THE ALTITUDINAL DISTRIBUTION OF THE GENUS *PINUS* IN THE
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ABSTRACT

The altitudinal distributions of members of the genus *Pinus* were studied on mountain ranges in the western United States and Mexico. The community of pines on each mountainside consists of members of three major groupings — long-needed *Diploxylon* species, short-needed *Diploxylon* species and *Haploxylon* species. Long-needed *Diploxylon* species form a core sequence of altitudinally replacing species over whose distribution are superimposed sequences of members of one of the other two groups. In the northern mountains ranges *Haploxylon* species formed this second sequence while in the southern ranges short-needed *Diploxylon* species assumed this role. Some morphological characteristics of these species were examined and random associations of species pairs generated using these characteristics. The results suggest that resource partitioning between altitudinally associated species does not occur but rather that a successional situation exists with long-needed *Diploxylon* species being replaced by either *Haploxylon* in the northern ranges or short-needed *Diploxylon* species in the southern ranges.

RESUMEN

Se estudió la distribución altitudinal de miembros del género *Pinus* en las sierras del oeste de Estados Unidos de América y México. La comunidad de pinos de cada ladera consiste de miembros de tres grupos mayores. Especies *Diploxylon* de agujas largas, especies *Diploxylon* de agujas cortas y especies *Haploxylon*. Las especies *Diploxylon* de agujas largas forman un núcleo secuencial de reemplazamiento altitudinal sobre cuya distribución se superimponen secuencias de miembros de alguno de los otros grupos. En las sierras del norte, las especies *Haploxylon* forman la segunda secuencia, en tanto que en las sierras del sur las especies *Diploxylon* asumen ese papel. Algunas características morfológicas de las especies fueron examinadas y con ellas se asociaron pares de especies al azar. Los resultados indican que no existe repartición de recursos

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entre especies asociadas altitudinalmente, sino que se presenta una situación sucesional en la que las especies *Diploxylon* de agujas largas son reemplazadas por especies *Haploxylon* en las sierras del norte o por *Diploxylon* de agujas cortas en las sierras del sur.

INTRODUCTION

Storer and Usinger (1963) and Yeaton (MS) have described the community organization of the seven species of the genus *Pinus* occupying a 3 000 m altitudinal gradient on the western slopes of the Sierra Nevada in central California. Abrupt altitudinal replacements occur among species with equivalent needle numbers per fascicle such that associations of pines which form consist of a 5-needled species with a 2 and/or 3-needled species. Yeaton (MS) has shown that needle number per fascicle reflects the total leaf surface area of seedlings when associated species with different needle numbers per fascicle are compared and has hypothesized that interspecific competition between seedlings for water is the mechanism by which the community is organized. Species with different needle numbers per fascicle may co-occur extensively altitudinally by utilizing microhabitats with different seasonal moisture regimes, 5-needled species occupying relatively shadier and wetter sites than 2 and/or 3-needled associates. Species with equivalent needle numbers per fascicle are displaced over the altitudinal gradient due to their ecological (and presumably physiological) similarity with the lowest species in each sequence adapted to a long growing season and summer drought stresses and the upper species adapted to a short growing season and winter drought stresses.

My purpose in this paper is to demonstrate that the community structure observed on the western slopes of the Sierra Nevada in central California is not unique but that the patterns observed are repeated on other mountain ranges with different species of the genus *Pinus*. More specifically I want to answer the following questions:

1. Are there common types of species of *Pinus* around which members of the pine community are organized?
2. Under what conditions are species of *Pinus* added or deleted from the pine community?
3. How general is the observation that species of *Pinus* which form extensive associations, either altitudinally or latitudinally, differ greatly in their morphological characteristics?

STUDY SITES AND METHODS

The distribution of pines over altitudinal gradients was quantified on the east and west slopes of the Sierra Nevada in central California; in the mountains of southeastern Arizona; in the Sierra Madre Oriental in the state of Nuevo Leon, Mexico; on the east and southwest slopes of the Sierra Madre Occidental in the state of Durango, Mexico; and on the southeast and northwest slopes of the volcanoes, Popocatepetl and Ixtaccihuatl, in the Distrito Federal and the state of Puebla, Mexico. The specific localities and their access roads are listed in Table 1. For comparative purposes other areas were studied in qualitative fashion.

The distribution of pines over each altitudinal gradient was quantified at 77 m (250') elevational intervals (154 m intervals in the Sierra Madre Occidental) by driving over access roads. At least 50 trees with trunks 16 cm or more in diameter

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were censused on line transects 10 m in width at each elevation. As my purpose was to show only the general pattern of distribution, particularly where each species enters and drops out on the altitudinal gradient, no attempt was made to gather census data from only one slope aspect or slope angle.

After the trees were censused, only individuals of the genus *Pinus* were included in the data analysis. At each elevational site the relative percentages of each species of pine in the stand were calculated and a graph of relative percentage against altitude made. Species were grouped in three categories at each site:

1. *Diploxylon* species with long, multi-needed fascicles; taxonomically all the species in this category belong to the sections *Ponderosa*, *Montezumae* and *Pseudostrobus* (Martínez, 1948). I grouped all these species together in the initial stages of the study because of their similar appearance and relative abundances.

2. *Diploxylon* species with shorter and generally fewer needles per fascicle than associated species in category 1 above; taxonomically all species are members of the sections *Leiophylla*, *Teocote* and *Serotinos*.

Table 1. Areas in which the altitudinal distribution of pines were quantified.

Range	Slope	Latitude	Longitude	Access Road(s)
Sierra Nevada	western	38°40'N	120°10'W	Highway 88 Jackson to Carson Pass
	eastern	38°40'N	120°0'W	Highway 88 Carson Pass to Woodfords
Santa Catalina*	eastern	32°30'N	110°35'W	Mt. Lemmon Road
Sierra Madre Oriental (Cerro Potosí)	eastern	24°53'N	100°15'W	road NW of Galeana, Nuevo León
Sierra Madre Occidental	eastern	23°25'N	105°20'W	Rt. 40 from El Salto east to Durango
	south-western	24°0'N	104°50'W	road south from El Salto into valley of the Rio Acaponeta
Transverse Range	southeast	19°8'N	98°37'W	Paso de Cortés east to Cholula
(Popocatepetl and Ixtaccihuatl)	northwest	19°8'N	98°37'W	Paso de Cortés west to Amecameca

* supplemented by lower elevation samples from the Santa Rita Mountains.

3. *Haploxylon* species.

All species identifications are based upon Little (1962) supplemented by Martínez (1948). Nomenclature is after Martínez (1948) for Mexican species and Mirov (1967) for pines found outside of Mexico.

A literature survey was conducted to examine the generality of the observation that species which form extensive associations, either altitudinally or latitudinally, are different in the morphological characteristics of their needle bundles such that there are major differences in their leaf surface areas. These differences may arise from differences in the spacing of needles along branches, needle numbers per fascicle, or needle length within a bundle. Only those species co-occurring extensively altitudinally (as shown in Mirov, 1967, p. 301-303 and by personal observation) or where there is no extensive altitudinal relief latitudinally (as shown in the range maps of Critchfield and Little, 1966) are included in this analysis. Overlaps in the tails of an altitudinal or latitudinal distribution are not included. Figure 1 serves

Fig. 1. The altitudinal distribution of *Pinus* on the western slopes of the Sierra Nevada in central California. Long-needled *Diploxylon*: ● = *P. sabiniana* (3 needles per fascicle, total needle length per fascicle = 75.0 cm). ○ = *P. ponderosa* (3, 72.0 cm). x = *P. jeffreyi* (3, 72.0 cm). Short-needled *Diploxylon*: ● = *P. contorta* (2, 8.0 cm). *Haploxylon*: ● = *P. lambertiana* (5, 42.5 cm). ○ = *P. monticola* (5, 35.0 cm). x = *P. albicaulis* (5, 27.5 cm).

as an example of what is meant by extensively associated species. The altitudinal distribution of *Pinus contorta* overlaps extensively the altitudinal distribution of *P. monticola*, *P. albicaulis* and *P. jeffreyi* but not the altitudinal distribution of *P. lambertiana*, *P. ponderosa* or *P. sabiniana*. Hence *P. contorta* is involved in three pine associations on the western slopes of the Sierra Nevada. When the associations of *P. lambertiana* with *P. ponderosa* and *P. albicaulis* with *P. jeffreyi* are included, a total of five pairwise associations are found on this mountain slope. As I searched the literature (mainly *Ecology*, *Botanical Gazette*, and various publications specifically about the genus *Pinus*), I recorded all instances where more than one species of pine were listed in a study as occurring together and then checked the Mirov (1967) and Critchfield and Little (1966) references to see if these species are extensively overlapping (i.e., 80% or more) altitudinally or latitudinally. For species with a large overlap I compared the morphological characteristics of needle number per fascicle and needle length as given in Shaw (1914) for species outside of México and Martínez (1948) for Mexican species to see how different the associated species actually are.

I next calculated ratios from the measurements of total needle lengths per fascicle for associated pairs of species by dividing the larger value by the smaller. I then compared the relative frequencies of these ratios with a large sample (700 plus) of randomly generated ratios using a Kolmogorov-Smirnov two sample test (Siegel, 1956). The random ratios were generated by computer using as measurements for total needle length per fascicle the same values as those contained in the data for observed associations of species. Since no species by definition may be associated with itself, only ratios for different species were included in the randomly generated associations. A similar random analysis could not be constructed for species replacing each other altitudinally since needle lengths and needle number per fascicle of different species may vary as a result of the large differences in climate that occur over long altitudinal gradients.

RESULTS

The altitudinal distributions of species of *Pinus* over five different mountain ranges in the western United States of America and México are shown in Figures 1-8. On all the mountain slopes studied the communities of pines are composed of at least one member of each of the three groups. However, the number of species and their relative abundances vary from slope to slope. The community of pines is organized around the members of the long-needled *Diploxylon* group. As on the western slopes of the Sierra Nevada, altitudinal sequences of species with equivalent needle numbers per fascicle occur (Figs. 1, 4, 5, 7, and 8). These sequences are predominantly found among the long-needled *Diploxylon* species. Species in this group show the greatest relative abundances in each range particularly on the slopes which receive more rainfall and do not have rain-shadow deserts or arid zones at their bases (Figs. 1, 4, 6). Where such arid conditions are present short-needled *Diploxylon* species increase in their relative abundances, usually at the lower elevations (Figs. 2, 3, 5, 7, and 8). *Haploxylon* pines form altitudinal sequences predominantly in the northern ranges and in the Sierra Madre Oriental (Figs. 1, 3, 6). Further south these sequences of *Haploxylon* species are lost and extensive sequences of short-needled *Diploxylon* species occur (Figs. 4, 5, 7, 8).

Patterns in needle number per fascicle and total needle length per fascicle also occur. In those ranges with arid zones at their bases the lower species within the altitudinally replacing sequence of pines may have a lower number of needles per fascicle (Figs. 3, 5, 6). Within each group of taxonomically related and altitudinally replacing sequences of pines with equivalent needle number per fascicle, there is a decrease in the total needle length per fascicle (Figs. 1, 4, 7). Long-needled *Diploxylon* species generally have the longest total needle lengths per fascicle and the species with the highest value for this measurement is found at intermediate elevations in comparison with the total range of *Pinus* distributions over a mountain-side (Figs. 3, 4, 5, 7, 8). Finally, if species with relatively similar total needle lengths per fascicle are graphed together, similar patterns of abrupt replacements occur indicating that members of one taxonomic group may substitute for members of another group as ecological replacements (Figs. 2, 3, 6, 7, 8). The majority of these ecological replacements occur between members of the short-needled *Diploxylon* and the *Haploxylon* groups.

Fig. 2. The altitudinal distribution of *Pinus* on the eastern slopes of the Sierra Nevada in central California. Long-needled *Diploxylon*: ● = *P. jeffreyi* (3, 72.0 cm). Short-needled *Diploxylon*: ● = *P. contorta* (2, 8.0 cm). *Haploxylon*: ● = *P. monophylla* (1, 4.0 cm). ○ = *P. monticola* (5, 27.5 cm).

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Fig. 3. The altitudinal distribution of *Pinus* on the mountains of southeastern Arizona. Long-needled *Diploxylon*: $\bullet$ = *P. engelmanni* (3, 100.5 cm). $\circ$ = *P. ponderosa arizonica* (5, 125.0 cm). $\times$ = *P. ponderosa scopularum* (3, 72.0 cm). Short-needled *Diploxylon*: $\bullet$ = *P. leiophylla* (3, 33.0 cm). *Haploxylon*: $\bullet$ = *P. cembroides edulis* (2, 8.0 cm). $\circ$ = *P. strobiformis* (5, 30.0 cm).

Fig. 4. The altitudinal distribution of *Pinus* on the western slope of the Sierra Madre Occidental in Durango, Mexico. Long-needled *Diploxylon*: $\bullet$ = *P. douglasiana* (5, 145.0 cm). $\circ$ = *P. engelmanni blancoi* (5, 167.5 cm). $\times$ = *P. durangensis* (5, 120.0 cm). Δ = *P. lutea* (5, 35.0 cm). Short-needled *Diploxylon*: $\bullet$ = *P. oocarpa* (5, 92.5 cm). $\circ$ = *P. lumboltzii* (3, 72.0 cm). $\times$ = *P. teocote* (3, 45.0 cm). Δ = *P. leiophylla* (5, 55.0 cm). Haploxylon: $\bullet$ = *P. ayacahuite* (5, 75.0 cm).

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Fig. 5. The altitudinal distribution of *Pinus* on the eastern slopes of the Sierra Madre Occidental in Durango, Mexico. Long-needled *Diploxylon*: ● = *P. engelmanni* (3, 100.5 cm). ○ = *P. engelmanni blancoi* (5, 167.5 cm). x = *P. lutea* (5, 35.0 cm). Short-needled *Diploxylon*: ● = *P. chihuahuana* (3, 33.0 cm) ○ = *P. leiophylla* (5, 55.0 cm). *Haploxylon*: ● = *P. cembroides* (3, 12.0 cm)

Fig. 6. The altitudinal distribution of *Pinus* on the western slope of the Sierra Madre Oriental in Nuevo Leon, Mexico. Long-needled *Diploxylon*: ● = *P. arizonica stormae* (3, 75.0 cm). ○ = *P. montezumae* (5, 87.5 cm). x = *P. rudis* (5, 66.2 cm). Short-needled *Diploxylon*: ● = *P. greggii* (3, 32.2 cm). *Haploxyylon*: ● = *P. cembroides* (3, 12.0 cm). ○ = *P. strobiformis* (5, 30.0 cm). x = *P. culminicola* (5, 24.0 cm).

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Fig. 7. The altitudinal distribution of *Pinus* on the western slopes of Popocatepetl and Ixtaccihuatl, Mexico. Long-needled *Diploxylon*: ● = *P. montezumae* (5, 87.5 cm). ○ = *P. pseudostrobus* (5, 140.0 cm). x = *P. radiis* (5, 66.2 cm). Δ = *P. hartwegii* (5, 66.2 cm). Short-needled *Diploxylon*: ● = *P. leiophylla* (5, 55.0 cm). ○ = *P. lawsoni* (3, 54.0 cm). *Haploxylon*: ● = *P. ayacahuite* (5, 75.0 cm). ----- indicates extensive agricultural development.

Fig. 8. The altitudinal distribution of *Pinus* on the eastern slopes of Popocatepetl and Ixtaccihuatl, Mexico. Long-needled *Diploxylon*: ● = *P. michoacana cornuta* (5, 167.5 cm). ○ = *P. rudis* (5, 66.2 cm). x = *P. hartwegii* (5, 66.2 cm). Short-needled *Diploxylon*: ● = *P. leiophylla* (5, 55.0 cm). ○ = *P. lawsoni* (3, 54.0 cm). *Haploxylon*: ● = *P. ayacahuite* (5, 75.0 cm).----- indicates extensive agricultural development.

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The number of species on any mountain slope is relatively constant, ranging from a low of four species on the dry eastern slopes of the Sierra Nevada to a maximum of nine species on the western slopes of the Sierra Madre Occidental. The number of species within an altitudinally replacing sequence of pines increases from a maximum of three species in the north to a maximum of four species in the south (compare Figs. 1, 3 with Figs. 4, 7). Within each range drier slopes have fewer species of *Pinus* than do the wetter slopes (compare Fig. 1 with 2, 4 with 5, 7 with 8). Concurrent with these observations the largest values for total needle lengths per fascicle increase towards the south.

The associations formed by pines are morphologically different from one another with respect to the measurements of needle number per fascicle and needle length. Of 85 pairwise associations gleaned from the literature, only 8 show values less than 1.2: 1 for the ratio of total needle lengths of associated pairs of species. In general, species are different from one another by a factor of 1.2 or more (Fig. 9). These differences, however, can be generated by random processes. No significant difference is found between the ratios calculated from the literature for associations of pines and those obtained from a random generation of associations (Kolmogorov-Smirnov two sample test, $D = 0.088$, not significant).

Fig. 9. The cumulative frequency distribution for ratios of total needle length per fascicle for naturally occurring and randomly generated pairs of associated pines. Natural associations ———. Random associations. ———

DISCUSSION

Associations of pines occurring over elevational gradients are organized around an altitudinally replacing sequence of long-needled *Diploxylon* species. In each mountain range long-needled *Diploxylon* pines make up the longest sequences of altitudinal replacements and are generally more abundant than their short-needled *Diploxylon* and *Haploxylon* associates. These long-needled *Diploxylon* pines may form the structural framework of the community of pines on a mountainside as a result of their successional status. In general, members of the genus *Pinus*, may be considered as early successional species (Pessin, 1933; Grant, 1934; Turner, 1935; Billings, 1938; Stabelin, 1943; Potzger and Potzger, 1948). In situations where the disturbed sites are described as having long growing seasons and ample moisture, the long-needled *Diploxylon* species colonize and grow rapidly (e. g. Wenger and Trousdell, 1958 for *P. taeda*). In situations where the disturbed sites are described as being of "poor" quality, either due to lack of moisture, nutrients, or time for a long growing season, the short-needled *Diploxylon* species colonize and grow rapidly (e.g. Brown and Curtis, 1952 for *P. banksiana*). Little information is available for the successional status of *Haploxylon* species. Where more than one species of *Pinus* are involved in a succession, the *Haploxylon* pine replaces the *Diploxylon* species (Huberman, 1935, Braun 1950). Studies of the reproductive ecology of *Haploxylon* and *Diploxylon* pines also suggest that the latter occurs later in succession (Yeaton, 1978a). In general, *Diploxylon* species associated altitudinally with *Haploxylon* pines occupy more open sites and are represented by many more individuals in the smaller (younger) size classes (Whittaker and Niering, 1965; Yeaton, unpublished data). The growth rate of seedlings of *Haploxylon* pines is slower than that of their *Diploxylon* associates (Yeaton, unpublished data). The combination of more individuals of long-needled *Diploxylon* species occupying open sites with many rapidly growing individuals serves to organize the altitudinal associations of pines found on each mountainside by providing shadier conditions required for establishment and growth of later successional species.

Short-needled *Diploxylon* and *Haploxylon* species function in one of two roles on these mountainsides. Some of these species have their altitudinal distributions superimposed over those of the long-needled *Diploxylon* species while other species become abundant at elevations where conditions are not favorable for the successful establishment and growth of long-needled *Diploxylon* species. Species whose distributions are superimposed over those of long-needled *Diploxylon* pines generally establish later in succession where conditions are shadier and potential rates of evapotranspiration are lower. In the northern mountain ranges studied and at higher elevations in the southern ranges, these are usually *Haploxylon* pines other than members of the group *Cembroides*. At intermediate elevations in the southern mountain ranges short-needled *Diploxylon* species appear to fill the ecological role of *Haploxylon* pines. Little is known about the ecology of these short-needled *Diploxylon* species in Mexico, particularly with respect to their requirements for establishment, subsequent growth and reproduction. As seedlings they generally have larger leaf surface areas than their long-needled *Diploxylon* associates of equivalent stem diameter (Yeaton, unpublished data for the pines of the southeastern slopes of the Sierra Madre Occidental in Durango, México). This pattern is similar to that found for *Haploxylon* and *Diploxylon* associates on the western slopes of the Sierra Nevada in California (Yeaton, MS) and suggests that they may require access to greater

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amounts of soil moisture than their long-needed *Diploxylon* associates. The increased leaf surface area in each case arises as a result of increased branching in seedlings of *Haploxylon* pines and short-needed *Diploxylon* species found in México.

In situations in which conditions are not favorable for the establishment of long-needed *Diploxylon* species, *Haploxylon* or short-needed *Diploxylon* pines achieve numerical dominance. These sites are usually characterized by low moisture availability and high potential rates of evapotranspiration. Members of the group *Cembroides* were isolated during interglacial periods in areas experiencing severe drought and developed adaptations to this stress, such as reduced number of needles per fascicle, decreased needle length and reduction in stomata numbers (Mirov, 1967). Despite these adaptations, seedlings of *Cembroides* species still require shaded moist sites for successful establishment and participate in a successional sequence with other plant species (McClay and Yeaton, in prep.). To a lesser extent short-needed *Diploxylon* species dominate moisture-stressed sites in this study. For examples, *Pinus contorta* occupies high elevational sites on the steep east-facing slopes of the Sierra Nevada and *P. lawsoni* dominates the low and relatively arid elevations of the high volcanoes in southern México.

Due to lack of information about the biology of short-needed *Diploxylon* species in México, it is difficult to state why these species replace *Haploxylon* pines at intermediate elevations. *Haploxylon* pines are slow growing and are found in shady sites with low rates of evapotranspiration. In southern México the common *Haploxylon* pine *P. ayacahuite* is found either at very high elevations on north-facing slopes or at lower elevations in the bottoms of cold-air drainage channels (pers. obs.). Perhaps slow growth rates of *Haploxylon* species contribute to their replacement at intermediate elevations by competition from faster growing short-needed *Diploxylon* species. Also these southern forests are composed predominantly of pines and oaks, while the number of other coniferous species are much reduced. Other coniferous species representing the genera *Abies*, *Cupressus*, *Libocedrus*, *Picea*, *Pseudotsuga* and *Tsuga* are much more prevalent in the northern mountain ranges and provide the dense shade conditions in which *Haploxylon* pines appear to be more successful. In contrast the mountain ranges of México are depauperate in species of these genera, and the pines usually intermingle with species of *Quercus* which provide more open conditions necessary for the establishment of short-needed *Diploxylon* species.

Several patterns of total needle length per fascicle are delineated by the distribution of species. These differences represent the result of adaptation to different climatic regimes. Over altitudinal gradients climatic conditions vary. Rainfall increases while temperature decreases with increasing altitude. At very high elevations, plants experience short growing seasons as a result of seasonally cold temperatures and winter drought stress. At lower elevations, plants experience summer drought stresses which also tend to shorten the length of the growing season. The best situation for rainfall and temperature appears to be at intermediate elevations. The climatic characteristics of these elevations affect the total needle lengths per fascicle. At very low elevations the number of needles in a fascicle are reduced. *Pinus engelmannii* has three needles per fascicle at low elevations on the eastern slopes of the Sierra Madre Occidental in Durango, México and five needles per fascicle at higher elevations along the same gradient. The longest total needle lengths per fascicle are found in those species occupying intermediate elevations. These values for species occupying higher elevations decrease. Likewise a similar pattern may be observed along a latitudinal gradient. Generally both rainfall and

length of growing season increase to the south (Sanders, 1921; Looks, 1951). Concurrently, the total needle lengths per fascicle increase for species occurring farther to the south. Yeaton (1978a) has suggested that total needle length per fascicle reflects the leaf surface area over which photosynthesis may occur and over which water may be lost by transpiration. Additionally, needle lengths may be reduced to prevent needle loss due to rime ice formation. The formation of rime ice increases with increasing elevation (Sprugel, 1976).

Finally ecologists are concerned with two situations of apparent co-existence of species (Grime, 1979). One is the traditional view of interspecific competition leading to resource partitioning and co-existence (*e. g.* Cody, 1974). The other concept involves a successional situation where two species appear to co-exist but actually are replacing one another over very long periods of time on a site-by-site basis (Forcier 1975, Yeaton 1978b). Hutchinson (1959) and many other authors have suggested that a minimum difference of at least 1.2: 1 must occur in those morphological characteristics which involve resource utilization for co-existence through partitioning of a limited resource. The fact that associations of pines may attain these values by chance alone would seem to suggest that these species are undergoing a long term successional replacement rather than resource partitioning. The observed differences among seedlings in total needle lengths per fascicle between early successional pines *i.e.*, long-needed *Diploxylon* species) and later successional species *i.e.* *Haploxylon* pines) reflects adaptation first to open sites in which rates of evapotranspiration are high and, second, subsequent replacement of these pines by species adapted to shadier sites where evapotranspiration is reduced. Investigations into these successional patterns are being conducted among the associated pines of the western slope of the Sierra Nevada.

ACKNOWLEDGEMENTS

I wish to thank the American Philosophical Society for its generous support of this research. Additional thanks are due to R. Karban, R. Ray, R.W. Yeaton and L.C. Yeaton for assistance in the field and to the Stampfer and González families for their hospitality while in México.

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