class three. Slightly upward pointing prickles were placed in class four, and those turning upward sharply, inscribing an arc greater than 45 degrees, in class five. The class frequencies were compared with the geographical source of the cone.

Dendrometer Studies

The general location of the dendrometer study sites in the area between the Palisades Ranger Station and Mt. Bigelow was mentioned in the description of the phytosociological study sites of the Santa Catalina Mountains.

This study area, located between 8190 and 8250 feet on the Lookout Trail between Palisades Ranger Station and Mt. Bigelow, was approximately two and one-half acres in area. The slope angle at the site averages 8.4 degrees (range 5 - 18 degrees). The slope direction is primarily south, ranging from SSE to SSW (160 - 200 degrees from magnetic north).

The soil in this area is a shallow, coarse textured Lithosol. The average soil depth around the trees studied is two inches, ranging from one inch to four and one-half inches as determined with auger samples near the base of the trees. The trees are comparable in size, development, and degree of shading from adjacent trees. Table 6 lists for the trees the needle classification, elevation at tree base, angle of the slope upon which the trees are found, diameter breast high (DBH), qualitative crown density, crown diameter and degree of shading from adjacent trees.

Air temperature was recorded with a thermograph housed in a US Weather Bureau type shelter at Palisades Ranger Station located less than one-fourth mile away from the site. A sheltered maximum-minimum thermometer was located in the center of the study area to check the reliability of the Palisades temperature data. It was determined during the term of the investigation that temperatures recorded at the two sites were comparable. Weekly maximum-minimum temperatures

TABLE 6. Site comparison for the trees used in the dendrometer study, Santa Catalina Mountains.

Tree Classification	Elevation at Tree Base (feet)	Slope Angle (degrees)	DBH (inches)	Crown Density (%)	Crown Diameter (feet)	Shade from Adjacent Trees (%)
Three-needle	8255	5	15.5	50	13	50
	8250	5	11.2	80	12	35
	8230	7	14.4	60	10	60
	8250	9	25.2	50	20	20
	8250	7	18.5	65	16	10
	8275	10	15.1	40	17	80
	8255	6	19.0	80	18	20
	8255	5	18.2	65	14	70
Mean	8265	7	17.1	61	16	43
Mixed-needle	8255	5	17.2	70	16	30
	8190	8	19.0	55	15	25
	8200	12	18.7	70	14	25
	8200	12	15.0	20	6	20
	8230	10	20.6	70	16	25
	8255	5	21.9	65	15	70
	8255	5	19.2	50	17	65
	8255	5	20.4	55	17	70
Mean	8230	8	19.0	57	15	41
Five-needle	8230	10	17.7	50	13	25
	8275	12	14.0	40	13	65
	8190	8	16.5	40	10	50
	8200	10	20.9	50	15	35
	8200	18	22.4	45	18	65
	8200	12	20.2	40	17	60
	8200	8	20.6	50	16	35
	8230	16	17.4	40	14	25
Mean	8215	12	18.7	44	15	45

were most often determined by the thermometer located in the study area.

Daily precipitation data were also collected at Palisades Ranger Station by Coronado National Forest personnel during the study period. Some error may be present in the precipitation values since the open area around the rain gauge was less than three times the height of the nearest trees. However, the determinations were considered to be sufficiently accurate to compare the time and the relative quantity of precipitation during the term of the study. Soil temperature and soil moisture were not monitored.

Radial growth of ponderosa pine has interested workers for some time, and different methods of determining this factor have been employed. MacDougal (1924, 1936) devised a dendrograph for continuously recording the radial fluctuations of tree trunks. He studied radial growth of different age classes of ponderosa pine in northern Arizona. Radial growth, needle elongation and height growth of ponderosa pine were compared by Fowells (1941) at different elevations in the Sierra Nevada Mountains of California. Daubenmire and co-workers have reported several studies in which radial expansion of ponderosa pine was compared with environmental factors (Daubenmire, 1945, 1946, 1950; Daubenmire and Deters, 1947). Turner has more recently reported investigations of growth and reproduction of ponderosa pine in northern Idaho (Turner, 1956). Hess (1960) has reported investigations of ponderosa pine growth correlated with ecological and environmental factors in the central Rockies of Colorado.

Trees studied were selected and classed on the basis of the number of needles per fascicle taken from each tree. Spur branches were collected from three different locations on each tree. Needles were stripped from the spur branches and segregated into groups from three seasons. Twenty fascicles in each group from each tree were selected randomly and enumerated. On the basis of the needle-class determined for a tree, three groups of trees were recognized. (The procedure for classing trees into groups has already been described in the section on stomates.) In the mixed-needle trees, at least twenty-five percent of the fascicles contained four needles per fascicle. Following examination of the trees, eight trees in each of the three groups were selected for radial expansion studies.

Daubenmire type dendrometers (1945) were used in this study to determine if detectable radial expansion differences were present among the three groups of trees. Two Daubenmire type dendrometer stations were installed on different radii approximately three feet above the base of each tree. Usually the northeast and northwest sides were utilized to minimize expansion of the brass anchor screws resulting from insolation.

Daubenmire type dendrometers give an estimate of the radial expansion at the time of measurement only, and it is not known if the periodic measurements are recorded at the time of greatest expansion or at some submaximal value because of diurnal fluctuation. To minimize this difficulty, readings were always taken at or near sunrise, the time of greatest daily trunk expansion.

Dendrometer measurements were made from December, 1960, starting before the onset of spring growth, and were terminated in October, 1961, after radial expansion had ceased for the season.

RESULTS

Habitat Studies

Phytosociological Relationships

Results of the quarters studies are summarized in tabular form (Tables 7 to 10). Quarters quadrats were established in four areas, and the results are presented by geographic region: Table 7, Santa Catalina Mountains; Table 8, Rincon Mountains; Table 9, Pinaleno Mountains; and Table 10, Chiricahua Mountains. As was stated earlier, only south-facing slopes were examined.

In the Santa Catalina Mountains (Table 7), ponderosa pine reaches its most prominent status on the upper slopes of the range. It appears, on the basis of importance values, to be the dominant species above 7250 feet in each contour studied. From 8000 to 8500 feet, ponderosa pine is associated mostly with other conifers, but it is, nevertheless, the overwhelming dominant of the community. Below 8000 feet, the oaks increase, and at the lower three stations, silver-leaf oak (*Quercus hypoleucoides*) competes with ponderosa pine for species importance.

The Rincon quarters data, Table 8, demonstrate even more strikingly the importance of ponderosa pine at higher elevations. From 8000 to 8500 feet, almost pure stands of

TABLE 7. Relative density, relative dominance, relative frequency and importance values of tree species in the quarters quadrats on the Santa Catalina Mountains from 8500 to 7000 feet.

Elevation (feet)	Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value
8500	Pinus ponderosa	72.5	88.8	52.5	213.8
	Pinus strobiformis	17.5	7.0	28.3	52.8
	Pseudotsuga menziesii	2.5	1.2	5.3	9.0
	Quercus reticulata	5.0	1.6	5.3	11.9
	Quercus hypoleucoides	2.5	1.4	10.5	14.4
8250	Pinus ponderosa	77.5	85.4	62.5	225.4
	Pinus strobiformis	10.0	4.6	18.8	33.4
	Pseudotsuga menziesii	12.5	10.0	18.8	41.3
8000	Pinus ponderosa	52.5	87.2	45.5	185.2
	Pinus strobiformis	25.0	4.6	27.3	56.9
	Quercus hypoleucoides	22.5	8.2	27.3	58.0
7750	Pinus ponderosa	56.3	73.1	50.0	179.4
	Pinus strobiformis	9.4	3.9	18.8	32.1
	Quercus hypoleucoides	34.4	23.0	31.2	88.6
7500	Pinus ponderosa	28.1	35.7	27.2	91.0
	Pinus strobiformis	15.6	13.2	18.3	47.1
	Quercus hypoleucoides	31.3	33.3	27.2	91.8
	Quercus reticulata	25.0	17.8	27.2	70.0
7250	Pinus ponderosa	50.0	52.7	50.0	152.7
	Pinus strobiformis	2.5	4.3	5.0	11.8
	Quercus hypoleucoides	42.5	38.3	40.0	120.8
	Quercus reticulata	5.0	4.8	5.0	14.8
7000	Quercus hypoleucoides	32.5	35.9	42.2	110.6
	Quercus reticulata	2.5	1.4	5.3	9.2
	Arctostaphylos sp.	65.0	62.6	52.5	180.1

TABLE 8. Relative density, relative dominance, relative frequency and importance values of tree species in the quarters quadrats on the Rincon Mountains from 8500 to 7250 feet.

Elevation (feet)	Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value
8500	Pinus ponderosa	100.0	100.0	100.0	300.0
8250	Pinus ponderosa	90.0	95.1	83.3	268.4
	Pinus strobiformis	5.0	1.7	8.3	15.0
	Juniperus deppeana	5.0	3.4	8.3	16.7
8000	Pinus ponderosa	90.0	97.1	83.3	270.4
	Pinus strobiformis	10.0	2.9	16.6	29.5
7750	Pinus ponderosa	20.0	30.4	26.3	76.7
	Pinus strobiformis	5.0	3.6	5.3	13.9
	Pinus leiophylla	2.5	9.6	5.3	17.4
	Quercus hypoleucoides	67.5	54.4	52.5	174.4
	Quercus reticulata	5.0	2.0	10.5	17.5
7500	Pinus ponderosa	20.0	31.9	23.1	75.0
	Pinus strobiformis	15.0	4.6	15.4	35.0
	Quercus hypoleucoides	40.0	47.1	38.4	125.5
	Quercus reticulata	20.0	15.1	15.4	50.5
	Juniperus deppeana	5.0	1.3	7.7	14.0
7250	Pinus strobiformis	10.0	5.8	7.7	23.5
	Pinus leiophylla	30.0	48.6	30.8	109.4
	Quercus hypoleucoides	35.0	22.6	30.8	88.4
	Quercus reticulata	25.0	22.9	30.8	78.7

ponderosa pine are present. At 7750 feet, silver-leaf oak becomes dominant and ponderosa pine is secondary. A similar trend is observed in the Santa Catalina Mountains. This sharp change may be the result of exposure differences since the lower quadrats are located on southwest slopes.

Douglas fir does not appear on the south slopes of this range in the quarters studies. Since Douglas fir is usually found at higher elevations than ponderosa pine, it is evident that the elevation in the Rincon Mountains is insufficient for the development of Douglas fir on southerly slopes. However, Marshall (1956) noted the presence of Douglas fir on the north slopes of the Rincons.

The elevational range of the quarters studies on the Pinaleno Mountains (Table 9) was broader than for the other areas investigated. Quarters contours were established from 7000 feet to 10,000 feet. Ponderosa pine was present in the uppermost contour; however, its contribution is insignificant (18.4 importance value units out of 300). Ponderosa pine does not assume dominance until 8500 feet. The oaks appear to assume their greatest importance at elevations below 8500 feet.

In the Pinaleno Mountains, Douglas fir occurs in a well-developed zone from 8750 to 9750 feet; white pine (*Pinus strobiformis*) appears as the dominant at the highest stations. Engelmann spruce (*Picea engelmanni*) is a significant member

TABLE 9. Relative density, relative dominance, relative frequency and importance values of tree species in the quarters quadrats on the Pinaleno Mountains from 10,000 to 7000 feet.

Elevation (feet)	Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value
10000	Pinus ponderosa	5.0	5.1	8.3	18.4
	Pinus strobiformis	62.5	71.9	41.6	176.0
	Picea engelmanni	20.0	14.7	29.2	63.9
	Pseudotsuga menziesii	12.5	8.3	20.8	41.6
9750	Pinus strobiformis	45.0	33.5	47.5	125.0
	Picea engelmanni	2.5	2.2	5.3	10.0
	Pseudotsuga menziesii	50.0	64.0	42.3	116.3
	Abies concolor	2.5	0.3	5.3	8.1
9500	Pinus ponderosa	5.0	17.6	8.7	31.3
	Pinus strobiformis	50.0	29.7	34.8	114.5
	Picea engelmanni	2.5	0.4	4.4	7.3
	Pseudotsuga menziesii	35.0	49.0	39.2	123.2
	Abies concolor	5.0	2.5	8.7	16.2
	Jamesia americana	2.5	0.9	4.4	7.8
9250	Pinus ponderosa	40.0	46.4	37.5	123.9
	Pinus strobiformis	20.0	23.7	25.0	68.7
	Pseudotsuga menziesii	37.5	25.0	33.3	95.8
	Abies concolor	2.5	4.9	4.2	11.6
9000	Pinus ponderosa	7.5	12.8	9.1	29.4
	Pinus strobiformis	15.0	10.7	18.2	43.9
	Pseudotsuga menziesii	55.0	64.8	45.5	165.3
	Abies concolor	22.5	11.8	27.3	61.6
8750	Pinus ponderosa	15.0	28.5	20.0	63.5
	Pinus strobiformis	32.5	16.1	28.0	76.6
	Pseudotsuga menziesii	35.0	50.1	28.0	115.1
	Abies concolor	12.5	4.4	20.0	36.9
	Quercus gambelii	5.0	0.9	4.0	9.9

TABLE 9. Continued.

Elevation (feet)	Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value
8500	Pinus ponderosa	40.0	73.8	34.6	148.4
	Quercus gambelii	10.0	9.8	15.4	35.2
	Quercus reticulata	27.5	6.8	19.3	53.6
	Cercocarpus sp.	22.5	9.8	30.8	63.1
8250	Pinus ponderosa	32.5	43.3	33.4	109.2
	Pinus strobiformis	2.5	1.7	4.8	9.0
	Quercus hypoleucoides	7.5	4.0	14.3	25.8
	Quercus reticulata	57.5	51.0	47.5	156.0
8000	Pinus ponderosa	37.5	58.7	31.8	128.0
	Quercus hypoleucoides	22.5	12.4	27.3	62.2
	Quercus reticulata	40.0	28.9	40.8	109.7
7750	Pinus ponderosa	22.5	24.3	33.3	80.1
	Quercus reticulata	77.5	75.7	66.6	219.8
7500	Pinus ponderosa	15.0	21.6	25.0	61.6
	Quercus reticulata	80.0	75.6	62.5	218.1
	Quercus hypoleucoides	2.5	2.5	6.3	11.3
	Juniperus deppeana	2.5	0.4	6.3	9.2
7250	Pinus ponderosa	40.0	47.3	40.0	127.3
	Quercus reticulata	55.0	48.7	50.0	153.7
	Quercus hypoleucoides	5.0	4.0	10.0	19.0
7000	Quercus reticulata	50.0	60.4	50.0	160.4
	Fallugia paradoxa	50.0	39.6	50.0	139.6

of the plant community at the highest station studied. It was noted that extensive spruce and white pine stands occurred at stations higher than the 10,000 foot contour; however, no quadrats were established here since no ponderosa pine was observed above 10,000 feet.

The quadrats in the Chiricahua Mountains were less complete than those in the other ranges since only four contours were established. The results from these quadrat studies are shown in Table 10. Ponderosa pine is dominant at only one station (9000 feet). At the highest station (9500 feet), aspen (Populus tremuloides) is dominant on the basis of the quarters established. Below 9000 feet the oaks become the dominant species. It should be pointed out that below the 9000 foot station rather steep rocky slopes were encountered, resulting in extremely arid conditions except in the riparian situations. The 8500 foot station was situated on a narrow rocky ridge that afforded only enough space to complete five quarters stations.

While it may appear that ponderosa pine does not have great importance in the Chiricahua Mountains, extensive ponderosa pine forests occur on the high plateau. The plateau area corresponds to the 9000 foot station. The large importance value of ponderosa pine at the 9000 foot station is characteristic of many ponderosa pine stands in the Chiricahua Mountains.

TABLE 10. Relative density, relative dominance, relative frequency and importance values of tree species in the quarters quadrats on the Chiricahua Mountains from 9500 to 8000 feet.

Elevation (feet)	Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value
9500	Populus tremuloides	75.0	48.9	52.5	176.4
	Pinus strobiformis	5.0	2.4	5.3	12.7
	Pseudotsuga menziesii	20.0	48.8	42.0	110.8
9000	Pinus ponderosa	65.0	84.3	58.8	208.1
	Pseudotsuga menziesii	35.0	15.7	41.2	91.9
8500	Pinus ponderosa	15.0	42.0	20.0	77.0
	Pinus strobiformis	10.0	2.7	13.3	26.0
	Pinus leiophylla	5.0	9.4	6.7	21.1
	Pseudotsuga menziesii	20.0	27.7	20.0	67.7
	Quercus reticulata	40.0	15.5	33.3	88.8
	Quercus hypoleucoides	10.0	2.7	6.7	19.4
8000	Pinus ponderosa	15.0	23.4	20.0	58.4
	Pinus strobiformis	5.0	13.8	6.7	25.5
	Pinus engelmanni	15.0	22.7	13.3	51.0
	Pseudotsuga menziesii	5.0	10.1	6.7	21.8
	Quercus reticulata	25.0	12.3	26.6	63.9
	Quercus hypoleucoides	35.0	17.7	26.6	79.3

<u>Needle Factor</u>

Needle information from the quarters stations and from the trail sampling procedures is tabulated for each mountain range studied (Table 11). With two exceptions, an increase in needle number appeared from higher to lower elevations. The increase was more pronounced the more southerly the mountain range. High frequencies of five-needle fascicles were found in the Santa Rita, Huachuca, and Chiricahua Mountains. The intermediate ranges, Santa Catalina and Rincon Mountains, demonstrated this phenomenon also, except that the frequency of higher-numbered fascicles was slightly less at most elevations. The Galiuro and Pinaleno Mountains showed a strikingly different pattern for this character.

On the basis of needle-number studies in the quarters of the Pinaleno Mountains, no five-needle fascicles were found. Only two four-needle fascicles were discovered among more than 1000 fascicles counted. Since the trees from which needle samples were collected in the Pinaleno Mountains were found exclusively in the quarters, no bias was present in the manner of selecting trees for needle enumeration.

It should be pointed out that a greater quantity of higher-numbered fascicles was encountered along Swift Trail in an earlier needle collection. Swift Trail samples from Lady Bug Flat to Riggs Lake yielded approximately 4 percent four-needle fascicles. A sample of 25 fascicles on the north side

TABLE 11. Needle factor for ponderosa pine by elevation in several mountain ranges of southeast Arizona.

Elevation (feet)	Mountain Range						
	Pinaleno	Galiuro 1/	Rincon	Santa Catalina	Santa Rita 1/	Huachuca 1/	Chiricahua
10000	3.00						
9500	3.00						
9000	3.00				3.04 2/		3.19 2/
8500	2.97		3.20 2/	3.16 2/	3.30		5.00
8000	3.01		3.05	4.79	3.00	4.97 2/	5.00
7500	3.01		4.88	4.43	4.00	-	-
7000	3.00	3.00 2/	-	4.67	4.40	-	-
6500	-	3.02	-	-	5.00	-	-
6000	-	3.00	-	-	-	-	-

1/ Trail samples only.

2/ Highest topographic feature studied.

- Ponderosa pine no longer appeared on slope studied.

of the mountain range at the lower limit of ponderosa pine had 36 percent five-needle fascicles.

More than 400 samples were counted from collections made while traveling by horseback in the Galiuro Mountains. In all situations investigated, no five-needle fascicles were collected, and only three four-needle fascicles were found.

Needle samples from El Tigre Mountains were selected along a trail on a west facing slope. The number of trees was not recorded, but the sample size exceeded 500 fascicles. Only one tree was found with four-needle fascicles and the remainder were five-needle.

Samples from northern Arizona stations, i.e., Hannegan Meadows, along the Mogollon Rim, near Flagstaff, Coconino Plateau, and near Prescott, in nearly all cases yielded three-needle fascicles. A few two-needle fascicles were found. Collection records were not kept, and these data are omitted from the comparison.

Morphological Characters

Needles

Needle characters investigated were total length and stomate number per unit length.

The average needle length is given in Table 12, with the location, standard error, and sample size of each collection. In addition, the trees from the dendrometer study

TABLE 12. Average length of ponderosa pine needles from locations studied in Arizona and Sonora.

Location	Mean Length (mm)	Standard Error (mm)	Sample Size
Santa Catalina Mountains			
Mt. Bigelow			
Three-needle	136	17.6	85
Mixed-needle	142	15.1	55
Five-needle	153	31.2	83
Rincon Mountains	130	27.9	10
Huachuca Mountains	121	15.3	19
Chiricahua Mountains	128	15.4	14
El Tigré Mountains, Sonora	147	26.8	23
Pinaleno Mountains	127	28.4	20
Prescott	163	27.1	14

are grouped according to the number of needles per fascicle (Table 12).

The number of stomates per unit length is presented graphically in Figures 4 and 5.

Figure 4 presents the frequency of stomate numbers per mm from the several populations investigated. The distributions are arranged in a north-to-south sequence. The Prescott samples were the most northerly and the samples from El Tigré Mountains the southernmost. These two stations are approximately 325 air miles apart.

The determination of the number of stomates per mm in the three classes of trees recognized in the Mt. Bigelow study area is found in Figure 5. Small differences are apparent between the five-, mixed-, and three-needle populations, and the populations appear to be similar for this character.

Pollen

Mean size and standard deviation for pollen-grain width and bladder width were determined for each sample in the Mt. Bigelow dendrometer study area. Table 13 summarizes the values calculated for 25 sample grains from 18 different trees. The samples are divided into three putative populations, *i.e.*, three-needle trees, mixed-needle trees, and five-needle trees.

In addition to the mean and standard deviation, the samples are analyzed further by analysis of variance for

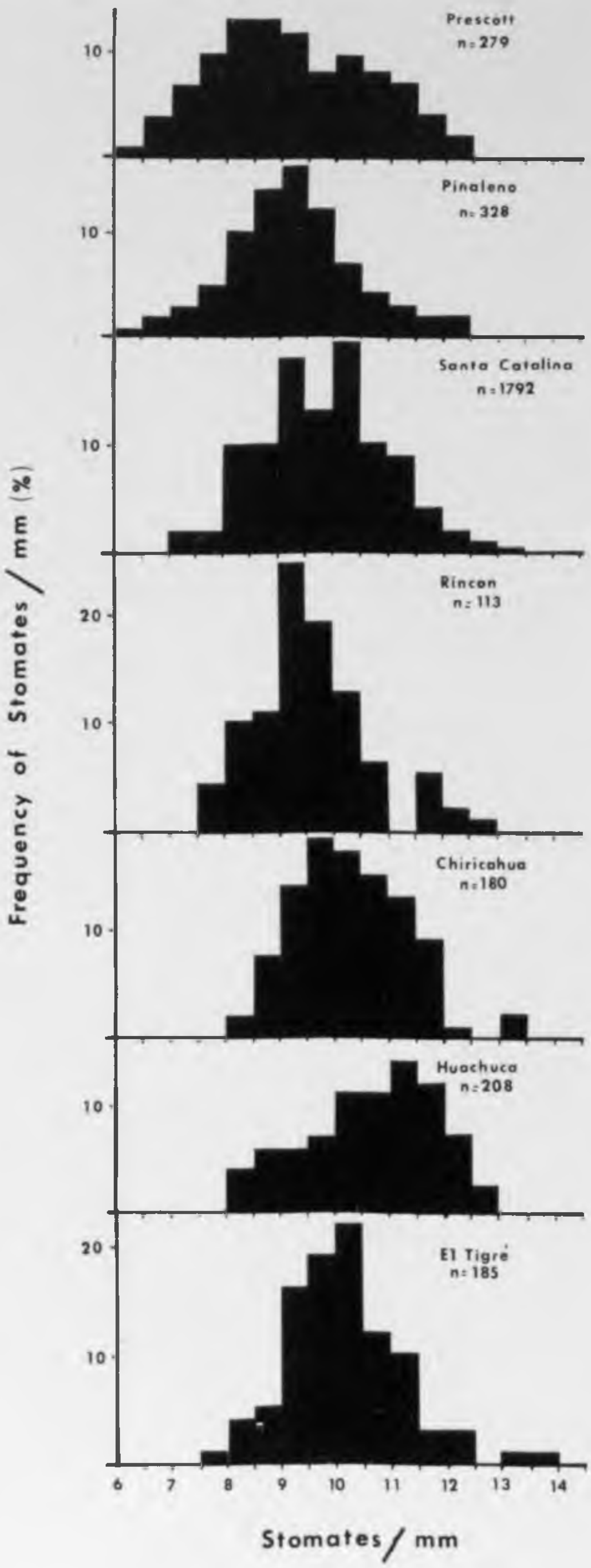

Figure 4. Frequency distributions showing number of stomates/mm in 0.5 mm classes. Data from ponderosa pine in Arizona and Sonora.

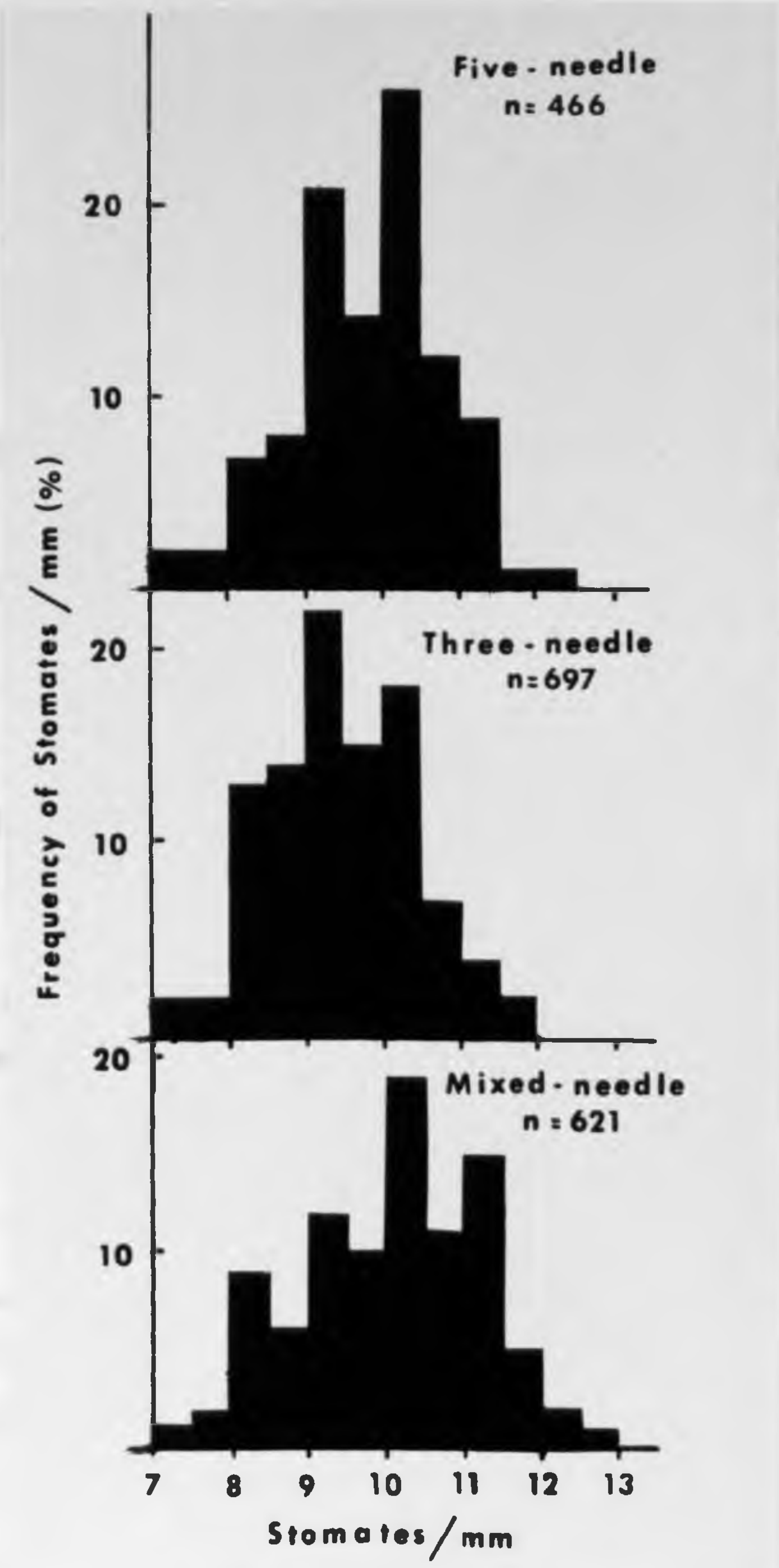

Figure 5. Frequency distributions showing number of stomates/mm in 0.5 mm classes. Data from ponderosa pine in Mt. Bigelow study area, Santa Catalina Mountains.

TABLE 13. Mean and standard deviation of the pollen-grain diameter and bladder width of three putative populations of ponderosa pine on Mt. Bigelow, Santa Catalina Mountains. Six trees from each population. Twenty-five measurements of each character from each tree.

Population	Pollen Grain Diameter		Bladder Width	
	Mean (μ)	Std. Dev. (μ)	Mean (μ)	Std. Dev. (μ)
Three-needle	48.2	9.9	29.0	1.7
	46.4	2.3	26.0	1.3
	46.0	2.0	31.4	1.9
	52.0	3.2	32.8	2.0
	49.2	2.1	31.4	2.0
	44.4	2.7	28.2	2.0
Mixed-needle	51.0	2.4	29.8	1.7
	51.8	1.6	32.0	2.0
	49.6	2.5	29.0	1.1
	49.6	1.8	29.6	1.6
	51.2	2.9	31.4	1.9
	52.4	3.4	27.8	1.3
Five-needle	51.4	3.2	32.2	1.6
	52.0	2.4	30.4	2.3
	48.4	1.3	29.8	1.9
	51.6	3.0	29.6	1.5
	50.4	4.8	29.0	2.2
	49.0	3.1	29.4	2.2

samples within samples (Snedecor, 1956). Thus, the pollen grain measurements are treated as samples within the tree within three populations. This analysis is presented in Table 14.

On the basis of the pollen-grain size analysis, no significant difference is found among the three putative populations. There is, however, a highly significant difference among the individual trees within the populations.

The pollen grain bladder width is subjected to the same statistical treatment, and the results are presented in Table 15. Similar results are obtained from the analysis of variance of the bladder width, *i.e.*, no significant difference among the three populations and a high degree of variance within the trees of the population.

Axelrod and Ting (1960) recommended determining a ratio between the body diameter and the bladder width. This ratio is determined for the Mt. Bigelow material, and the analysis of variance is presented in Table 16.

The same conclusion is drawn from the analysis of the bladder-width to grain-diameter ratio as shown in the analysis of the individual characters, *i.e.*, no significant difference among the populations but a high level of individual variation within a population.

In addition to the sample drawn from the Mt. Bigelow area, pollen grains from other areas were collected and

TABLE 14. Analysis of variance of pollen grain size from trees within three putative populations of ponderosa pine on Mt. Bigelow, Santa Catalina Mountains.

Source of Variation	DF	SS	MS
Populations (3)	2	0.62	0.31 n.s.
Trees in population (6)	15	50.66	3.38 *
Determinations from trees (25)	432	81.18	0.19
Total	449	132.46	

n.s. Not significant.
* Highly significant difference.

TABLE 15. Analysis of variance of pollen grain bladder widths within three putative populations of ponderosa pine on Mt. Bigelow, Santa Catalina Mountains.

Source of Variation	DF	SS	MS
Populations (3)	2	0.06	0.03 n.s.
Trees in population (6)	15	17.23	1.15 *
Determinations from trees (25)	432	15.71	0.04
Total	449	33.00	

n.s. Not significant.
* Highly significant difference.

TABLE 16. Analysis of variance of the ratio between pollen grain diameter and bladder width from three putative populations of ponderosa pine on Mt. Bigelow, Santa Catalina Mountains.

Source of Variation	DF	SS	MS
Populations (3)	2	0.01	0.005 n.s.
Trees in population (6)	15	1.03	0.069 *
Determinations from trees (25)	432	0.85	0.002
Total	449	1.89	

n.s. Not significant.
* Highly significant difference.

measured. The mean size of the grain and the mean width of the bladders are shown in Table 17 for samples collected in the Pinaleno, Galiuro, and Santa Rita Mountains.

A marked size difference determined for the northern Arizona samples resulted in a re-examination of the material. This further study showed the grains to be immature, i.e., the exine of the grain was smooth and no reticulation was present. These are common features of immature grains, as the exine configuration appears only at maturity. When the staminate cones for this collection were removed from the fixing solution, the pollen sacs had to be crushed to release the grains. Thus, the pollen was not yet ready for release and was not fully mature. These samples, therefore, were excluded from the comparison shown in Table 17.

Pistillate Cones

Length. Table 18 lists the geographical regions in which cones were collected for length comparisons. The mean length, range and standard deviation for each collection are tabulated in Table 18. The data from this table are, in addition, presented graphically in Figure 6.

Density. The calculated cone density values were grouped by frequency classes and geographical location. Frequency-class histograms are presented in Figure 7.

Cone Prickle. The umbo spine or prickle on the cone scale was placed in one of five categories. The average class

TABLE 17. Comparison of the mean and standard deviation of the pollen-grain diameter and bladder width of pollen grains collected in the Pinaleno, Galiuro, and Santa Rita Mountains, Arizona.

Location	Pollen Grain Diameter		Bladder Width	
	Mean (μ)	Std. Dev. (μ)	Mean (μ)	Std. Dev. (μ)
Pinaleno Mts.	49.6 52.8	3.1 11.0	31.4 31.6	2.0 4.3
Galiuro Mts.	48.4	3.7	31.4	2.4
Santa Rita Mts.	50.4	3.5	29.8	2.3

TABLE 18. Mean length, range, standard deviation, and sample size for cones collected at several stations in Arizona and Sonora.

Location	Mean Length (cm)	Range (cm)	Standard Deviation (cm)	Sample Size
Northern Arizona	8.0	5.9 - 11.4	1.40	47
Pinaleno Mts.	8.1	5.6 - 10.8	1.52	57
Southern Arizona	7.7	5.9 - 9.8	1.07	62
Santa Catalina Mts.	8.3	6.3 - 9.8	0.95	36
Rincon Mts.	7.0	5.8 - 8.5	0.87	14
Chiricahua Mts.	6.3	5.9 - 6.7	0.30	5
Huachuca Mts.	7.0	6.4 - 7.5	0.41	7
El Tigré Mts., Son.	8.2	6.2 - 11.3	1.94	14

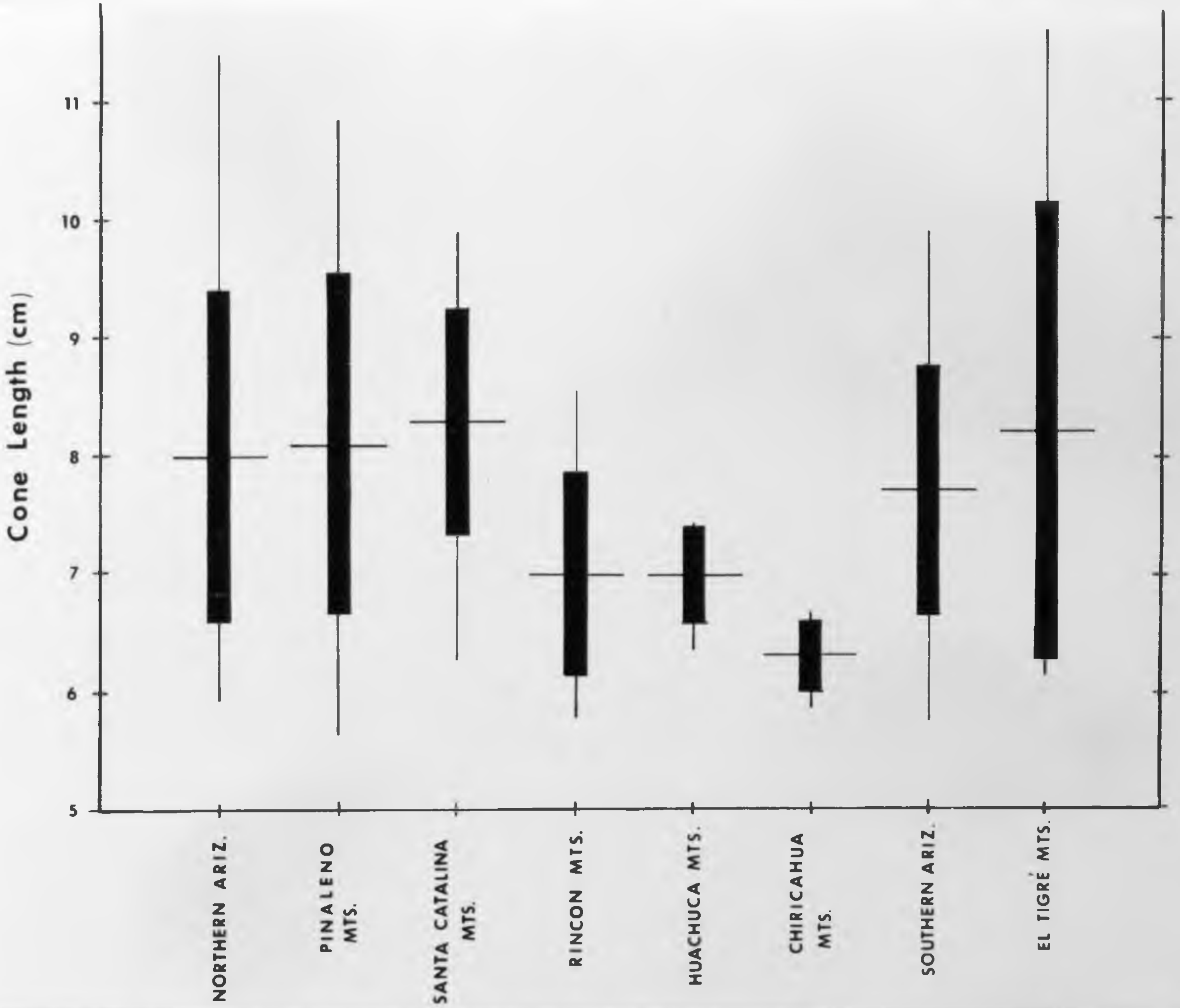

Figure 6. Mean length, range and standard deviation for cones from several populations of ponderosa pine.

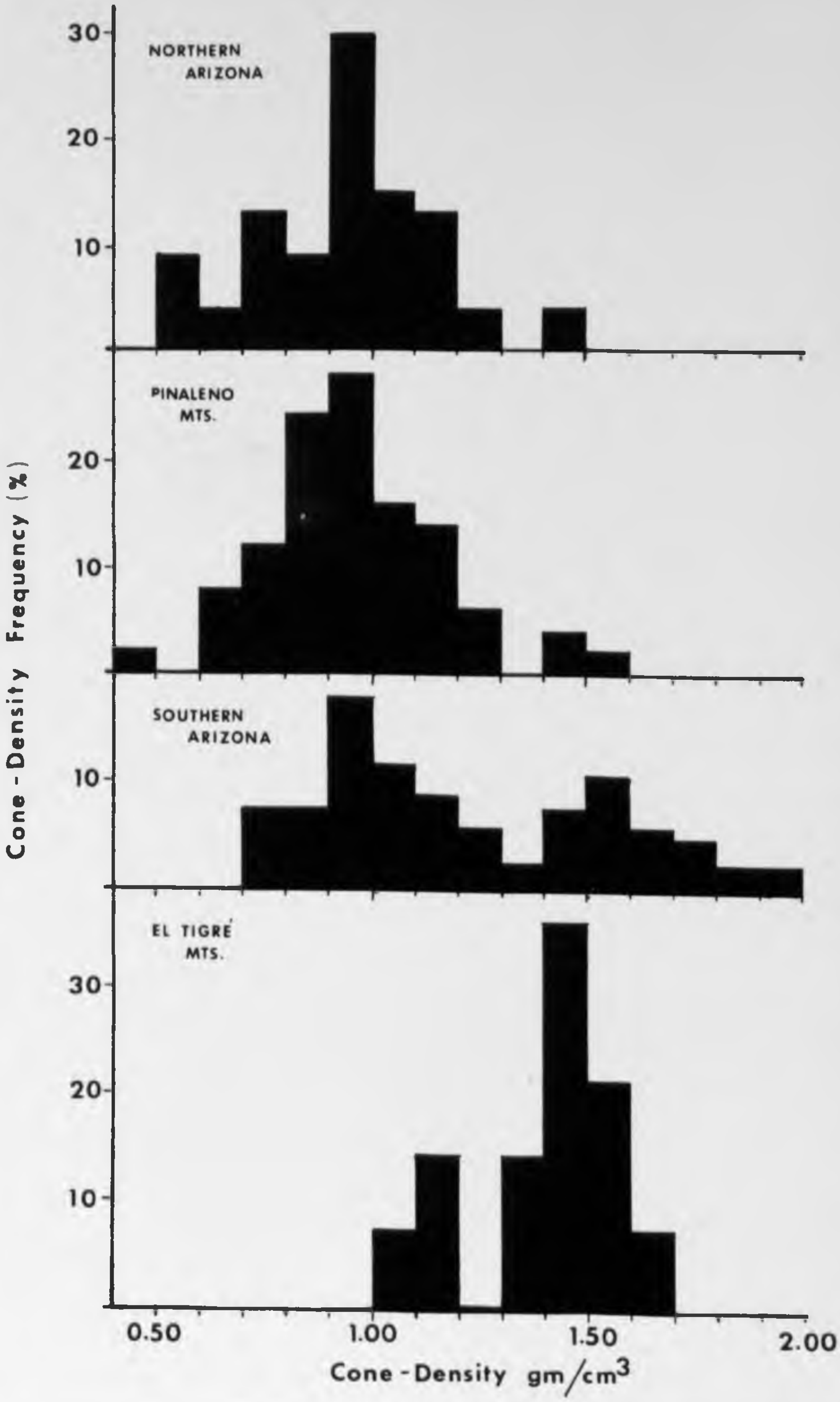

Figure 7. Frequency distribution of cone density for ponderosa pine populations.

is tabulated in Table 19 for the populations observed. The populations are arranged in a north-south sequence. The prickle direction more often points upward in the northern and central stations (northern Arizona and Pinaleno Mountains) and downward in the southern sites. The spine direction more often appears intermediate in the Santa Catalina Mountains.

Figures 8 to 10 show representative illustrations of cones from each of the three geographical areas studied, i.e., northern Arizona (sample from Prescott), southeast Arizona (sample from Rincon Mountains), and Sonora (sample from El Tigré Mountains).

Figure 8 shows a cone and a cone scale from Prescott and demonstrates the characteristic cone scale spine. In this case the spine is curved outward. In addition, the spine is quite stout and broad at its base where it is attached to the umbo.

Figure 9, a cone from the Rincon Mountains, shows the typical inward-curved umbo spine seen in many southeast Arizona ponderosa pine populations. As in the northern sample, the spine is stout and broad at the base where it is attached to the umbo.

In Figure 10, an illustration of a cone and cone scale from El Tigré Mountains, the spine also curves inward, but the spine is small and delicate and arises from the umbo as a small prickle without a broad base.

TABLE 19. Cone prickle designation and sample size for stations in Arizona and Sonora.

Location	Prickle Class	No. Cones Observed
Northern Arizona	4.52	46
Pinaleno Mts. - Total	3.61	57
9250 feet elevation	4.00	9
8750 feet elevation	3.60	5
8500 feet elevation	3.40	12
8000 feet elevation	3.12	8
7500 feet elevation	3.45	11
7000 feet elevation	4.00	12
Santa Catalina Mts. - Total	2.95	42
9000 feet elevation	3.67	15
7500 feet elevation	2.40	15
7000 feet elevation	2.75	12
Rincon Mts.	2.31	16
Huachuca Mts.	2.28	7
El Tigré Mts., Son.	2.14	14

Figure 8. Typical cone from Prescott showing recurved cone-scale prickle.

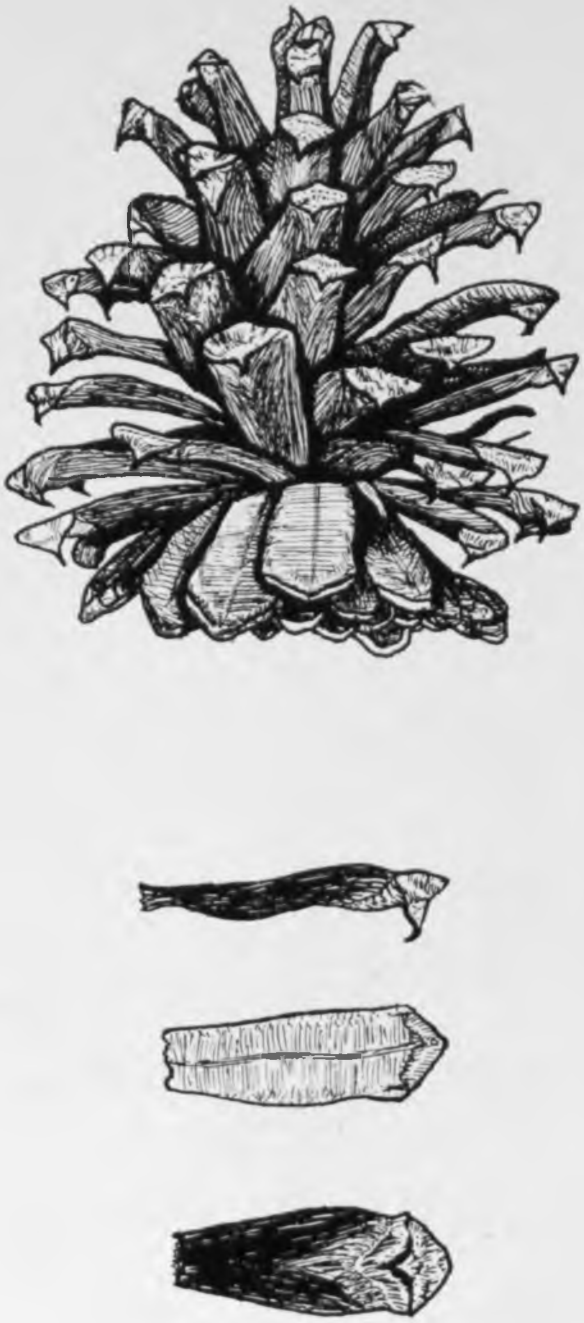

Figure 9. Typical cone from Rincon Mountains showing incurved cone-scale prickle.

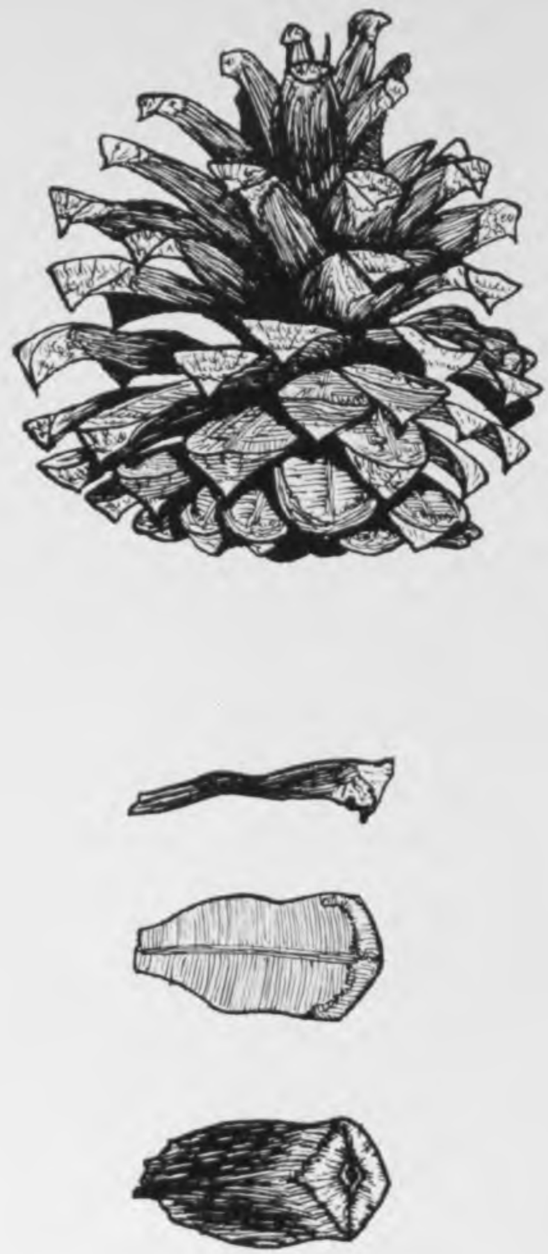

Figure 10. Typical cone from El Tigré Mountains showing small, delicate cone-scale prickle turning inward.

The cone samples from the Rincon and Huachuca Mountains have prickles with the broadened basal character, while many of the Santa Catalina Mountain samples have delicate spines like the samples from El Tigré Mountains. The latter character was especially evident at lower elevations in the Santa Catalina Mountains. Frequency of samples within prickle classes from the several geographic locations are presented in Figure 11.

Dendrometer Studies

Figures 12 and 13 summarize the data collected from the dendrometer study sites. From these illustrations it can be seen that the trees classed as three-needle and mixed-needle commenced radial expansion before the five-needle trees.

In Figure 12, dendrometer data for the three putative populations are expressed as increase in radial expansion over the previous visit. For ease of comparison, the data are plotted as the percentage of the total seasonal expansion for the populations. Maximum and minimum temperatures which occurred between visits, and the daily precipitation during the period of the study, are also plotted in Figure 12.

The three-needle and mixed-needle trees appeared, on the basis of data shown in Figure 12, to be alike since they exhibited radial increases prior to the five-needle trees. The three-needle group showed greater radial activity at this

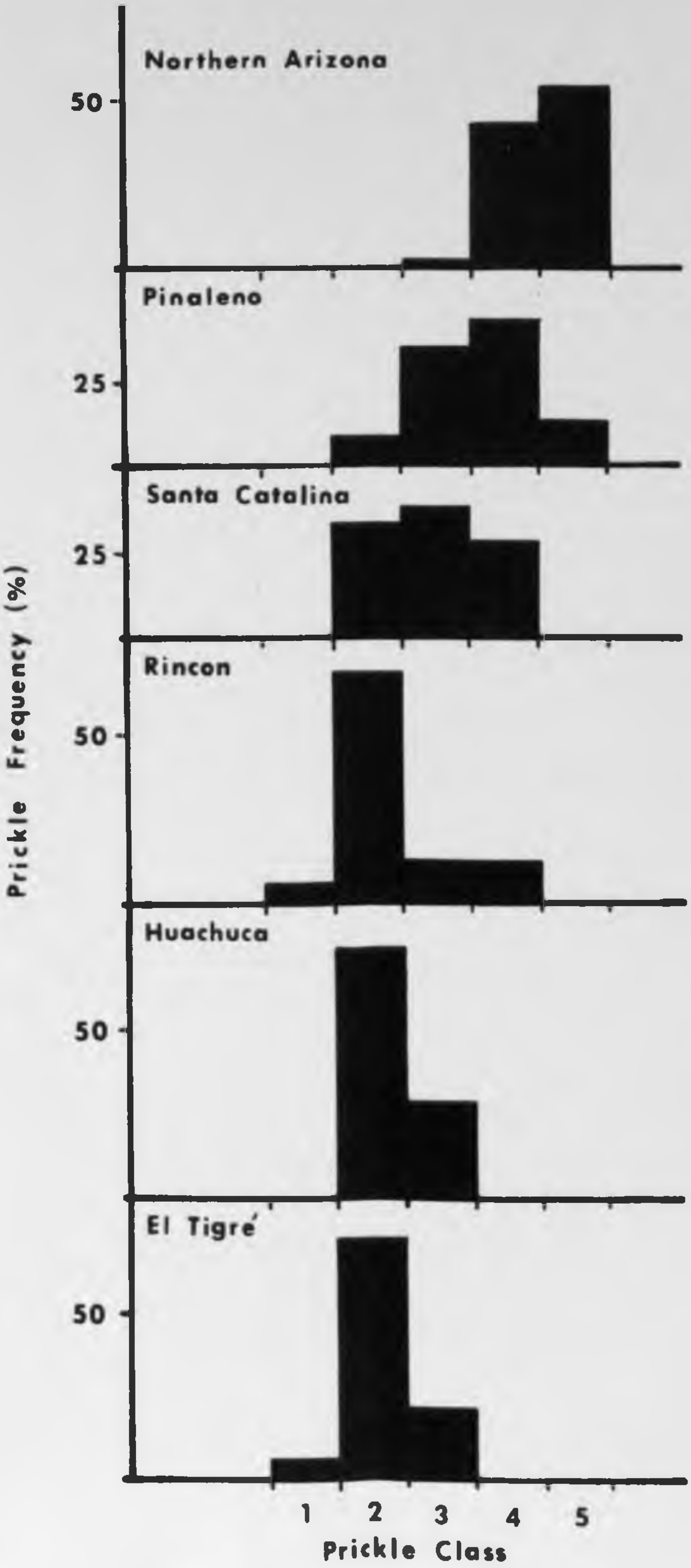

Figure 11. Frequency distribution of cone-scale prickle classes for a north-to-south array of ponderosa pine populations.

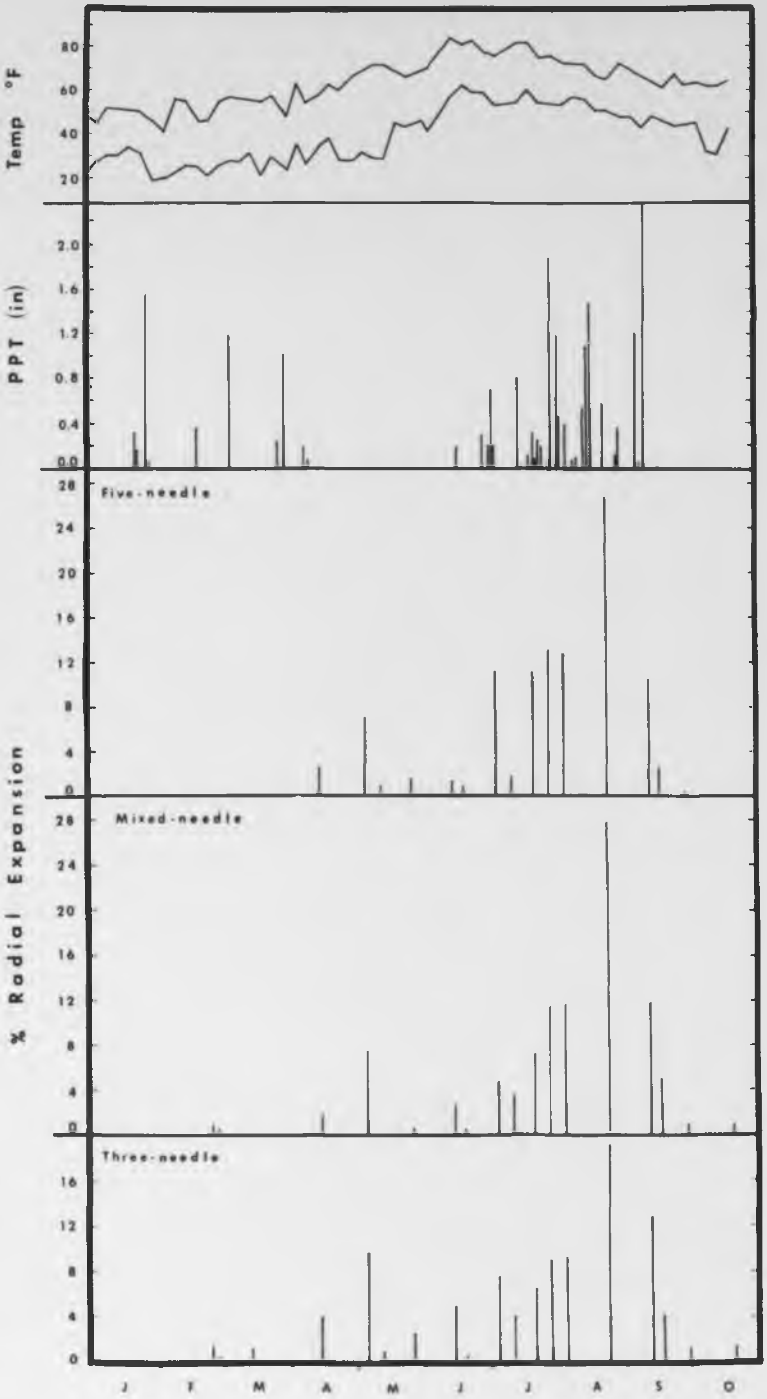

Figure 12. Radial expansion (as percent of growing-season total) for three populations of ponderosa pine which have been distinguished by differences in number of needles per fascicle. Radial expansion data show average percent increase of stem radii in excess of values obtained on previous date measured. Temperature data are maximum and minimum values occurring between visits. Precipitation data are daily values. All data are from the Mt. Bigelow study area.

time (first indication of increase was February 24, 1961) than did the mixed-needle trees.

The five-needle trees did not show any radial expansion until six weeks after the other two groups (April 14). Most radial expansion took place during the summer months for all three groups. All three classes of trees ceased radial expansion at approximately the same time.

The dendrometer data are plotted another way in Figure 13. The curves are arranged to show an accumulation of total radial increments rather than an increment increase from one reading to the next, as in Figure 12. The cumulative curves show the mean radial increase from approximately 18 determinations in each class. One standard deviation above and below the mean was determined for each dendrometer recording date.

The time each class of tree reached its 5 and 95 percent total is also indicated (Figure 13). The growth phase between these two values was termed the grand period by Büsgen and Münch (cited by Jackson, 1953). Figure 13, like Figure 12, demonstrates that the three-needle trees commenced their grand period prior to the five-needle trees, and the mixed-needle trees were intermediate during the season studied. The completion of 95 percent total expansion occurred at about the same time for each group.

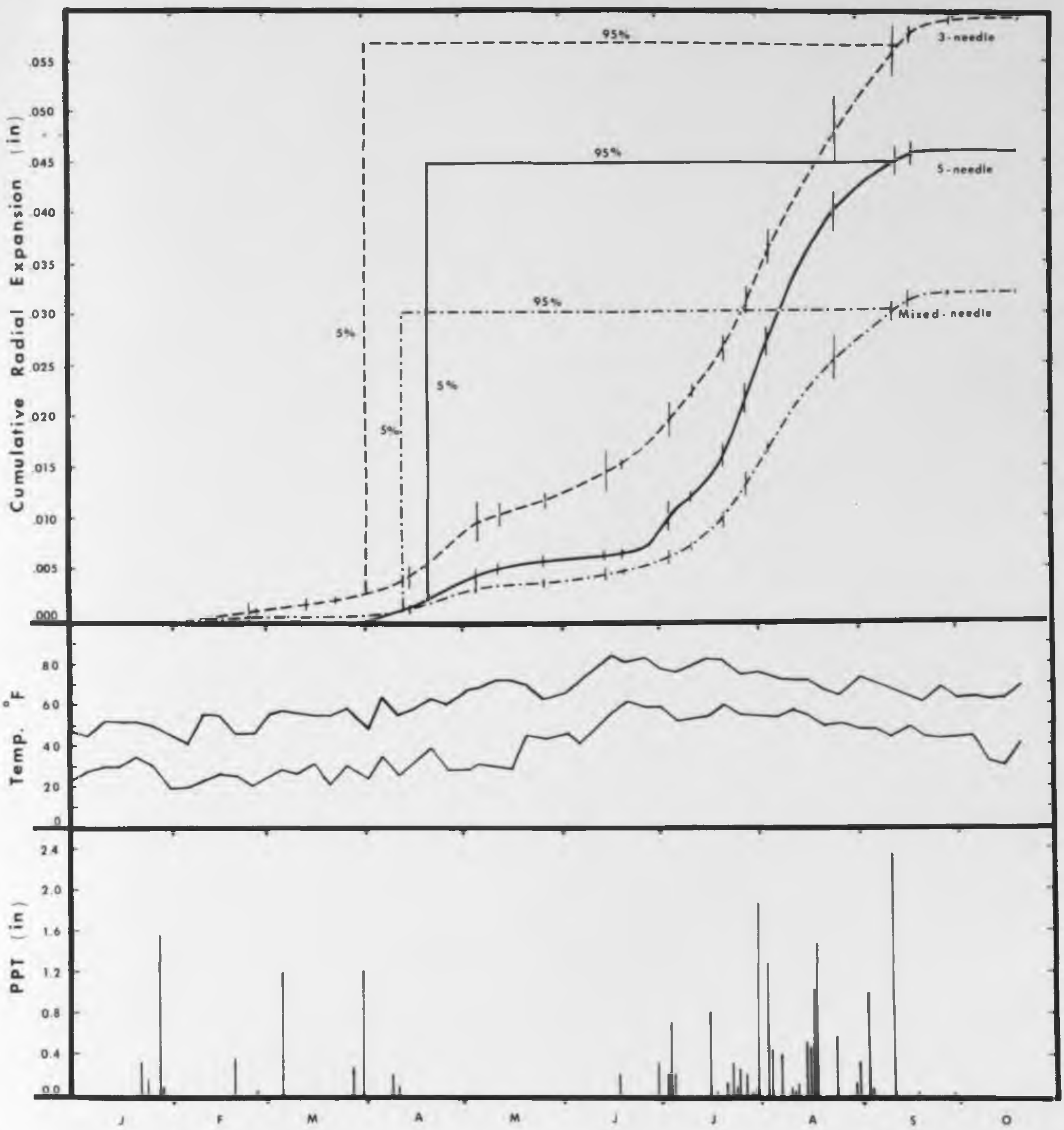

Figure 13. Cumulative radial expansion for three populations of ponderosa pine. Temperature data are maximum and minimum values occurring between visits. Precipitation data are daily values. All data are from the Mt. Bigelow study area.

A chronology was determined by the Laboratory of Tree Ring Research of the University of Arizona from the core samples taken from the trees in the dendrometer study. The average ring width during the last 80 years for the three classes of trees was 1.41 mm $\pm$ 0.01 mm for the three-needle, 1.41 mm $\pm$ 0.01 mm for the mixed-needle, and 1.53 mm $\pm$ 0.05 mm for the five-needle trees. In addition to ring widths, the number of intra-annual rings for the tree groups was determined. The five-needle trees showed 12.8 percent intra-annual rings, the mixed-needle 14.2 percent, and the three-needle 28.3 percent in a 60 year chronology.

DISCUSSION

Habitat Studies

Phytosociological Relationships

Characterization of ponderosa pine habitats with quarters quadrat studies in mountain ranges of southeast Arizona showed the relative contribution this species makes to the composition of the montane forests. The altitudinal range of ponderosa pine in the mountains studied is from approximately 7250 to over 9000 feet.

In the Santa Catalina Mountains, ponderosa pine is dominant throughout its range. From 7250 feet to 8000 feet it is associated with oaks. Above 8000 feet, however, the forest is composed of conifers, and at these stations ponderosa pine asserts commanding dominance on the forest structure. Shreve (1915) early recognized the striking change that occurs in the vegetation gradient at the start of the ponderosa pine zone in the Santa Catalina Mountains. He perceived the dual nature of ponderosa pine associations. He cited the rich array of elements from the Encinal (oak woodland) extending upward into the forest region to 8000 feet, and above 8000 feet he observed that ponderosa pine forests assume a more open character, principally because the oaks are absent.

The dual nature of the ponderosa pine zone in the Santa Catalina Mountains is portrayed graphically in Figure 14. The importance values of the species shown were determined from the quarters analysis and are presented in Table 7. The dominance of ponderosa pine thus determined is apparent, and its dual associations with other conifers in the upper portion and with oaks in the lower portion of its range is illustrated.

The Santa Catalina Mountains do not have sufficient elevation to provide distinct Douglas fir habitats on the south slope. The geomass of Mt. Lemmon is small, and this habitat tends to be more arid than would be expected at this elevation if greater mass were present. Suitable ponderosa pine habitats extend to the summit on the south-facing slopes of the Santa Catalina Mountains.

Increasing aridity near the summit of the study transect is suggested by the observed decrease of Douglas fir as the summit (Mt. Bigelow, 8550 feet) is approached (Figure 14). Douglas fir has its greatest development on south slopes at approximately 8000 feet, well within the forest interior. Apparently the habitat is more mesic here than at the higher exposed positions.

The oak component of the forest community is restricted primarily to the lower altitudinal range of ponderosa pine. Oak also appears at the highest elevation

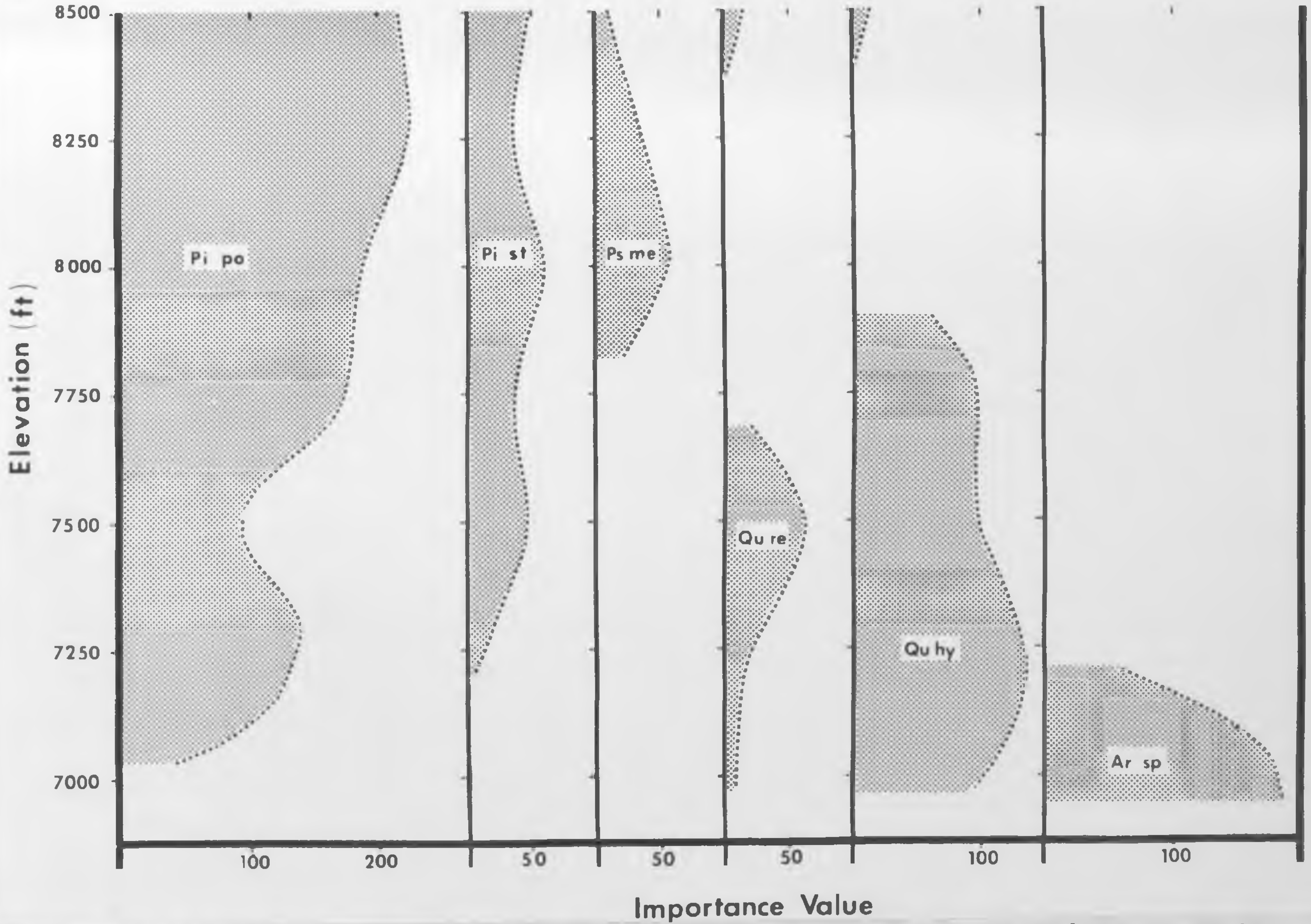

Figure 14. Importance values for major tree species in the Santa Catalina Mountains quarters stations. Pi po = Pinus ponderosa, Pi st = P. strobiformis, Ps me = Pseudotsuga menziesii, Qu re = Quercus reticulata, Qu hy = Q. hypoleucoides, Ar sp = Arctostaphylos sp.

sampled. This is perhaps further evidence for the increased aridity at the summits of the several prominences in this area.

Ponderosa pine distribution in the Rincon Mountains is similar to that in the Santa Catalina Mountains. On the uppermost slopes, well-developed ponderosa pine forests appear. At the uppermost stations (8500 feet), the community is essentially monotypic, since no tree associates appear with ponderosa pine in the 40 quarters established. Ponderosa pine remains dominant to 8000 feet. Below this, the oaks assume dominance, and at 7250 feet, ponderosa pine is no longer present on exposed slopes. Figure 15, constructed in the same manner as Figure 14, illustrates the almost total dominance of ponderosa pine in the Rincon Mountains at the upper elevational range. In addition, the conifer-oak relationship recognized in the Santa Catalina Mountains is repeated.

In the Santa Catalina and Rincon Mountains, ponderosa pine is seldom found with more than two or three tree associates. The structure of the tree zone seems fairly simple, and throughout the altitudinal zone, ponderosa pine is responsible for much influence on the forest composition. This is not the case in the Pinaleno Mountains.

The Pinaleno Mountains quarter studies indicate a more complex vegetation composition throughout the forest zone (Figure 16). Ponderosa pine is found at the highest

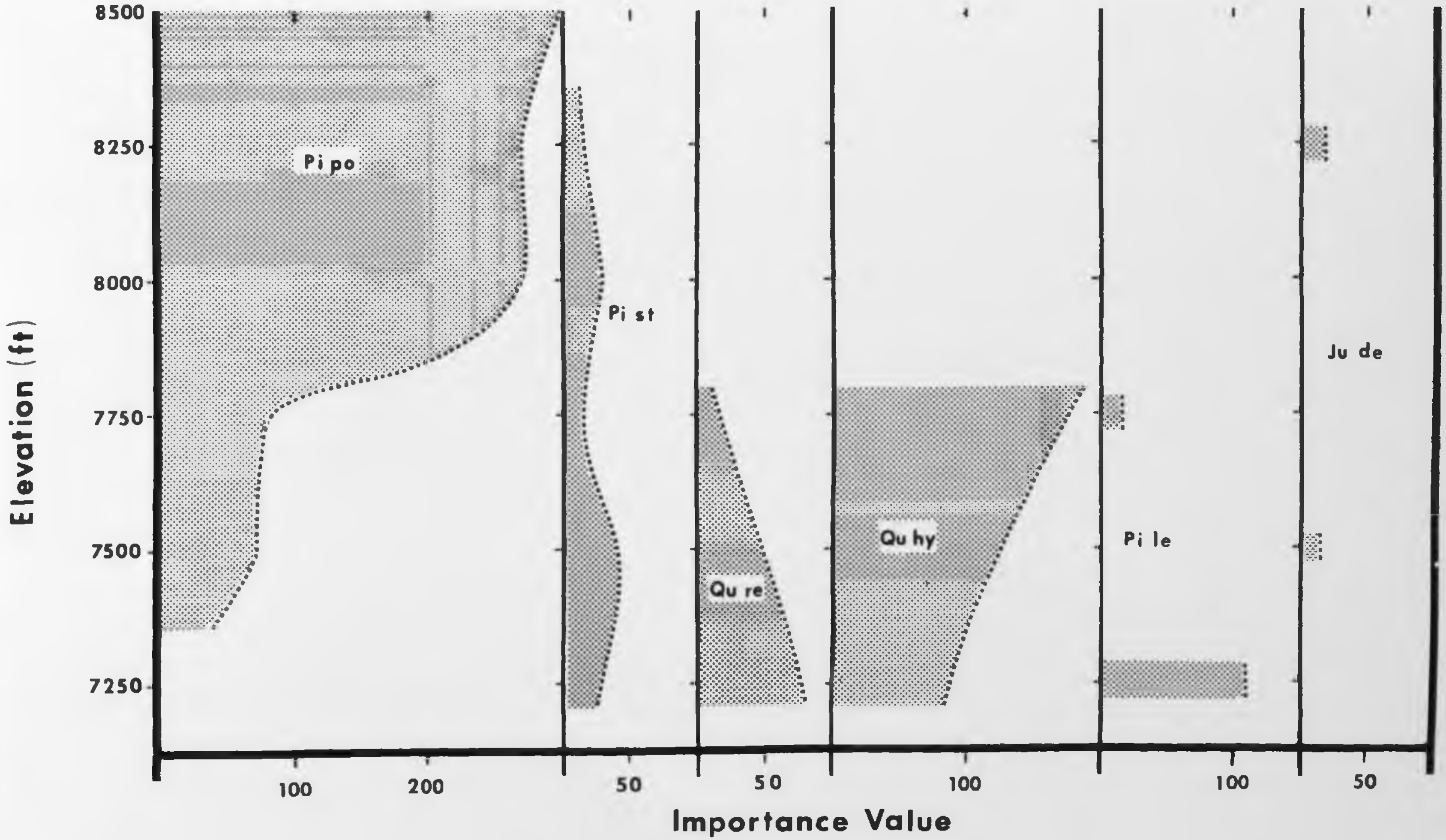

Figure 15. Importance values for major tree species in the Rincon Mountains quarters stations. Pi po = Pinus ponderosa, Pi st = P. strobiformis, Pi le = P. leiophylla, Qu re = Quercus reticulata, Qu hy = Q. hypoleucoides, Ju de = Juniperus deppeana.

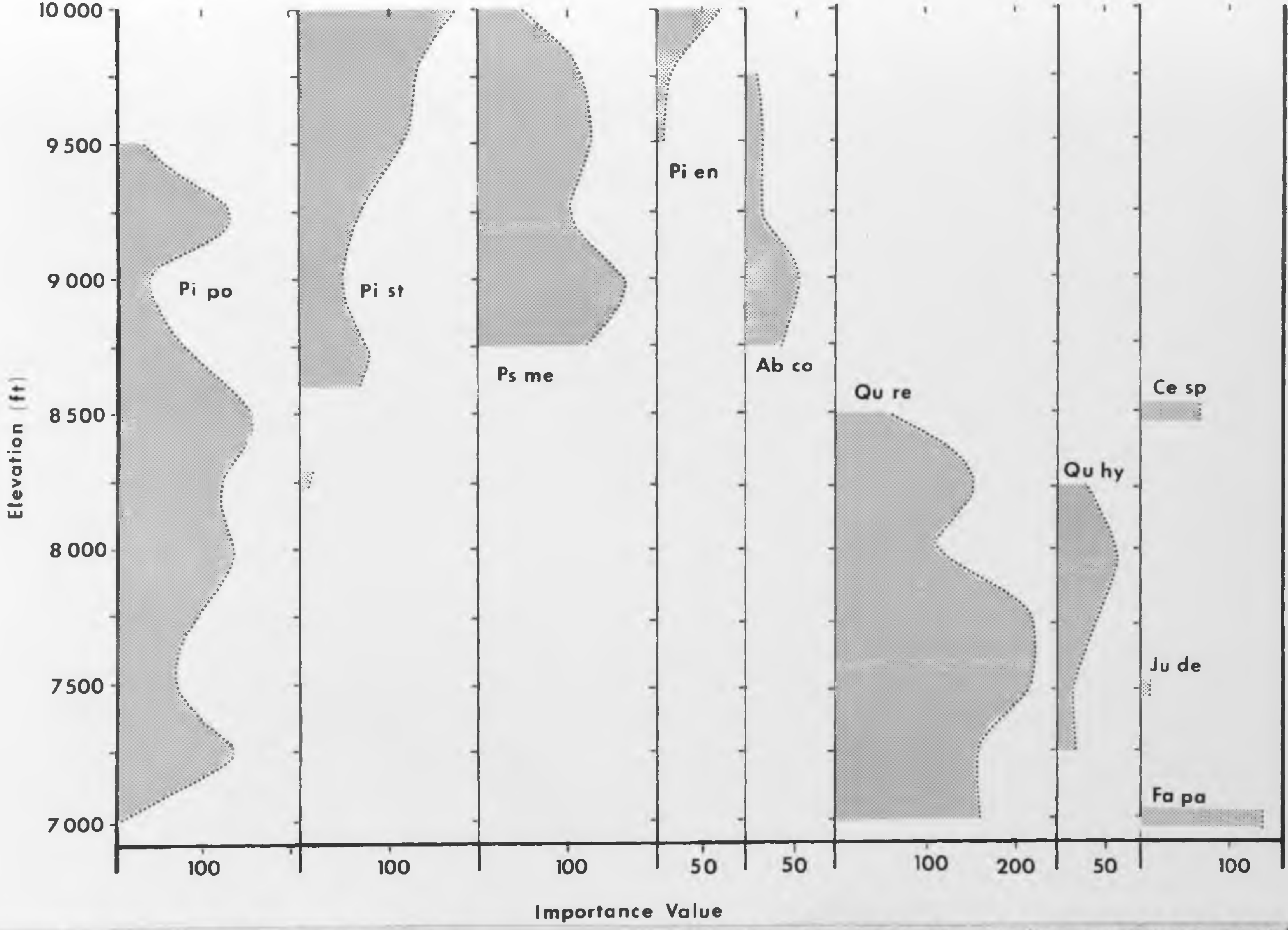

Figure 16. Importance values for major tree species in the Pinaleno Mountains quarters stations. Pi po = Pinus ponderosa, Pi st - P. strobiformis, Ps me = Pseudotsuga menziesii, Pi en = Picea engelmanni, Ab co = Abies concolor, Qu re = Quercus reticulata, Qu hy = Q. hypoleucoides, Ce sp = Cercocarpus sp., Ju de = Juniperus deppeana, Fa pa = Fallugia paradoxa.

elevation sampled (10,000 feet) and occurs down to 7250 feet. The importance values for ponderosa pine are nowhere as great in the Pinaleno Mountains as they are in the Santa Catalina and Rincon Mountains. The greatest importance value recorded for ponderosa pine in the Pinaleno Mountains is approximately 50 percent (148.4/300.0) at the 8500 foot elevation station. Ponderosa pine importance diminishes above this station and Douglas fir increases. Below 8500 feet, the oaks assume a dominant role in the appearance of the community.

The Pinaleno Mountains represent the only range investigated which has a well developed Douglas fir zone on the south slopes. In addition, elements of the spruce zone appear at the higher stations on the south slope. Since the land mass at the higher elevations is considerably greater here than in the other ranges investigated, the upper slopes appear to be less arid, and more mesic communities are present as indicated by the presence of such plants as Douglas fir and Engelmann spruce.

Perhaps the explanation for more mesic vegetation types found in the Pinaleno Mountains can be attributed to the "Merriam Effect" (Lowe, 1961). Lowe referred to the profile prepared by Merriam (1890) of San Francisco and O'Leary Peaks north of Flagstaff, and emphasized the effect of geomass on vertical distribution of vegetation communities as recognized by Merriam. Merriam (1890) noted that on a large mountain geomass like San Francisco Peak, the spruce zone occurred as low as 8500 feet, but was absent on nearby O'Leary Peak (9000 feet). Ponderosa pine only reaches to 8200 feet on San Francisco Peak but was found to 8800 feet on the smaller O'Leary Peak. This effect was attributed to the greater geomass of the San Francisco Peak. A similar situation was recognized by Lowe (1961) in the Pinaleno Mountains where, as a result of greater geomass, this mountain range is able to support more mesic vegetation types than the other mountain ranges thus far mentioned in this study.

The dominance of ponderosa pine in the Pinaleno Mountains is also significantly reduced at mid-elevations (8000 - 8500 feet), because the oak association reaches to higher elevations than in the other ranges discussed. In the Santa Catalina and Rincon studies, oaks are nearly absent above 7750 - 8000 feet. The oak community in the Pinaleno Mountains, however, extends above 8500 feet. This may be explained by the generally precipitous nature of the slopes below 8500 feet on the Pinaleno Mountains and the resulting aridity of these stations.

The community status of ponderosa pine in the Chiricahua Mountains appears confused. This is explained partly because extremely arid habitats appear on precipitous slopes below 8500 feet on the south end of the mountain range.

Additional confusion results from the presence of Apache pine (<u>Pinus latifolia</u> Sarg. = <u>P</u>. <u>engelmanni</u> Carr.) in this range (Table 10).

Apache pine is ponderosa-like. It differs from ponderosa pine by its longer needles (12 - 16 in.), greater cone size (3.7 - 4.8 in.), and generally shorter growth form. Apache pine has needles in threes and sometimes fives. Taxonomists agree that this pine is distinct from ponderosa pine (Martinez, 1948; Little, 1950; Kearney and Peebles, 1951, 1960).

In the Chiricahua Mountains, Apache pine replaces ponderosa pine at the lower altitudinal range of the latter. In Rucker Canyon, at 7000 feet elevation on the south end of the Chiricahua Mountains, Apache pine is the prevalent yellow pine.

Well developed ponderosa pine forests in the Chiricahua Mountains are found on the plateau connecting the several high peaks along the ridge of the mountain system. These areas have relatively gentle topography and appear to be less arid than the steep south slopes. The quarters station at 9000 feet (Table 10) probably best characterizes the ponderosa pine forest structure in the Chiricahua Mountains.

In the Huachuca, Santa Rita, and Galiuro Mountains, ponderosa pine does not appear to be dominant on the south slopes. In these areas, the Encinal (Shreve, 1915) is the more prevalent vegetation type.

In the mountain ranges of southeast Arizona, the lower altitudinal range of ponderosa pine appears to be limited by the arid conditions occurring on the exposed, often precipitous south slopes. Daubenmire (1943) concluded that probably the most important factor determining the lower limit of ligneous dominants of the Rocky Mountain vegetation units was the intolerable degree of aridity which occurred at lower elevations. Shreve (1915, 1917) early recognized the influence of drought at the lower limit of vegetation types in the Santa Catalina Mountains. In the Rincon Mountains, Blumer (1910) observed that the west slopes were more arid than were the east because of the desiccating effect of prevailing westerly winds. The resulting aridity causes vegetation zones on the west slopes of the Rincons to be higher. Daubenmire (1943) observed that the lowest extension of trees was in mesic sites, such as canyon bottoms or north-facing slopes. He cited this as further evidence for the lower limit of plants being determined by drought.

The lower limit of ponderosa pine in all mountains examined in this study is obviously bordering on arid regions. In the Santa Catalina, Pinaleno, and Chiricahua Mountains, it was noted that stumps and dead trees of ponderosa pine are present at stations lower than the last station containing living ponderosa pine. This may indicate a general rise in the lowest extent of ponderosa pine in those areas.

Ponderosa pine forests are dominant to the highest topographic features on the south slopes of the Santa Catalina and Rincon Mountains. In the Pinaleno Mountains, ponderosa pine does not assume a dominant role at elevations as high as in the Santa Catalina and Rincon Mountains. The upper south-facing slopes of the Pinaleno Mountains are sufficiently mesic to support stands of Douglas fir and Engelmann spruce.

Bates (1923, 1924) suggested that available heat was responsible for the upper limit of Douglas fir and ponderosa pine. He cited the presence of these species on open ridge tops and south-facing slopes at their upper altitudinal limits as evidence for a heat requirement. In addition, he noted the invasion from lower vegetation types occurs after disturbance has cleared an area. This, he concluded, was because the invaders find warmer conditions at the higher elevations after disturbance.

Pearson (1931) carried on transplant studies with Douglas fir, ponderosa pine, and other conifers, in which he planted seedlings above their natural ranges. In all cases the plants died. He suggested that the heat requirements of the seedlings during the growing season determined the natural upward limit of the species. This limit was established by a short growing season and a deficit of heat during the growing period.

The only ranges sampled in which ponderosa pine is not present at the highest elevation are the Pinaleno and Chiricahua Mountains. The forests in the Pinaleno Mountains are well-developed above 8500 feet and are dominated by Douglas fir and white pine. The highest station on Mt. Graham (Pinaleno Mountains) at which ponderosa pine was found bordered an open mountain meadow, and only two ponderosa pine individuals were present in the quarters. This may support Bates' (1924) hypothesis that invaders from lower elevations are usually found only in open sites where additional heat can reach the ground for the establishment of seedlings.

Needle Factor

Average needle number is shown to increase from the upper to the lower altitudinal range of ponderosa pine in Table 12. This gradient was observed in the Santa Catalina, Rincon, Chiricahua, Huachuca, and Santa Rita Mountains, but not in the Galiuro or Pinaleno Mountains. This gradient may be a response to changing environment, or it may result from the presence of intergrading populations of Arizona and ponderosa pine.

Haller (1962b) discussed the presence of ponderosa pine in the eastern part of its range with high frequencies of two-needle fascicles. The typical Rocky Mountain ponderosa pine is most often considered to have three-needle fascicles.

Squillace and Silen (1962) indicated that two-needle ponderosa pine was more common to northeastern ranges in the Rockies.

Haller (1962b) supported the hypothesis that reduction of needle number was caused by unidentified habitat factors. His data suggest that needle number reduction is a response to more mesic environments. In the more arid sites, he found an increase in the quantity of three-needle fascicles in Rocky Mountain ponderosa pine. He noted that two-needle trees show fewer effects of cold damage, suggesting that three-needle trees are less-suited to the colder habitat sites.

If the number of needles per fascicle is a result of habitat response, and greater frequency of high-number fascicles appears with increasing aridity, then an explanation may be provided for the increase in number of needles per fascicle as one moves downslope through the ponderosa pine zone in southeast Arizona. Haller (personal communication) suggested that ponderosa and Arizona pine in the Santa Catalina Mountain studies are the same taxa but show different needle numbers in response to environmental conditions.

Haller's hypothesis might be attractive if a similar relationship were observed in the Galiuro and Pinaleno Mountains, since the lower south-facing slopes of the Pinaleno Mountains appear to be as arid as those observed in habitats with five-needle trees. Martin and Fletcher (1943) cited evidence that the Pinaleno Mountains may be drier than the Santa

Catalina Mountains. The Galiuro Mountains appear to provide even more arid habitats for ponderosa pine, and yet, no five-needle fascicles were collected in this range.

Rather than morphological response to environment, the absence of five-needle trees in the Pinaleno and Galiuro Mountains may be a result of five-needle Arizona pine not yet appearing in these mountain ranges in sufficient quantities to influence the community.

Martin (1961) noted that a peculiar feature of the southwestern biota is the large number of Madrean Mexican species which find their northern limits in the montane forest populations. He suggested that the arrival of the Mexican species was quite recent (interconnection as recent as 3000 - 8000 years) and that Rocky Mountain representatives of the biota were well-established when the Mexican elements arrived.

Pollen analysis of a 42 meter core from Wilcox Playa (Martin, 1963) indicated that 95 to 99 percent of the extracted pollen is pine at a depth dated in excess of 20,000 years. This past period of pine dominance corresponds to the pluvial. Martin (1963) compared these pollen frequencies with modern pollen rains and determined that similar pollen quantities could be found from soil samples obtained beneath coniferous trees in the Santa Catalina Mountains near 8500 feet (Hevly and Martin, 1961). This evidence suggests that coniferous forests dominated the desert grassland now surrounding

Wilcox Playa (c.a. 30 miles south of the Pinaleno Mountains) during the pluvial. A 4000 foot vertical displacement upward to the location of the present coniferous forests is represented by this evidence. It appears that in times past, the mountains of southeastern Arizona may have been dominated by coniferous forest with arcto-tertiary origins (Chaney, 1947). Later, as warming and drying occurred, Madrean Mexican species invaded the region. Apparently, these invaders from the Mexican Highland floras have not reached the Galiuro and Pinaleno Mountains in sufficient quantities to influence the pine forest composition, but have become significant counterparts of the other mountains considered in southeast Arizona.

Lowe (1961) recognized a difference between the mountain ranges in southeast Arizona. He considered the Santa Rita, Huachuca, and Chiricahua Mountains as "outlying 'Sierra Madrean Mountains,'" distinct from the Santa Catalina and Rincon "outlying 'Rocky Mountains.'" Presumably, he would include the Galiuro and Pinaleno Mountains in the outlying Rocky Mountain group. The evidence observed from the needle number per fascicle studies in the several mountain ranges tends to support differences between (1) the Santa Rita, Huachuca, and Chiricahua Mountains and (2) the Santa Catalina and Rincon Mountains, as recognized by Lowe (1961).

On the basis of the interpretations by Martin and Lowe, and data to be discussed, the needle-number cline found in the several ranges of southeast Arizona is attributed to the presence of Rocky Mountain-ponderosa pine and Sierra Madrean-Arizona pine appearing at the border of the Madrean-Rocky Mountain junction. The greatest expression of this junction is apparently in the Santa Catalina and Rincon Mountains.

Morphological Characters

Needles

No differences in needle length between southeast Arizona and Sonoran populations were observed; between northern and southern Arizona populations, slight differences appeared. These results were not unexpected since the range of needle size cited in taxonomic descriptions (Table 1) shows similar overlap.

The study of stomates has yielded a subtle, but nevertheless, interesting relationship. While the differences appear to be slight, comparison of the several populations suggests a subtle shift toward increased stomate number with decreasing latitude. Additional observations reveal that samples from the Prescott area and the Pinaleno Mountain populations appear more nearly alike for this character than do the Pinaleno and remaining southern Arizona samples.

Mergen (1958) found no correlation between this character and latitude, average number of frost-free days or average warm-season precipitation. He found slight clinal relationships from east to west between 81° and 88° east longitude. The magnitude of the difference in number of stomates was small (8.4 - 8.9 per mm) and for ecological considerations may be considered insignificant. Mergen tested the importance of environment and found that highly significant differences in the number of stomate-rows reflect small environmental differences. However, no variation was found for number of stomates per unit length. He considered the number of rows to be variable but the number of stomates per unit length to be under "fairly rigid genetic control."

The difference in longitude between the populations studied in Arizona and Sonora is small (109° - 111° 30') and the effect of longitude is considered to be minor. If Mergen's hypothesis of rigid genetic control is valid, it appears that a slight increase in stomate number per unit length occurs from north to south. This is perhaps due to the increased intergradation of Arizona pine into the ponderosa pine populations from north to south. The population in the Pinaleno Mountains is apparently little influenced by Arizona pine. Arizona pine exerts increased weight on the pine community farther south, and higher frequencies of stomates per unit length are observed in the populations.

The rows of stomates are extremely variable throughout the range, except that three-needle fascicles tend to have more rows of stomates than the five-needle. On three-needle fascicles, as many as 21 rows of stomates were observed on the three sides. On five-needle fascicles, as few as two rows per side and as many as 11 rows per needle were recorded. Although the number of stomates per unit length and number of needles apparently increases with increasingly arid habitats, the total stomatal area is probably less in five-needle than in three-needle populations, because the number of stomate rows is fewer in Arizona pine.

Pollen

No differences in pollen dimension were found between the several sampling areas. The study lacked a critical comparison in that northern pollen samples were not included. The standard deviations overlap in all samples. Pollen size distributions do not offer additional information concerning the relationship of Arizona and ponderosa pine. Wodehouse (1935) stated that grains from different pine species are scarcely distinguishable on the basis of size. He also recognized the small size differences and large overlap found in the different pine species. Axelrod and Ting (1960) studied the problem of similar pollen size in different species of pine. They made a dimensional distribution diagram of known pollen size frequencies and were able to prepare size-range charts of known material to compare with unknown material. Unfortunately, the distributions of their size-frequency diagrams often overlapped to a degree that only grains with extreme size variations could be identified.

Significant differences in pollen size distribution are not observed between members of the closely related ponderosa pine complex in southeast Arizona, and this avenue seems closed for identification of the two taxa.

Pistillate Cones

Length. Total cone length comparisons (Figure 6 and Table 18) demonstrate a wide size range in natural populations. These data show the error of describing *P. arizonica* as having smaller cones than *P. ponderosa*, because this character is not valid.

The apparent cline in cone size observed from north to south (Figure 6), especially in the Santa Catalina, Rincon, Huachuca, and Chiricahua populations, is probably influenced by small sample size rather than population differences between the several mountain ranges. The grouped southeast Arizona sample, combining these small individual mountain samples, appears similar to the northern Arizona and Sonora populations.

Density. Direct cone-size measurement was shown to be a poor character for identification of the pine taxa studied. Indirectly, however, the size, as it relates to volume and density, appears to show differences. Data plotted in Figure 7 demonstrate a definite north to south change. Northern Arizona populations have less dense cones; the Pinaleno samples appear to be nearly like the northern Arizona collection. Samples from El Tigré are the most dense, while samples from southeast Arizona are bimodally intermediate between the two extremes. It is significant that members of each geographic sample show slight tendencies toward bimodal cone density distributions. The cone densities of the populations studied are not sufficiently divergent to allow for identification of the taxa, but slight differences are noted.

Haller (1962a) noted a clinal relationship between elevation and cone density in P. jeffreyi at certain locations and no relationship in others. He indicated that environment may influence this character. The cones collected in the southeast Arizona study are not separated by elevation, but rather, represent geographic samples, usually from two or more elevations.

The difference noted between north and south stations may be a result of environmental response and have no significance in demonstrating population variability. Many more samples should be collected and densities determined before a definite conclusion can be reached.

Cone Prickle. Cone prickle-class observations show an obvious shift from upward-pointing prickles in northern stations to downward-pointing prickles in the southern stations. Data presented in Figure 11 show this character and demonstrate the change observed in prickle direction with decreasing latitude. The apparent intermediate position of the southeast Arizona populations, when compared to the northern Arizona and Sonoran samples, further indicates the presence of dual components in these populations; samples from the Prescott area and El Tigré Mountains only slightly overlap.

A basic problem associated with identification of the taxa is illustrated by the comparison of the most widely divergent populations. If the populations are observed at the extreme ends of the range, sufficient differences occur to justify specific status for Arizona pine. However, when the intermediate populations are considered, the significance of this taxonomic separation is reduced and apparent subspecific designation for Arizona pine is indicated.

Dendrometer Studies

Radial expansion curves for the tree classes in the Mt. Bigelow study demonstrate apparent time differences for the commencement of radial expansion activities. The three-needle and mixed-needle trees commenced radial activity approximately six weeks prior to the five-needle trees (February 24 versus

April 14 in this year of study). The daily temperatures during this period were probably not limiting and the daily maximum temperature exceeded 40° F at this time. It would appear that sufficient moisture was present since two classes of trees showed radial-increment increases. The factors controlling initiation of radial expansion in the trees of this study are not known.

Daubenmire (1950) studied 41 trees from 14 different locations, including a population from northern Arizona, and concluded that day-length appears to have no influence on growing season. Wort (1962) thought cambial activity was climatically controlled in trees, but attributed the date of readiness of cambial activity to heredity. In the Santa Catalina study, a dual factor of genetic control plus environmental conditioning may prevail in regulating the onset of radial activity in the defined ponderosa pine populations.

The early onset of radial activity in the three-needle trees may be a genetic expression of Rocky Mountain rain pattern influence, while the later-starting five-needle response is conditioned by Madrean rain patterns. The Rocky Mountain rain pattern is of a fairly constant, generally heavy nature from March to the end of summer, while the Madrean climatic influence produces biseasonal rainfall with a spring drought period between summer and winter precipitation regimes. Because of the biseasonal rainfall pattern, radial expansion in the three- and mixed-needle trees in the Mt. Bigelow study began earlier under the influence of the winter rain, but did not continue rapid expansion during the spring drought common to this region. The spring drought could interrupt radial expansion in the trees, and this interruption could account for intra-annual rings. Onset of growth early in the season, followed by cessation of activity during the spring drought and resumption with summer rains, may cause such a ring pattern to appear. This growth pattern would possibly be disadvantageous; that is, growth in response to summer rains might be sluggish because a significant portion of the stored materials were utilized in the earlier flush. Such a phenomenon might be responsible for the greater number of intra-annual rings found in the three-needle group.

The average ring width reported by the tree-ring studies is greater in the five-needle trees. This greater average accumulation of growth increments was not demonstrated during the single year of this study, since the three-needle trees accumulated greater radial increments than the five-needle trees. Jackson (1953) cited three types of growth pattern in forest trees: species starting late but growing rapidly; those starting early but with moderate to slow growth rates; and those of intermediate character, having a moderately steady rate of growth. It appears, on the basis of the Mt. Bigelow study, that three-needle trees fall into the second of Jackson's categories, five-needle into the first, and perhaps mixed-needle into the last category.

The dendrometer studies add still more evidence to the concept that two different ponderosa pine populations are present in the mountains of southeast Arizona, and apparent intergradation between Arizona and ponderosa pine is occurring in these mountain ranges.

Fritts (1963a, 1963b) has made available data derived from the 36 increment cores collected from the trees of the Mt. Bigelow study. He found considerably more difference between the three- and five-needle trees than between the three- and mixed-needle trees.

He measured yearly ring widths from 1881 to 1960, calculated "group standardized values," and compared the three-, mixed- and five-needle classes. The yearly standardized values for each core, tree, and groups of trees were derived (Figure 17). The correlations among the group standardized values were: three- and mixed-needle, 0.96; five- and mixed-needle, 0.86; and three- and five-needle, 0.81.

In addition, Fritts (1963a, 1963b) analyzed the component variances in the yearly standardized values. He found the percent variance retained by the mean yearly groups to be: 42 percent for the five-, 64 percent for the mixed-, and 65 percent for the three-needle group. This indicates that the year-to-year growth response is considerably more similar

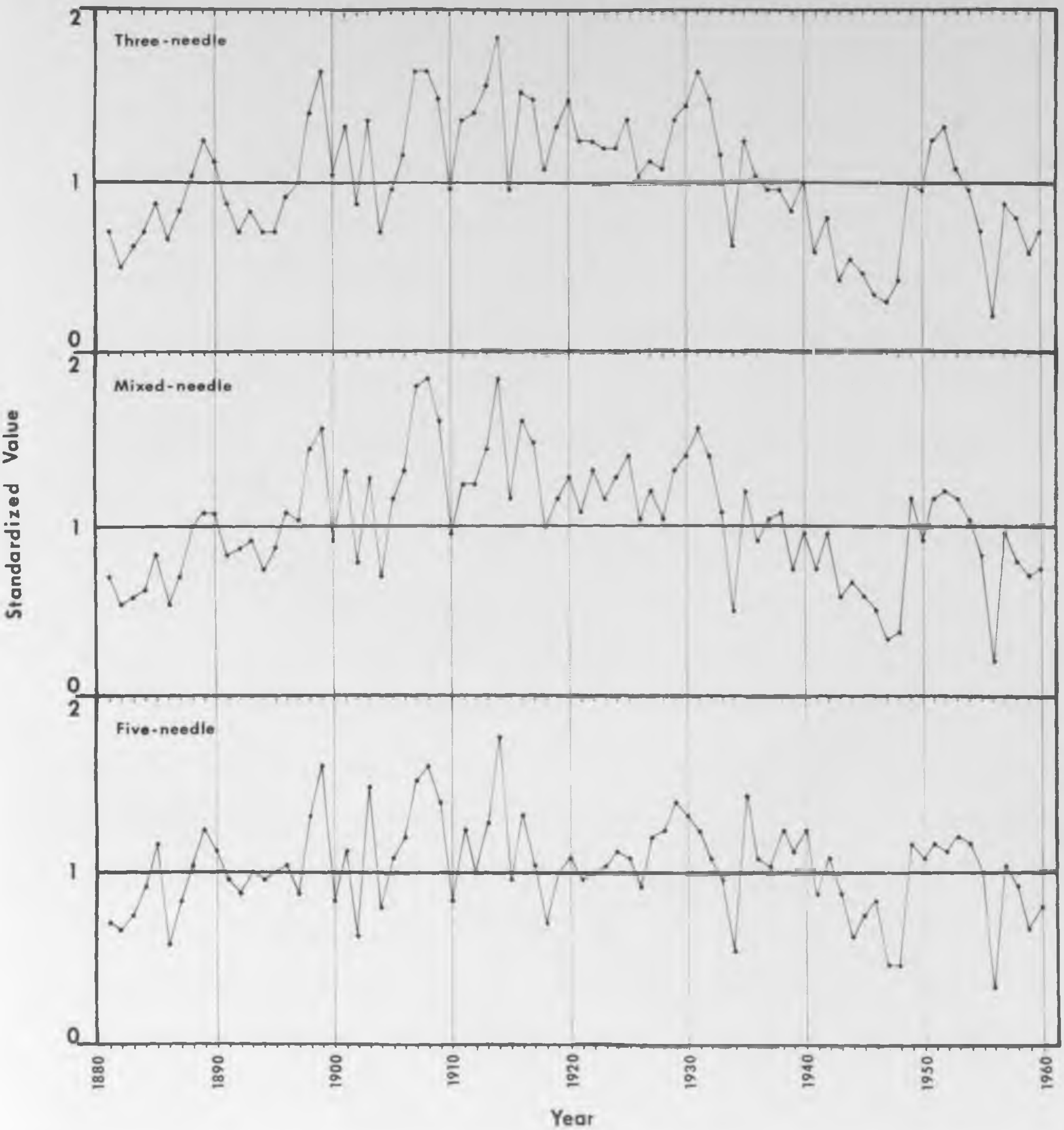

Figure 17. Average yearly standardized values for tree rings taken from the three-, mixed-, and five-needle groups in the Mt. Bigelow dendrometer study. Each series represents the mean of twelve cores from six trees for the years 1881 - 1960.

among trees and cores within the three- and mixed-needle groups than among the trees and cores of the five-needle group. Fritts concluded from the similarity of the growth response, and from comparison to other studies, that since the component variances were higher in the three- and mixed-needle groups, climatic conditions were more frequently limiting to these populations. He cites other analyses (1963b) which indicate that high percent variance retained is typical of trees near the lower limit of their range.

Thus it appears, on the basis of dendrometer studies and Fritts's results, that two ponderosa pine populations are present in the Mt. Bigelow study area, and that here the three-needle ponderosa pine is near its lower limit.

When the dendrometer studies were begun, the only character used to differentiate the putative populations was needle number. The results of the dendrometer study and subsequent studies, including examination of morphological and anatomical features, have demonstrated the validity of this single character for differentiation of the members of the Arizona-ponderosa pine complex.

The several studies concluded illustrate an apparent pattern of intergradation between two different populations of ponderosa pine. Little of the evidence presented is of such nature as to conclusively separate the taxa. No marked differences are found to justify elevation of Arizona pine to specific status. Nevertheless, the overall pattern emerging points to justification for designating Arizona pine as different, perhaps in a minor degree, from the Rocky Mountain ponderosa pine.

I am reluctant to recommend even subspecific status for Arizona pine, since the population appears to be a continuation of a large group of populations from the Central American Highlands to British Columbia. The designation of Arizona pine as a variety of ponderosa pine may set this population apart from the other taxon, when, in reality, from an ecological point of view, Arizona pine is a member of a widespread population with varying characters.

Langlet (1962) recognized this problem in European populations of Scots pine. Scots pine has been divided into northern and southern subspecies, although few apparent differences exist. Langlet cited Huxley (1939): "When gradation exists within a group, the mere conferring of a subspecific or specific name gives a false impression of the homogeneity of the group."

Langlet (1962) proposed recognition for continuous and discontinuous differentiations so that segments of overall populations do not become endowed with special Latin names. Nothing is gained by splitting a species, except that an incorrect impression results and special cases become emphasized. Langlet proposed that an ecologic concept be introduced for continuous changes over a geographic area, and special taxonomic categories should be minimized. His desire to show uniformity rather than emphasize disparity has been echoed by other writers.

Daubenmire (1943) suggested similar ideas, though perhaps not as strongly. He rejected the concept of species in Rocky Mountain ponderosa pine and stated that the variety concept was more useful from an ecological point of view, because it emphasized similarities rather than differences between the several variable populations of ponderosa pine.

Dallimore (1929) early recognized the geographical rather than botanical distinctions between _P. arizonica_ and _P. ponderosa_. He recommended inclusion of _P. arizonica_ in the _P. ponderosa_ complex, along with other members of the broad group.

The data presented above in the habitat and morphological studies illustrate a minor clinal change between the ponderosa and Arizona pine populations studied. After examining the slight changes which occurred, little foundation remains to designate Arizona pine a species distinct from _P. ponderosa_.

From an ecological point of view, Arizona pine represents a geographic divergence within the broad ponderosa pine community. From a taxonomic point of view, however, the differences observed indicate Arizona pine should be recognized as a variety of ponderosa pine. Designation of Arizona pine as _P_. _ponderosa_ var. _arizonica_ is not objectionable if considered in terms recognized by Daubenmire (1943) and others.

SUMMARY

1. A study to determine differences between Arizona and ponderosa pine and the preferred habitats of these taxa has been made in southeast Arizona. Morphological characters between the southeast Arizona ponderosa pine populations and other regions are also compared. Phytosociological studies have been carried on in the Santa Catalina, Rincon, Pinaleno, and Chiricahua Mountains to determine relationships within and among the populations of the ponderosa pine complex.

2. Ponderosa and Arizona pine populations are generally found between 7000 and above 9000 feet elevation on the open south slopes of the mountain ranges investigated. From approximately 7000 to 8500 feet, ponderosa pine is associated with oaks. Above 8500 feet, other coniferous species increase and the oaks are less common.

3. Ponderosa and Arizona pine occur to the summits of peaks in the Santa Catalina and Rincon Mountains, and at the higher elevations, assume almost complete dominance of the coniferous elements of the montane forest on south-facing slopes. In the Pinaleno and Chiricahua Mountains, ponderosa pine nowhere exhibits the great importance, based on phytosociological consideration, that it does in the aforementioned

mountain ranges. In the Pinaleno Mountains, greater high-elevation geomass is present and more mesic habitats result. In these positions, well developed Douglas fir and Engelmann spruce zones are present on the south slopes.

4. Determination of the number of needles per fascicle demonstrated that this ratio increases with decreasing elevation in the Santa Catalina, Rincon, Santa Rita, Chiricahua, and Huachuca Mountains. This is interpreted as indicating that the five-needle Arizona pine intergrades with the three-needle ponderosa pine in mountain ranges where the two taxa appear. No needle-characters of Arizona pine were found in the study areas of the Galiuro and Pinaleno Mountains, which suggests that Arizona pine populations are not present in these ranges.

5. Needle lengths determined for the populations studied showed no differences useful for identification of the taxa. Samples collected in northern Arizona, southern Arizona, and Sonora were compared.

6. The number of stomates per unit length of needles was found to increase slightly from north to south. However, in the Santa Catalina Mountains, little difference was found in this character among trees classed as three-needle, mixed-needle, and five-needle.

7. No differences were found between pollen grain and bladder width measurements from groups of trees classed

as three-, mixed-, and five-needle. Within trees of a group, however, considerable variability was indicated. Comparison of pollen grain dimensions from other mountain ranges yielded similar results, i.e., no detectable differences among the populations.

8. Pistillate cones were compared among stations in northern Arizona, southern Arizona, and Sonora. Mean length, range, and standard deviation calculations from the several sample populations demonstrated the inability to separate Arizona and ponderosa pine with this character, even though this character has been classically referred to as a diagnostic difference between the two taxa. Comparison of cone density among the sampled populations showed a marked trend toward denser cones from north to south as the degree of intergradation of Arizona pine into ponderosa pine populations increased. The El Tigré Mountain samples, considered to be exclusively Arizona pine, showed the greatest density, and the densities from here only slightly overlapped the northern Arizona samples. Cone-scale-prickle direction was found to shift from upward pointing in the northern Arizona ponderosa pine populations to downward pointing in southern Arizona and Sonoran pine populations. Outward-pointing prickles occurred in more intermediate ranges.

9. Dendrometer studies demonstrated differences between the three-needle trees and the five-needle trees. The

ponderosa pine three-needle groups commenced radial activity prior to the Arizona pine five-needle groups. Intermediate and presumably hybrid mixed-needle trees responded more like the ponderosa pine group for this character.

10. Evidence is discussed which implies that mountains of southeast Arizona are varied junctions between Rocky Mountain and Mexican Madrean floristic provinces, and in these mountains, Arizona pine is intergrading with ponderosa pine. Evidence presented suggests that the Pinaleno and Galiuro Mountains are more influenced by Rocky Mountain ponderosa pine; the Santa Catalina and Rincon Mountains are intermediate but probably closer to the Rocky Mountain types; and the Santa Rita, Huachuca, and Chiricahua Mountains are under greater influence from the Madrean Arizona pine type.

11. Arizona pine is considered to be a variety of ponderosa pine (e.g., *Pinus ponderosa* Laws. var. *arizonica* (Engelm.) Shaw (1909)). It is shown that there are no distinct, consistent differences between the two taxa, but rather, a close relationship among a series of intergrading populations on a generally north-south gradient in this southwestern region of North America.

LITERATURE CITED

Axelrod, D. I., and W. S. Ting, 1960. Late pliocene floras east of the Sierra Nevada. Univ. of Calif. Press, Los Angeles and Berkeley, Calif. 117 p.

Bates, C. G., 1923. The transect of a mountain valley. Ecology 4:54-62.

__________, 1924. Forest types in central Rocky Mountains as affected by climate and soil. U. S. Dept. Agr. Bull. 233, 152 p.

Beals, E. W., and G. Cottam, 1960. The forest vegetation of the Apostle Islands, Wisconsin. Ecology 41:743-751.

Blumer, J. C., 1910. A comparison between two mountain sides. Plant World 13:134-140.

Chaney, R. W., 1947. Tertiary centers and migration routes. Ecol. Monographs 17:139-148.

Cottam, G., and J. T. Curtis, 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

Curtis, J. T., 1950. Original forest structure. Paper at AAAS Symposium on Structure of Plant Communities. Cleveland, Ohio. December.

__________, and R. P. McIntosh, 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology 31:434-455.

Dallimore, W., 1929. The yellow pines of North America. Kew Bull. Misc. Inform. 1929:330-335.

Daubenmire, R. F., 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. 9:326-387.

__________, 1945. An improved type of precision dendrometer. Ecology 26:97-98.

Daubenmire, R. F., 1946. Radial growth of trees at different altitudes. Bot. Gaz. 107:462-467.

__________, 1950. A comparison of cambial growth in different geographic races of Pinus ponderosa. Bot. Gaz. 112:182-188.

__________, and M. W. Deters, 1947. Comparative studies of growth in deciduous and evergreen trees. Bot. Gaz. 109:1-12.

Engelmann, G., 1878. Coniferae, p. 255-264. In: Wheeler, G. M., Report upon United States geographical surveys, west of the one hundredth meridian. Vol. VI - Botany. Gov. Print. Of., Wash.

Fenneman, N. M., 1931. Physiography of western United States. McGraw-Hill Book Co., N. Y. 534 p.

Forrester, J. D., 1958. Geologic map of Graham and Greenlee Counties, Arizona. Ariz. Bur. of Mines, Univ. of Ariz., Tucson, Ariz.

__________, 1959. Geologic map of Cochise County, Arizona. Ariz. Bur. of Mines, Univ. of Ariz., Tucson, Ariz.

__________, 1960. Geologic map of Pima and Santa Cruz Counties, Arizona. Ariz. Bur. of Mines, Univ. of Ariz., Tucson, Ariz.

Fowells, H. A., 1941. The period of seasonal growth of ponderosa pine and associated species. J. of Forestry 39:601-608.

Fritts, H. C., 1963a. A Physiological program for evaluating the use of tree rings as climatic indicators. Seventh Annual Meeting, Ariz. Acad. Sci., Biol. Sec., Tucson, Ariz.

__________, 1963b. Statistical evaluation of tree-ring series. Seventh Annual Meeting, Ariz. Acad. Sci., Biol. Sec., Tucson, Ariz.

Haller, J. R., 1957. Taxonomy, hybridization and evolution in Pinus ponderosa and P. jeffreyi. Ph.D. Thesis, Botany Dept., Univ. of Calif. Los Angeles, Los Angeles, Calif. 170 p.

Haller, J. R., 1962a. Variation and hybridization in ponderosa and Jeffrey pines. Univ. of Calif. Publ. in Bot. 34:123-166.

__________, 1962b. Variation in needle number in Pinus ponderosa. Paper given at AIBS Meetings, Systematics Section, Corvallis, Ore., Aug. 1962. Abstr. in Amer. J. Bot. 49:675-676.

Hess, D. W., 1960. Ecological studies of the growth of ponderosa pine on the east slope of the Rocky Mountain front range in Boulder County, Colo. Ph.D. Dissert., Univ. of Colo. 100 p. Univ. Microfilms, Ann Arbor, Mich. (60-1067). (Dissert. Abstr. 20:3935.)

Hevly, R., and P. S. Martin, 1961. The geochronology of pluvial Lake Cochise. I. Pollen analysis of shore deposits. J. Ariz. Acad. Sci. 2:24-31.

Jackson, L. W. R., 1953. Radial growth of forest trees in the Georgia piedmont. Ecology 33:336-341.

Johnston, I. M., 1943. Plants of Coahuila, eastern Chihuahua, and adjoining Zacatecas and Durango. J. Arnold Arbor. 24:306-339, 375-421.

Kearney, T. H., and R. H. Peebles, 1942. Flowering plants and ferns of Arizona. U.S. Dept. Agr. Misc. Publ. No. 423. 1069 p.

__________, and __________, 1951. Arizona flora. Univ. of Calif. Press, Berkeley, Calif. 1032 p.

__________, and __________, 1960. Arizona flora. 2d ed. Supplement by J. H. Howell and E. McClintock, p. 1035-1085. Univ. of Calif. Press, Berkeley, Calif. 1085 p.

Langlet, O., 1962. Ecological variability and taxonomy of forest trees. p. 357-369. In: T. T. Kozlowski, ed. Tree growth. The Ronald Press Co., N. Y.

Lindsey, A. A., 1956. Sampling methods and community attributes in forest ecology. For. Sci. 2:287-296.

__________, J. D. Barton, and S. R. Miles, 1958. Field efficiencies of forest sampling methods. Ecology 39:428-444.

Little, E. L., 1950. Southwestern trees. U.S. Dept. Agr. For. Serv. Agr. Handb. No. 9. 109 p.

Lowe, C. H., Jr., 1961. Biotic communities in the sub-Mogollon region of the inland southwest. J. Ariz. Acad. Sci. 2:40-49.

MacDougal, D. T., 1924. Growth in trees and massive organs of plants. Dendrographic measurements. Carn. Inst. Wash. Publ. No. 350. 89 p.

__________, 1936. Studies in tree-growth by the dendrographic method. Carn. Inst. Wash. Publ. No. 462. 256 p.

Marshall, J. T., 1956. Summer birds of the Rincon Mountains, Saguaro National Monument, Arizona. The Condor 58:81-97.

Martin, P. S., 1961. Southwestern animal communities in the late pleistocene. New Mex. Highlands Univ. Bull., Catalog Issue, 1961:56-61.

__________, 1963. Geochronology of pluvial Lake Cochise, southern Arizona. II. Pollen analysis of a 42 meter core. Contrib. No. 56. Program in Geochronology, Univ. of Ariz., Tucson, Ariz. Ditto Report. 15 p.

Martin, W. P., and J. E. Fletcher, 1943. Vertical zonation of great soil groups on Mt. Graham, Arizona, as correlated with climate, vegetation and profile characteristics. Ariz. Agr. Exp. Sta. Tech. Bull. 99 p.

Martinez, M., 1948. Los pinos Mexicanos. 2d ed. Ediciones Botas, Mexico. 361 p.

Mergen, F., 1958. Genetic variation in needle characteristics of slash pine and some of its hybrids. Silvae Genetica 7:1-9.

__________, 1959. Applicability of the distribution of stomates to verify pine hybrids. Silvae Genetica 8:107-109.

Merriam, C. H., 1890. Results of a biological survey of the San Francisco Mt. region and desert of the Little Colorado in Arizona. North American fauna. No. 3. 136 p.

Nichol, A. A., 1952. The natural vegetation of Arizona. Univ. of Ariz. Tech. Bull. No. 127:188-230.

Pearson, G. A., 1931. Forest types in the southwest as determined by climate and soil. U.S. Dept. Agr. Tech. Bull. No. 247. 143 p.

Phillips, E. A., 1959. Methods of vegetation study. Henry Holt and Co., Inc., N. Y. and San Fran. 107 p.

Ransome, F. L., 1923. Description of the Ray quadrangle. U.S. Geol. Surv. Folio 217.

Sargent, C. S., 1905. Manual of the trees of North America. Houghton Mifflin Co., Boston. 826 p.

__________, 1922. Manual of the trees of North America. 2d ed. Houghton Mifflin Co., Boston. Second Corrected Edition, Dover Public., Inc., N. Y. 2 vol.

Shaw, G. R., 1909. The pines of Mexico. Publ. Arnold Arbor. No. 1. 29 p.

__________, 1914. The genus *Pinus*. Publ. Arnold Arbor. No. 3. 96 p.

Shreve, F., 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Carn. Inst. Wash. Publ. No. 217. 112 p. 36 pl.

__________, 1917. The physical control of vegetation in rainforest and desert mountains. Plant World 20:135-141.

Snedecor, G. W., 1956. Statistical analysis. 5th ed. Iowa State College Press, Ames, Iowa. 534 p.

Squillace, A. E., and R. R. Silen, 1962. Racial variation in ponderosa pine. For. Sci. Monographs 2-1962. 27 p.

Stearns, F. W., 1949. Ninety years change in a northern hardwood forest in Wisconsin. Ecology 30:350-358.

Sudworth, G. B., 1917. The pine trees of the Rocky Mountain region. U.S. Dept. Agr. Bull. No. 460. 46 p.

Turner, R. M., 1956. A study of some features of growth and reproduction of *Pinus ponderosa* in northern Idaho. Ecology 37:742-753.

Wheeler, G. M., 1878. Report upon United States geographical surveys west of the one hundredth meridian. Vol. VI - Botany. Gov. Print. Of., Wash. 404 p. 30 pl.

Wodehouse, R. P., 1935. Pollen grains, their structure, identification and significance in science and medicine. McGraw-Hill Co., N. Y. 574 p.

Wort, D. J., 1962. Physiology of cambial activity, p. 89-95. In: T. T. Kozlowski, ed. Tree growth. The Ronald Press Co., N. Y.