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The Forest Vegetation at Higher Altitudes in the Chiricahua Mountains, Arizona

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ABSTRACT: Forty 250-m^2 plots were distributed at various aspects at altitudes above 2000 m. Tree diam were measured in each plot, and the frequencies of herbs and shrubs were counted in smaller quadrats. The plots were arrayed in a three-dimensional ordination according to the method of Bray and Curtis with modifications by the authors; other ordination techniques were used as well. An environmental index (essentially a moisture index), computed from aspect, altitude and slope, correlated significantly with the axes of the ordinations. The ordinations produced five well-separated groups of stands that exhibited characteristic vegetational and environmental properties.

The major tree species, ordered from xeric to mesic, are: *Quercus arizonica, Pinus leiophylla* var. *chihuahuana, P. ponderosa* (principally var. *arizonica*), *Q. gambelii, P. strobiformis, Pseudotsuga menziesii, Abies concolor, Populus tremuloides* and *Picea engelmannii.* The positions of *A. concolor* and *Q. gambelii* are less certain than those of the other species. Size structure reveals that *Pseudotsuga menziesii,* the dominant tree species in the study area, will be increasing in dominance in the future, mainly at the expense of *Pinus ponderosa,* particularly in moderately moist and shady sites. *Picea engelmanni* and *Pinus leiophylla* are stable in the stands that they dominate at the mesic and xeric ends of the gradient, respectively. *Populus tremuloides* is declining in the stands it now dominates due to the better reproduction and establishment of *Abies concolor* and *Picea engelmannii. Pinus strobiformis* is the species of second highest constancy and density, but it fails to dominate a single one of our stands.

Zonation is not particularly strong and may be changing. *Pinus ponderosa* dominates altitudes below 2600 m, *Pseudotsuga menziesii* dominates altitudes above 2800 m, and the two species share dominance between 2600 and 2800 m. Other species dominate stands throughout the region and are variously restricted by altitude and aspect. Our assessment of the rather incomplete early records, as well as the present data, leads us to conclude that *Pseudotsuga menziesii* has increased strongly since the fires that ravaged the region a century ago. If the present patchwork of stands dominated by a variety of species also reflects the great fires, then the region may become more strongly zoned and less diverse as time goes on.

INTRODUCTION

The Chiricahua Mountains of southeastern Arizona are the highest mountains close to the Mexican border. Because of the combination of high altitude and southern latitude, there is a unique mixing of floral elements typical of the Mexican Sierra Madre and the southern Rocky Mountains. The unusual flora and fauna of the Chiricahuas attracted the attention of early naturalists (Toumey, 1895a, 1895b; Kellogg, 1902; Blumer, 1909, 1911) and have inspired recent popular accounts (Heald, 1967). Blumer was the first to describe the vegetation ecologically. He assigned trees to the Merriam life zones as follows: Transition zone—*Pinus leiophylla;* Canadian zone—*P. ponderosa* and *Abies concolor;* Hudsonian zone—*Picea engelmannii. Pinus strobiformis* was observed in both upper zones but was more common near the summits; *Pseudotsuga menziesii* was present from 1950 m upward (Blumer, 1909). Blumer (1911) also noted the interaction of aspect and altitude upon the vegetation.

Royal Kellogg (1902), a representative of the Forest Service, made this concise statement about the forest above 2100 m: "This forest consists principally of *Pinus ponderosa,* with considerable *Pseudotsuga taxifolia* [=*menziesii*] and a less amount of *Abies concolor.* The ponderosa is fairly well distributed over all the slopes; but the Douglas Spruce [=fir] and White Fir are commonly found only on the northerly

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exposures. On the N slopes . . . , above 8700 ft, there is [sic] about 800 acres of dense *Picea engelmanni*[*i*]." The more recently published investigations have been confined to the lower elevations of the Chiricahua National Monument or the Southwest Research Station at Cave Creek Canyon (Roseberry and Dole, 1937; Marshall, 1957; Reeves, 1976).

The only prior quantitative work in the high Chiricahuas was that of Robinson (1968) who gathered information concerning the physical environment and described the vegetation from a dozen quadrats located above 2850 m. He found that N slopes were dominated by *Picea engelmannii* and that the dense tree cover made for a generally sparse herbaceous understory. Southern, eastern and western aspects were dominated by what he called an ecotonal admixture of *Pseudotsuga menziesii, Pinus ponderosa* and *P. strobiformis,* each species varying in dominance by aspect. *Pseudotsuga menziesii* and *Pinus strobiformis* were characterized as reproducing heavily. Martin (1963) briefly noted altitudinal ranges of some species in the Chiricahuas relative to their distributions in the Huachuca Mountains. He attributed the occurrence of *Picea engelmannii* (not present in the other southern Arizona mountain ranges of similar elevation, excepting the Pinalenos), as well as the generally lower species distributions by altitude, to the Merriam effect, a climatic factor caused by the massiveness of the mountain range.

Several studies have described the vegetational ecology of southwestern mountains in Arizona (Whittaker and Niering, 1964, 1975, and citations therein; Brady and Bonham, 1976) in New Mexico (Dick-Peddie and Moir, 1970; Hanks and Dick-Peddie, 1974) and in Texas (Gehlbach, 1967). The prolonged and detailed investigation by Whittaker and Niering makes the Santa Catalinas one of the better-studied mountain ranges in the United States. One cannot assume, however, that their results apply particularly well to the high Chiricahuas. Their sample plots extended from near the summit of Mount Lemmon (2801 m) to the desert plains below; thus the investigation was more broadly focused. In addition, the forests of the Chiricahuas differ compositionally and occupy a broader and higher area.

In this paper we describe the vegetation of the mixed conifer forests of the high Chiricahuas, relate component species to environmental gradients, infer successional trends for tree species and discuss the vegetation from a historical perspective.

STUDY AREA

The Chiricahua Mountains are located in eastern Cochise Co., Arizona, approximately 32 km W of New Mexico and 65 km N of Mexico. They are structurally typical of the mountains of the Basin and Range Province which in southeastern Arizona is characterized by ranges extending N and S with elevations of 2500 m or more and separated by alluvial valleys. The study centered in the Chiricahua Wilderness along the main crest of the range, extending 10 km from Rustler Park to Monte Vista Peak. Chiricahua Peak (2987 m) and Fly's Peak (2947 m) are the highest points in the range, and from Rustler Park to Monte Vista the elevation of the main crest does not drop below 2600 m. The area atop the crest resembles rolling hills atop a narrow, high plateau rather than distinct mountain peaks. This relatively flat area on top is bounded on the E and W by steep slopes (25-40°) and sharply dissected canyons dropping 1000 m or more into the adjacent valleys. Within the study area the undulating terrain provides a variety of slope exposures. In some places the land is broken by rock outcroppings, while other sites are characterized by gentle slopes or open parks, all of which contribute to a diversity of microhabitats.

The Chiricahuas are situated near the northwestern edge of the Mexican highlands volcanic field. West of the Cave Creek drainage, the Chiricahuas are overlain by volcanic rhyolites and monzonites of mid-Tertiary age (Marjaniemi, 1969). The volcanic rocks are primarily welded tuffs with minor associated late-stage volcanics. The only rocks of pre-Tertiary age that occur within the study area are the siltstones, shales and limestone beds of the Cretaceous Bisbee formation (Drewes and Williams, 1973). The Bisbee formation outcrops below the Winn Falls scarp in Cave Creek Canyon and is below the elevation of the majority of the quadrats.

The soils of the high Chiricahuas are derived from these acidic volcanic rocks except in the aforementioned eastern drainages where they are of sedimentary origin. Soils in the study area exhibit a wide range of development. On many of the S-facing slopes the soil consists of gravel thinly overlain by topsoil; in contrast, the N slopes have deep humus soils. Robinson (1968) described the soils in the vicinity of Fly's Peak as podzol lithosols, characterized by an azonal profile and a distinct lack of uniform particle size. By examining organic content and soil particle size for both N and S slopes, he concluded that at field capacity the soil moisture available to plants on the N slopes was nearly twice that on the S slopes. In addition, the measured soil moisture on the N slopes was consistently higher than that of the S slope in June, July and August.

The Chiricahuas fall into the Arizona climatic regime, characterized by moist winters, dry springs, wet summers and dry autumns (Lowe, 1964). The spring drought is the more severe because of the high temperatures associated with it. Following this arid spell is the summer monsoon season, when convectional thunderstorms account for over 50% of the annual precipitation. There are four stations in the Chiricahuas where weather data are taken; unfortunately none of these is at an elevation greater than 1900 m and thus cannot give exact records for the study area. Data from these four stations (mean elevation, 1660 m) give a mean winter temperature of 5.7 C. Mean annual temperature is 14.1 C. Mean precipitation by season and percent of annual precipitation are as follows: winter, 119 mm, 27%; spring, 35 mm, 8%; summer, 248 mm, 56%, and autumn, 42 mm, 9%. Mean annual precipitation from these four stations is 442 mm (Sellers and Hill, 1974).

Extensive research on altitudinal gradients and their effects on climate in Arizona have been summarized by Lowe (1964). For every 305 m increase in elevation, there is a corresponding 2.2 decrease in temperature and an increase of 100-125 mm in precipitation. Extrapolating from these figures, we can estimate the mean annual precipitation and temperature in the high Chiricahuas. These are 795 mm and 7.3 C at 2600 m, 850 mm and 6.2 C at 2750 m and 905 mm and 5.4 C at 2900 m. The figure of 905 mm is reasonably close to Robinson's (1968) figure of 864 mm for Fly's Peak in 1966.

METHODS

Sampling techniques.—Vegetation was assessed by the count-plot method for trees with a frequency count for shrubs and herbaceous plants (Mueller-Dombois and Ellenberg, 1974; Daubenmire, 1968). The sample plots were rectangular quadrats 10 X 25 m (0.025 ha) in size, placed so that the 25-m sides lay upslope. Trees were measured for diam at breast height (dbh) except that smaller saplings were measured at soil level. Along the central axis of the plots a 0.5 X 0.5 m wooden frame was placed every other 0.5 m, alternating on either side of the axis. Twenty-five small quadrats per large plot were taken with a total coverage of 6.25 m^2. All herbaceous and shrubby species and seedlings rooted within the small quadrats were recorded, and any species observed within a large plot but not occupying any of the small quadrats was listed as though it had occurred in one. The location of plots was recorded, as were elevation, slope angle and exposure, soil observations, the presence of epiphytes or parasites, and possible site disturbances. Cover by trees taller than 10 m, or shorter than 10 m, and by shubs and herbs was estimated.

After conducting a reconnaissance of the study area, quadrat sampling sites were selected. The criteria for determining sites followed Newsome and Dix (1968) and are: (1) the tree canopy must cover 60% of the ground; (2) the species composition must appear to be homogenous; (3) the stand must be continuous for more than 0.6 ha; (4) the habitat (topography) must be uniform, and (5) stands must be mature and free of obvious recent disturbance (due to windfall, fire or cutting). A total of 40 quadrats were established in May and June 1976. The goal was to representatively sample the forest vegetation over the range of slope aspects and angles above 2000 m. The majority of the stands lay between 2600 and 2900 m. The plots were checked through September to determine by flower and fruit those species exhibiting only vegetative characteristics in May and June. All identifications were checked at the herbarium of the Southwestern Research Station in Cave Creek Canyon, the herbarium of Chiricahua National Monument, or the herbarium of the University of Arizona with the assistance of Vincent Roth, William B. Murray or Charles T. Mason. Nomenclature follows Weber and Johnston (1976) and, for species not contained therein, Kearney and Peebles (1951). The varietal names in *Pinus leiophylla* var. *chihuahuana* and *P. ponderosa* var. *arizonica* will henceforth be omitted.

Analytical methods.—One-, two- and three-dimensional ordinations were constructed according to the methods of Bray and Curtis (1957) as modified by subsequent workers [*see* Mueller-Dombois and Ellenberg (1974) and Whittaker (1967)] and by the present authors. The objective of the ordination is to construct geometric arrays of stands in which the distances between pairs of stands show a high negative correlation to the vegetational similarities between pairs of stands. In short, similar stands should be located near one another, and dissimilar stands should be widely separated.

We used a modification of Sorensen's (1948) index of similarity ($IS = 200w/(A+B)$) in the determination of similarities between stands. A is the sum of all quantitative values for the species in one of the stands and B is the sum of all such values in the other stand; w is the sum of the smaller of the two values for each species from the two stands. The quantitative values were, for the trees, the dominance (basal area) expressed in dm^2 and, for the other species, the % frequency in the 25 0.25-m^2 quadrats through the center of the plots. We chose to express dominance in dm^2 because the numeric values obtained were similar in magnitude to the frequency values obtained for the other species. Consequently, we considered that neither the trees nor the other plants were unduly weighted in subsequent analyses. In further computations an index of dissimilarity (ID) was used in which $ID = 100\text{-}IS$.

Stands were located on the x axis of the ordination according to the formula of Beals (1960): $x = (L^2 + (dA)^2 - (dB)^2)/2L$. L is equal to the index of dissimilarity between two reference stands that were chosen, in our case, by a systematic trial-and-error method. One of the stands occupies the zero position of the x axis and the other stand occupies a position numerically equal to the ID between the two stands. Each of the other stands is positioned upon the x axis according to the formula above in which dA is the ID value between the stand and the reference stand at the zero position and dB is the ID value between the stand and the reference stand at the other end of the x axis. Subsequently, a y axis may be similarly constructed after two y-axis references stands have been selected. Stands may be located upon the y axis without regard to their x-axis positions provided the reference stands of the y axis are not widely separated on the x axis. [*See* Mueller-Dombois and Ellenberg (1974) for a discussion of the latter point.] At this stage the ordination is two-dimensional, and a three-dimensional ordination may be constructed subsequent to the establishment of a z axis.

The selection of terminal stands for ordinations is problematical. Our objective was to select from the 780 pairs the one pair that when used in the construction of the x axis would produce the best ordination, that is, the highest correlation between the interstand distances on the x axis ($\triangle x$) and the ID values. We tested all pairs with ID values $\geqslant 65$ and selected the pair that gave the highest correlation when used as the terminal stands. In order to select the terminal stands for the y axis of the two-dimensional ordination we tested first those stands that fit most poorly on the x axis, that is, those stands for which the value $(dA)^2\text{-}x^2$ was the highest. [*See* Mueller-Dombois and Ellenberg (1974) for further discussion.] The terminal stands for the z axis were selected similarly.

The ordination just described will henceforth be known as the vegetational ordination, as its construction depended solely upon the vegetation of the stands. Other ordinations were done that depended entirely upon the aspect, altitude and slope of the stands; these ordinations will be referred to as environmental ordinations. Vegetational and environmental measurements may be combined in order to construct a mixed environmental-vegetational ordination. The modifiers "environmental," "vegetational" and "mixed" have the same meanings as Whittaker's (1967) "direct," "indirect" and "weighted-average."

Only those species that occurred in four or more plots were used in the construction of ordinations. Other species have been included in such calculations as number of species per plot or total woody stem cover, but these species are not mentioned by name anywhere in the article. The few tree seedlings recorded in the small quadrats were not used in any of the analyses.

RESULTS

Vegetational ordination.—The stands are arrayed in Figure 1a according to their vegetational similarities. The correlations between the indices of dissimilarity between pairs of stands and the interstand distances are 0.707 for the x ordination, 0.782 for the two-dimensional xy ordination and 0.822 for the three-dimensional xyz ordination (not shown). Figures 1b and 1d display the tree species of highest dominance and highest density in the stands as arrayed in the vegetational ordination. The ordination tends to cluster those stands containing a particular species. For example, *Pinus ponderosa* and *Achillea lanulosa* are essentially confined to stand grouping III. One of the tree species, *Abies concolor,* however, is not clustered at all, and two others, *Pseudotsuga menziesii* and *Pinus strobiformis,* are clustered only weakly. The shrubs and herbs tend to cluster less strongly than the trees, but a half dozen species are tightly grouped within the ordination. In addition, certain species are strongly segregated from certain others. In particular, stands containing *Picea engelmannii* or *Populus tremuloides* are widely separated in the ordination from stands containing *Pinus leiophylla* or *Quercus arizonica.* The mean positions in the ordination for tree species are given in Figure 1c. In the computation of the mean position the position of each stand was weighted for dominance. The tendency for two species to occur together is indicated in part by the separation of the mean positions in Figure 1c.

It is standard practice, when ordinations are constructed on the basis of vegetation alone, to subsequently seek correlations between the axes of the ordination and a variety of other variables (Table 1). Several variables measured in the field were omitted from Table 1. These included slope and percent cover by trees under 10 m in height, by shrubs and by herbs. These variables were omitted because they failed to correlate significantly with any one of the three axes of the vegetational ordination. Of the variables measured, only aspect, altitude and slope are totally independent of vegetation. Both aspect and altitude correlate positively (and in three of six instances, significantly) with the three axes of ordination. In general, air temperature, soil temperature, precipitation and, consequently, soil moisture are strongly affected by aspect or altitude. Due to the coincidence of high insolation with the high afternoon temperatures, the SW exposure is assumed to be the warmest and dryest with the NE exposure taken to be the coolest and wettest. This assessment is in accordance with general thinking, but *see* Haase (1970). Aspect was ranked as follows: SW-1, S-2, W-3, SE-4, NW-5, E-6, N-7, NE-8. The influence of slope upon soil moisture is a complex function of soil porosity, latitude, aspect and season, but in general the illumination diminishes with increasing slope at lower latitudes during the growing season (Geiger, 1965).

Aspect, altitude and slope were combined in the calculation of an environmental index, which in turn is a measure of moisture, temperature and illumination. The

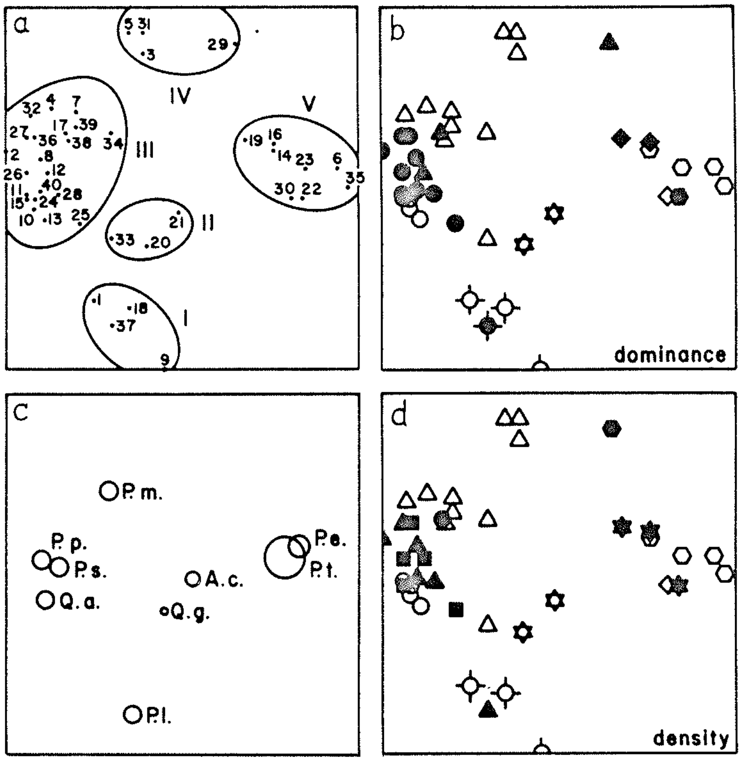

Fig. 1.—*1a.* Vegetational ordination of the stands. Stands are arrayed according to their relative similarities to the terminal stands of the x axis (stands 2 and 35) and the terminal stands of the y axis (stands 9 and 5). Each axis extends for 100 ID (index of dissimilarity) units. *1b.* Tree species of highest dominance in the stands as arrayed in 1a. Solid symbols indicate that the species of highest dominance is not the same as the species of highest density. ⬢ , *Picea engelmannii;* ◆ , *Populus tremuloides;* ✡ , *Abies concolor;* ▲ , *Pseudotsuga menziesii;* ■ , *Pinus strobiformis;* ● , *Pinus ponderosa;* ⌖ , *Pinus leiophylla. 1c.* Mean positions of the tree species in the vegetational ordination. A weighted-mean, x-axis position was calculated for each species by summing the products of the x-axis position and the dominance value for the species in each stand, then dividing by the sum of the dominance values. The y-axis position was similarly calculated. The size of the circle indicates the position of the z axis. *1d.* Tree species of highest density; symbols as in 1 b

equation EI = aspect + 0.007 altitude + 0.04 slope −20 generates values that correlate highly with each of the three axes of the vegetational ordination. The term −20 has no effect upon the correlations and was used simply to bring the EI values into a range similar to the aspect ratings. If one considers the range of values for the variables (aspect, 1-8; altitude, 2000-3000 m; slope, 0-90°), it can be seen that the coefficients bring aspect and altitude into about equal importance and slope into half the importance of the other two. The equation for EI was generated by a systematic trial-and-error procedure whose objective was to maximize the correlation between EI and the axes of the vegetational ordination.

Description of the stand groupings.—The two-dimensional ordination has segregated the stands into five discrete clusters, each having distinct vegetational and environmental characteristics that are summarized in Tables 2 and 3. Each stand of group I is characterized by a joint occurrence of *Pinus leiophylla* and *P. strobiformis* with the former species dominating. Despite the low EI values for the two oak species, the stands of group I are entirely free of *Quercus gambelii,* and *Q. arizonica* has but a minor presence in one of the stands. The following species achieve their highest mean dominance or frequency values in group I: *Pinus leiophylla, Thermopsis pinetorum* and *Muhlenbergia montana.* The stands have poor soil development, small trees and low aspect ratings, but altitudes are intermediate. The mean EI (1.96) is lower for group I than for any other group.

The three stands of group II are not very similar to one another. They happen to cluster together because each is quite dissimilar to the x and y terminal stands. For that reason the three plots occur in the center of the ordination. Nevertheless, the plots have several vegetational features in common. Each contains *Quercus gambelii* and one plot contains *Q. arizonica* as well. *Abies concolor* dominates two stands in the group and thus dominates the group as a whole. Despite widespread occurrence and its presence in all the other groups, *Pinus strobiformis* is absent from each of the plots in group II. The following species achieve their highest mean dominance or frequency values in group II: *Abies concolor, Q. gambelii, Muhlenbergia virescens, Agrostis scabra, Verbena bipinnatifida* and *Elymus arizonica.* Mean density and tree size are low, soil development is poor, but species diversity is high. As with group I the mean EI value is low (1.96) but for different reasons—altitude is low for two of the stands but aspect is intermediate.

Group III is characterized by the mutual occurrence of *Pinus ponderosa, Pseudotsuga menziesii* and *Pinus strobiformis. Pinus ponderosa* is nearly confined to

TABLE 1.—Correlation matrix for several stand variables. Values are expressed as correlation coefficients X 1000. N=40, p=0.05 at 0.308 and p=0.01 at 0.398

	Asp.	Alt.	Soi.	Cov.	Dom.	Den.	D/D	Spe.	EI	EVI	Z	Y
Aspect												
Altitude	−78											
Soil	680	−28										
Cover	389	114	503									
Dominance	409	365	365	613								
Density	60	273	−64	−333	75							
Dom./Den.	261	41	207	574	560	−591						
No. species	7	−335	78	−150	−55	−127	−74					
EI[a]	798	515	532	338	533	211	225	−158				
EVI[b]	628	385	533	428	597	−64	463	−152	761			
Z[c]	229	402	244	244	449	64	163	−370	474	620		
Y[c]	330	225	403	380	493	1	234	251	401	490	159	
X[c]	536	123	368	253	339	−43	257	−101	538	752	416	1

[a] Environmental index

[b] Environmental-vegetational index

[c] Axes of the vegetational ordination

group III and is the leading dominant, but the other two species have a significant presence in other groups. Within group III one sees a clear-cut gradient along the y axis with *Pseudotsuga menziesii* dominating the upper end and *Pinus ponderosa* dominating the lower end. *Pinus strobiformis* achieves higher dominance at the lower

TABLE 2.—Vegetational characteristics of the five groups of stands. For each species the mean dominance (for trees) or frequency (for shrubs and herbs) is tabulated for each group of stands. Also listed is the mean EI value for each species weighted for dominance or frequency

Tree species	EI	Group I	II	III	IV	V
Picea engelmannii	7.95	0	0	0	19.8	86.9
Populus tremuloides	6.51	0	0	0.6	1.6	66.0
Pseudotsuga menziesii	4.92	16.3	13.2	40.0	196.3	4.4
Pinus strobiformis	4.50	4.0	0	8.3	1.0	0.5
P. ponderosa	3.94	6.3	0	70.1	0	1.6
Abies concolor	3.80	1.6	23.2	1.0	0	7.1
P. leiophylla	2.18	85.9	3.7	0.2	0	0
Quercus arizonica	1.47	0.05	0.3	0.3	0	0
Q. gambelii	1.43	0	6.6	0.02	0	0
Nontree species						
Geranium richardsonii	6.93	0	0	0.6	11.0	5.0
Undetermined mosses	6.58	0	0	1.0	23.0	24.0
Acer glabrum	6.37	0	0	0	0	5.5
Oxalis grayi	6.16	0	0	1.0	16.0	2.0
Thalictrum fendleri	6.12	0	0	1.3	8.0	1.5
Helenium hoopesii	6.04	0	0	2.1	7.0	4.0
Calamgrostis canadensis	4.50	0	0	1.3	2.0	0
Vicia americana	4.42	2.0	0	1.9	2.0	0
Bromus marginatus	4.41	0	0	3.6	4.0	1.5
Pteridium aquilinum	4.36	3.0	2.7	8.4	0	0.5
Stipa pringlei	4.33	5.0	4.0	8.8	14.0	1.0
Achillea lanulosa	4.29	0	0	4.0	0	0
Thermopsis pinetorum	4.22	8.0	0	6.7	0	0
Muhlenbergia virescens	3.80	0	12.0	11.6	6	0
Senecio wootonii	3.63	1.0	0	4.8	0	0
Agrostis scabra	3.35	15.0	24.0	3.4	0	0
Verbena bipinnatifida	3.31	1.0	8.0	1.1	0	0
Senecio actinella	2.72	2.0	4.0	5.0	0	0
Muhlenbergia montana	2.56	8.0	0	1.5	1.0	0
Elymus arizonica	2.35	6.0	6.7	0.6	0	0.5

TABLE 3.—Mean values for stand variables within the groups generated by the vegetational ordination[a]

	Group I	II	III	IV	V
Aspect	2.00	4.67	4.02	5.38	6.75
Altitude	2696	2331	2733	2863	2811
Slope	27.0	24.3	21.9	15.8	22.1
Soil	1.25	1.67	1.90	3.00	2.88
Species	8.50	11.7	8.67	11.5	7.38
EI	1.96	1.96	4.03	6.04	7.31
Dominance	114.1	57.5	120.9	218.8	168.7
Density	64.2	39.0	65.3	51.0	66.1
Mean ID[b]	53.2	77.5	55.1	38.1	62.0

[a] The units of measurement for the variables are the following: aspect, 1 (for SW) to 8 (for NE); altitude, m; slope, °; soil, 1 (poorly developed) to 4 (well-developed); species, no. of species/plot; EI (environmental index), *see* formula in Results; dominance, dm^2/plot; density, no. of trees/plot; mean ID, (*see* Introduction)

[b] The mean ID (index of dissimilarity) between all 780 pairs of stands is 77.7

end and may come to dominate several stands in the central and lower portions of the group. The species that achieve their highest mean dominance or frequency values within the group are: *Pinus strobiformis, P. ponderosa, Quercus arizonica, Pteridium aquilinum, Achillea lanulosa* (occurs exclusively within the group), *Senecio wootonii* and *S. actinella.* A wide range of values are seen for aspect and altitude, producing an intermediate value for the mean EI (4.03).

Group IV is composed of stands strongly dominated by *Pseudotsuga menziesii* and having very high values for total stem cover. *Pinus ponderosa* is entirely absent from the group and so are *Abies concolor, Pteridium aquilinum* and *Elymus arizonica,* despite their presence in every other group. *Pinus strobiformis* shows a minor presence in each stand. *Picea engelmannii* and *Populus tremuloides* are beginning to show themselves in these rather mesic stands. Species achieving their highest mean dominance or frequency values within the group are the following: *Pseudotsuga menziesii, Geranium richardsonii, Oxalis grayi, Thalictrum fendleri, Helenium hoopesii, Calamgrostis canadensis, Bromus marginatus* and *Stipa pringlei.* Group IV shows the highest mean values for altitude, soil development, canopy cover, stem cover and tree size. The group is species-rich, more homogenous than the others, and the mean EI is 6.04.

Group V is characterized, in general, by the presence of *Picea engelmannii* (the leading dominant), *Populus tremuloides* and *Abies concolor,* although none of these species is present in every stand. *Pseudotsuga menziesii* is more poorly represented here than in any other group. Only *Picea engelmannii, Populus tremuloides,* undetermined mosses and *Acer glabrum* achieved their highest mean values for dominance or frequency in group V. The latter species occurs exclusively in group V. Species diversity is low and mean stem cover, density, tree size and aspect rating are high. The mean EI for this, the most mesic group of stands, is 7.31.

Environmental and mixed ordinations.—A unidimensional environmental ordination may be constructed by arranging the stands on an axis according to their EI values (Fig. 2). Only four species (*Picea engelmannii, Populus tremuloides, Pinus leiophylla* and *Quercus arizonica*) have clearly unimodal distributions; five have two peaks. As is generally observed, each species has a unique distribution except that *Abies concolor* and *Pinus strobiformis* have similarly shaped distribution curves. Four of the species (*Abies concolor, Pinus ponderosa, Pseudotsuga menziesii* and *Pinus strobiformis*) extend broadly across the moisture gradient. This broad amplitude could be inferred from the fact that each of these species except *Pinus ponderosa* clustered poorly in the vegetational ordination.

A mixed environmental-vegetational ordination was prepared after a technique developed by Whittaker (1967). For each stand the dominance value for each tree species was multiplied by the EI value for that species. The sum of these products was then divided by the sum of the dominance values. Similarly, the frequency value for each herbaceous species was multiplied by the EI for the species, and the sum of these products was then divided by the sum of all frequency values in the stand. Each stand was then positioned on a two-dimensional ordination according to the environmental-vegetational index (EVI) derived from trees (x axis) and other species (y axis). We have outlined the stands in Figure 3 according to the five groups of Figure 1a. It is apparent that both ordinations segregate the stands rather similarly. The mixed ordination did rearrange the stands somewhat, however. Stands 3, 5 and 31 are dominated by *Pseudotsuga menziesii.* Stands 16, 19 and 30 are dominated by *Populus tremuloides,* which is also present in stand 29. Stands 6, 14, 22, 23 and 35 are all dominated by *Picea engelmannii.* This new clustering, therefore, segregates spruce and aspen. The correlation coefficient for EVI for trees and the EVI for nontrees is 0.825, and note that the y ordination is necessary to separate group III from group IV. When the dominance of trees is plotted against a combined EVI for trees and nontrees, sharp unimodal curves are obtained in most cases. Once again, however, *Abies concolor* shows multiple peaks and a presence across the entire gradient (Fig. 4).

Succession.—In order to infer successional trends we carefully examined each species in each stand with respect to present dominance, density and size distribution. We concluded that in nearly every case the species of highest density is also likely to become the leading dominant in the future. Only in five stands does another species seem likely to compete seriously with the presently most numerous species. In only

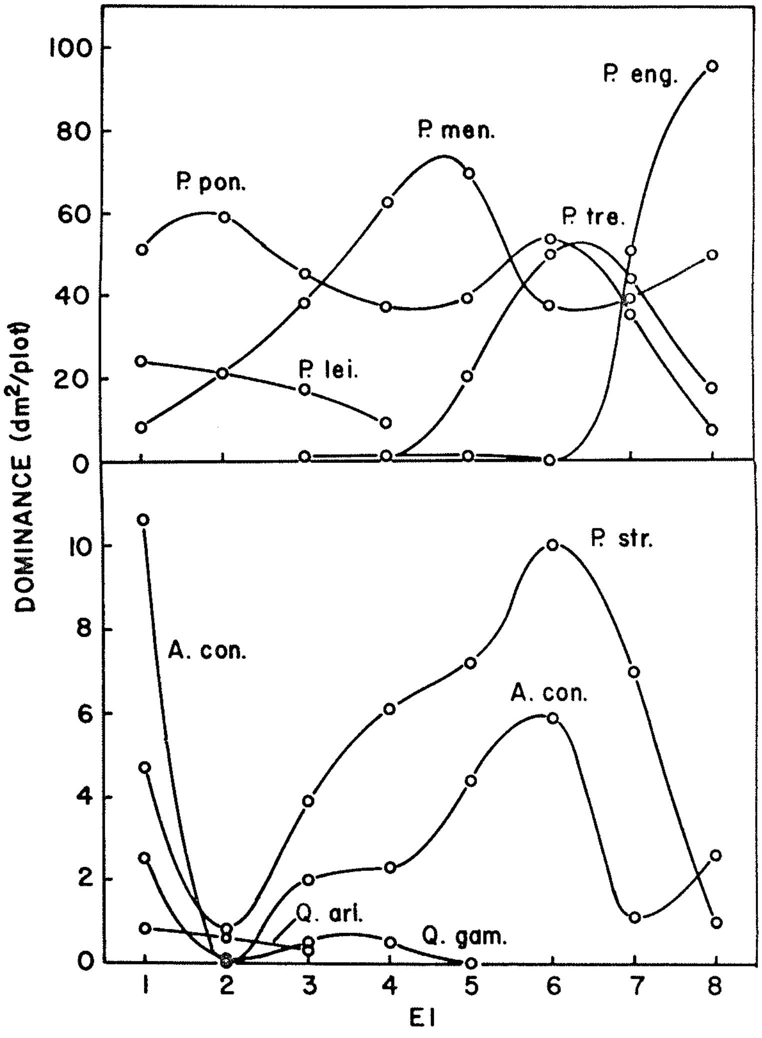

Fig. 2.—Environmental ordination of tree species. Mean dominance values for tree species are plotted against the environmental index (EI). The curves were smoothed by calculating the mean dominance from stands whose EI values occur within a two-unit range. Thus the points over EI = 5 pertain to stands with EI values of >4 and ⩽6

one instance is the most numerous species not represented by individuals < 10 cm dbh, but in that stand no other species is reproducing either. In only two stands is the most numerous species not represented by individuals ⩾ 10 cm dbh. Otherwise the size class distribution bodes well for the presently most numerous species, *i.e.*, the site appears to be favorable for both reproduction and growth. In 24 stands the species of highest density and the present leading dominant are the same. In another five stands the species of highest density is a codominant species (dominance ⩾ 1/2 the dominance of the present dominant species). Consequently, we have accepted the species of highest density as the apparent future dominant in each stand and are confident of introducing but a small error in so doing. Data that bear upon the successional trends in our stands are presented in Figure 1 and Table 4.

Pseudotsuga menziesii dominates the region (principally above 2600 m) as a whole. Both the mean density (trees per stand) and the dominance (stem cover in dm^2 per plot) are the highest for that species. *Pseudotsuga menziesii* occupies 31 stands, dominates 13 of them, and is the species of maximum density in 16 stands. Seventy-five percent of the trees are young (< 10 cm dbh) so there is much potential for future growth. If *Pseudotsuga* does come to dominate new stands it will be almost entirely in stands presently dominated by *Pinus ponderosa*. Only in three instances will *Pseudotsuga menziesii* give way to other species.

Pinus ponderosa is presently the species of second highest dominance throughout

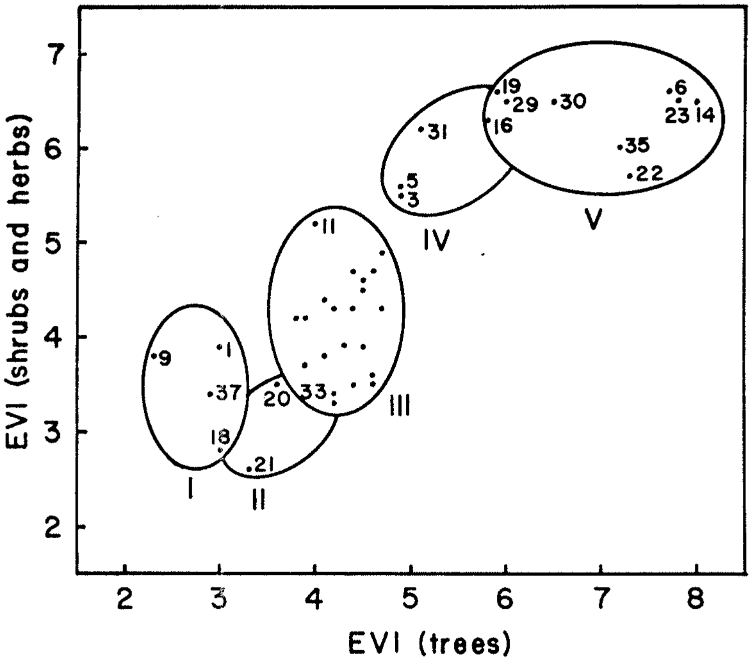

Fig. 3.—Mixed ordination of stands. An environmental-vegetational index (EVI) for each stand was calculated by summing the products of the dominance value and the mean EI value for each tree species, then dividing by the sum of the dominance values for all tree species. Another EVI is calculated similarly from the frequency of the nontree species. These EVI values were plotted on the x and y axes, respectively. The five groups of Figure 1 are encircled in the figure except that stand 33 belongs in group II and stand 29 belongs in group IV. The correlation between the two EVI's is 0.825

the region, but it appears to be giving way to *Pseudotsuga menziesii* and *Pinus strobiformis*. Though it presently dominates 13 stands, it is the species of maximum density in only five. In addition, only 43% of the individuals are < 10 cm in diam. Only *Populus tremuloides* has a lower percentage, and it is the other species that is reproducing poorly. *Populus tremuloides* is failing to reproduce in six of 10 stands occupied, and two of the stands that it currently dominates are giving way to *Abies concolor*.

Because of the large number of stands occupied by *Pseudotsuga menziesii* and *Pinus ponderosa*, it was possible to do more detailed analyses for these two species. Thirty-one stands contain at least three individuals of one or the other species. The

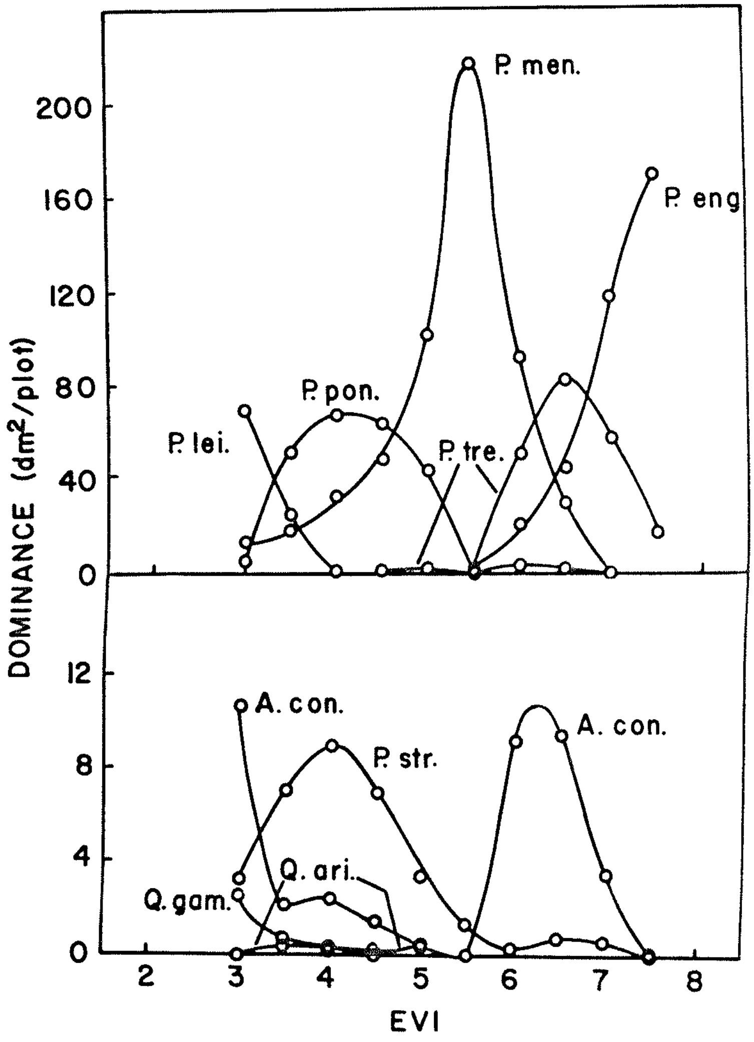

Fig. 4.—Mixed ordination of tree species. Mean dominance values for tree species are plotted against the environmental-vegetational index (EVI—*see* legend for Fig. 3). The curves were smoothed over a one-unit range in a manner similar to that described in Figure 2

TABLE 4.—Successional data for the tree species

Species	Mean dominance[a]	Mean density[b]	$\% < 10$ cm dbh	Stands occupied	Stands dominated	Stands codominated[c]	Stands where max. density	NR[d]
Picea engelmannii	19.4	3.7	47	7	5	1	5	1
Populus tremuloides	13.7	5.0	26	10	3	1	1	6
Pseudotsuga menziesii	44.2	20.1	75	31	13	4	16	2
Pinus strobiformis	4.98	11.5	92	29	0	1	5	1
P. ponderosa	37.8	8.9	42.5	23	13	6	5	4
Abies concolor	3.83	7.0	90	12	2	0	5	1
P. leiophylla	8.95	4.55	61.5	6	4	0	3	0
Quercus arizonica	0.196	0.250	80	4	0	0	0	1
Q. gambelii	0.505	0.325	54	4	0	0	0	1

[a] dm^2/plot

[b] trees/plot

[c] Dominance $\geqslant \frac{1}{2}$ dominance of leading species

[d] Not reproducing; that is, no individuals < 10 cm dbh

dency is for fir to reproduce better in stands that are moist or shady. Relative tes of reproduction were assessed in several ways, but the measurement finally osen is the following: No. of fir individuals < 10 cm dbh minus no. of pine individuals < 10 cm dbh, all divided by the total number of trees in the stand. This lue correlated significantly ($p<0.01$) with both EI and total stem cover. We nsider the latter to be a good index of shadiness.

Abies concolor and *Pinus strobiformis* are the two species showing the highest tes of reproduction. Both appear to have a very wide environmental amplitude to dge by their distributions in the ordinations, but the ascendancy of the former spees appears to be confined to the more mesic sites presently occupied by *Populus tremoides* and *Picea engelmannii*. *Pinus strobiformis* is interesting for a number of reasons. It is the second most widely distributed tree, occupying 29 stands; it also has the second highest mean density; but 92% of the individuals are less than 10 cm in diam and it dominates no stands. In five of the stands *Pinus strobiformis* has the highest density, and prospects for continued growth in those stands should be good for the reason that the total stem cover and the canopy cover are both somewhat less than the average whereas the environmental index is somewhat higher. Thus sunlight and moisture would seem to be adequate.

Two species appear to be stable in their positions at the extremes of the environmental gradient. *Picea engelmannii* may be destined to lose one of the stands it now dominates, but it may gain another. The percentage of individuals less than 10 cm in diam is an intermediate figure of 47, and the species is failing to reproduce in only one stand that it now occupies. *Pinus leiophylla* may give up one stand, but its future looks good with 62% of its individuals less than 10 cm in diam and no reproductory failure in any of the stands occupied.

In general the stands appear to be proceeding toward a more mesic vegetation. In 11 instances the species of highest density is more mesic (has a higher EI value) than the species of highest dominance; in five instances the opposite is true.

DISCUSSION

The ordinations.—The ordinations appear to have been successful for several reasons. For the vegetational ordination, the correlation between interstand distances in one, two or three dimensions and the ecological distances as measured by the index of dissimilarity is quite high. Each of the axes correlates significantly with the environmental (moisture) index, and, most importantly, the vegetational ordination clusters the stands into discrete groups whose members have obvious vegetational and environmental similarities. For the mixed environmental-vegetational ordination, the correlation (0.662) between interstand distances and ecological distance is highly significant. Each of the axes of Figure 3 correlates significantly with the environmental moisture index, and, in this ordination too, groups of stands can be delineated.

Each ordination has its relative merits. The vegetational ordination arrayed the stands with respect to indices of dissimilarity better than the mixed ordination. The mixed ordination did a creditable job in this regard, too, and we believe that the validity of our index of dissimilarity is supported thereby. Our vegetational ordination produced a somewhat more two-dimensional array of stands, and the stands were also more discretely clustered than in the mixed ordination. The mixed ordination has the advantage of a clear-cut relationship between the environmental variables and the vegetation itself. The stands in Figure 3 tend to be clustered along a diagonal from lower left to upper right proceeding from xeric to mesic, and the very high correlation between the EVI for trees and the EVI for nontrees indicates that our sampling techniques for both groups of plants were adequate.

The correlation between the combined environmental-vegetational index (EVI the distance along the diagonal in Fig. 3) and the environmental index is high, but not perfect. This may mean that the EI fails to take into account all of the significant factors of the physical environment and that the vegetation itself exerts a significant influence upon the individuals in the stand. Stands that lie above a regression line (not shown) for EI (x axis) vs. EVI (y axis) have a vegetation more mesic than the environment would seem to indicate and stands below the regression line, a more xeric vegetation. The stands above the line are more stable and the stands below, more seral. This was determined by comparing the number of individuals of the dominant species to the number of individuals of the nearest competitor (the species of highest density other than the dominant). This observation is consistent with the previously described tendency for successional stands to proceed toward more mesic vegetation. In any case, the vegetation itself may be the best indicator of moisture availability, an assumption upon which the validity of the mixed ordination depends. Consequently, Figure 4 (dominance vs. EVI) may be a more realistic representation of species distribution than Figure 2 (dominance vs. EI).

The EI ranking of tree species from mesic to xeric in Table 2 agrees with that of Whittaker and Niering (1964) except that *Abies concolor* and *Quercus gambelii* are ranked as more xeric. The discrepancy is due, at least in part, to the fact that we determined EI solely from aspect, altitude and slope and did not take into account the surrounding topography. Consequently, stands in low-altitude ravines could receive low EI ratings despite rather moist conditions. Stands 20 and 21 may be underrated as they do lie in a ravine; they are also the stands of highest dominance for *Abies concolor* and *Quercus gambelii*. We had considered adjusting the EI rating for surrounding topography but decided against the procedure for the sake of objectivity and simplicity. Further adjustment of EI would make very little difference except for the two species in question. *Abies concolor* probably should have a moisture rating about equal to *Populus tremuloides*, in agreement with the position of the main peaks in Figure 4 and with the fact that *Abies concolor* is the apparent future dominant in two stands presently dominated by *Populus tremuloides*. As for *Quercus gambelii*, we have insufficient data outside of stands 20 and 21 for an evaluation. Whittaker and Niering (1964) give the species a moisture status equal to that of *Pinus strobiformis*.

Succession.—Jones (1974) presents the following scheme for succession in southwestern mixed-conifer forests: *Pinus ponderosa* or *Populus tremuloides* is usually the first tree species to invade a disturbed area. *Pseudotsuga menziesii* and *Abies concolor* generally follow, but they may become established as the first tree species on the site. Succession may end there or it may proceed to the establishment of species of *Picea* and *Abies*. Upon mesic sites at higher altitudes these genera may follow *Populus tremuloides* directly or even become established as the first trees. *Pinus leiophylla* is not treated in that scheme, and *P. ponderosa* is given only seral status. Yet we believe that both species can dominate certain stands on appropriate sites for a very long time. We saw no encroachment of *Pseudotsuga menziesii* upon *Populus tremuloides*, nor did we see any significant occurrence of *Pseudotsuga menziesii* and *Abies concolor* mixed together. Otherwise our observations are in agreement with Jones' assessment. *Pinus strobiformis* (also not treated by Jones) remains problematical in light of its high constancy, high density and wide amplitude, coupled with its failure to dominate a single stand.

Much of the Chiricahuas would seem to be in a seral stage—an interpretation lent historical support by Kellogg (1902), who remarked that he could not detect a single place in the mountains that had not been burned in the previous 20-30 years. Yet we wonder whether the stands of group IV may have escaped fire for over a century as each stand has at least three trees over 60 cm dbh. Kellogg observed that *Pinus ponderosa* dominated the forest above 2100 m. He is supported indirectly by Blumer (1909) who lists *P. ponderosa* as characteristic of the Canadian zone (2100-2700 m). *Pseudotsuga menziesii* is not listed as dominating any zone, but Blumer merely comments that the tree is "present" from 2000 m upward. In agreement with Blumer, we found *Pinus ponderosa* to dominate, on the whole, our stands below 2800 m (*see* group III in Table 2), but our measurements (*see* Table 4) and those of Robinson (1968) clearly show *Pseudotsuga menziesii* to be the leading dominant for the region as a whole above 2600 m. Between 2600 and 2800 m the two species exhibit equal dominance. We conclude from the following considerations that *Pseudotsuga menziesii* has increased considerably since the great fires of a century ago: (1) The present apparent increase in dominance (present study), (2) the apparent unimportance of the species at the turn of the century (Blumer, 1909, and Kellogg, 1902), and (3) the behavior of the species in southwestern mixed coniferous forests as judged by other investigators (Jones, 1974).

Origin of the montane vegetation.—The means by which the mixed conifer forest became established in southwestern desert mountain ranges has been variously interpreted. Martin (1963) theorizes that the pluvial maximum of the Wisconsin glaciation caused a downward migration of the vegetational zones. Based on palynological evidence from the Wilcox playa, 65 km NW of the Chiricahuas, Martin and Mehringer (1965) diagram yellow-pine parkland as having been continuous in valleys adjoining the Chiricahuas; the major part of the massif was vegetated with a spruce-fir forest and, at the highest elevations, alpine vegetation. The spruce-fir forest was not continuous between mountain ranges, but the displacement was enough to enhance opportunities for migration across the valleys. With the closing of the pluvial phase, vegetation migrated up the mountains in response to more xeric conditions.

Wells (1966) agreed that there was a depression of vegetation during the Wisconsin pluvial maxima, but from examination of macrofossil evidence in fossil packrat middens in the Chisos Mountains, Texas, concluded that the depression was much greater (800 m) for xerophilous woodland vegetation (pinyon pine, juniper and oak) than for ponderosa pine and more mesophytic montane vegetation. Furthermore, because of the uneven distribution of coniferous species in the mountains of the Chihuahuan desert, he considered former continuity of montane forests to be an untenable mechanism for present distributions. He attributed dispersal of coniferous species to long-distance transport of propagules by birds, particularly the band-tailed pigeon (*Columba fasciata*).

The band-tailed pigeon is a relatively common summer resident in the mountains of southern Arizona, and there is uneven distribution of some tree species in the mountains of southeastern Arizona (*Abies lasiocarpa* is present only in the Pinalenos and Santa Catalinas, *Picea engelmannii* only in the Pinalenos and Chiricahuas). Nevertheless, the mixed-conifer forests of southern Arizona are essentially dominated by the same species (Whittaker and Niering, 1964, 1975; Wallmo, 1955; Brady and Bonham, 1976; Martin, 1963), and the differences can be rationalized. *Picea engelmannii* occurs only in the two highest and most massive mountain ranges. The lack of *Abies lasiocarpa* in the Chiricahuas, while curious, is not particularly telling because the species is infrequent in the Santa Catalinas and significant only in the Pinalenos which are higher and farther N than the Chiricahuas. The basic similarity of mixed conifer forest throughout southeastern Arizona does not support the need for an alternative to the hypothesis of migration to explain the distribution of forest components.

Martin (1963) concluded that the migration of Madrean pine-oak woodland from the S could not have occurred concurrently with the boreal invasion that accompanied the Wisconsin pluvial maximum. He suggests the Madrean invasion occurring during peak development of the Mexican monsoon in the altithermal period (4000-8000 BP). The plant geography of *Pinus strobiformis* is problematical in this scheme. It is a species that has its center of distribution in the Sierra Madre of Mexico (Critchfield and Little, 1966) and yet is not a component of the pine-oak woodland but of the mixed-conifer forest. In addition to this anomalous presence of a Madrean species in the boreal forest, the taxonomic status of the species is unclear. It is distinct from *P. flexilis* (Steinhoff and Anderson, 1973) but its relation to the *P. ayacahuite* complex remains unclear. As its importance in southwestern mixed-conifer forests appears to be on the increase (present in 73% of quadrats in this study), a clarification of its taxonomy would seem to be important. *Pinus leiophylla* is also of Madrean origin, but, as expected, occurs only in the most xeric sites when found at higher altitudes.

The forest communities of the Chiricahuas reflect the long-term historic events just described and the more recent fires that ravaged the mountains 100 years ago. *Pinus ponderosa* or *Populus tremuloides* presently dominates many stands, but these two species, which quickly invade burned-over areas, appear to be declining except that *Pinus ponderosa* may stabilize on certain sites. The stands lost to *P. ponderosa* and *Populus tremuloides* will become dominated by *Pseudotsuga menziesii, Abies concolor* and *Picea englemannii* unless new cycles of disturbance occur. Altitudinal zonation is weak above 2000 m; in our study only *Picea engelmannii* and the two oaks were strongly restricted by altitude. Instead, the vegetation reflects the topographic moisture availability and the local successional history of the stand. We would expect altitudinal zonation to become stronger if the mountains continue to be protected from fire. If this does occur, the southwestern aspen, mixed-conifer forest will lose some of its character as fewer species come to dominate more extensively.

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