

SEEDLING CHARACTERISTICS AND ELEVATIONAL DISTRIBUTIONS OF PINES (PINACEAE) IN THE SIERRA NEVADA OF CENTRAL CALIFORNIA: A HYPOTHESIS

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ABSTRACT

Seven species of the genus *Pinus* occupy a 3000-m elevational gradient on the western slope of the Sierra Nevada in central California. Three species of 3-needled pines replace each other abruptly over the mountainsides as do three species of 5-needled pines. The seventh species, a 2-needled pine, is found on the upper half of the mountainsides. Observed associations of pines on these slopes consist of a 2- or 3-needled species (or both) with a 5-needled species. A hypothesis is presented that interspecific competition between seedlings, ultimately for water, has led to the distributional patterns observed. This hypothesis is examined in terms of the morphological characteristics of seedlings and their needles that reflect their relative usage of water.

Storer and Usinger (1963) portray seven species of the genus *Pinus* forming a guild over a 3000-m elevational gradient on the western slope of the Sierra Nevada in central California. The distributional pattern of these seven species as described is striking. Three species of 3-needled pines replace each other sequentially over the elevational gradient, as do three species of 5-needled pines. When one species disappears, another appears with the same number of needles per fascicle. The change with elevation is portrayed as abrupt with little or no overlap occurring between species with similar needle numbers. Also, a 2-needled species of pine is found over the upper half of the elevational gradient. Up to about 915 m there is only a 3-needled species (*P. sabiniana*). From 915 m to timberline several associations of pines are found. Each of these higher-elevation groups is composed of a 2-needled or a 3-needled species, or both, associated with a 5-needled pine. At no place on the mountainside are two 3-needled or two 5-needled pines described as occurring together. If the distribution of pines depicted by Storer and Usinger is accurate, the pattern of needle numbers per fascicle requires explanation. I suggest that this distributional pattern represents an example of the competitive exclusion principle in which interspecific competition has led to the elevational separation of species with similar needle number. If so, there must be ecological differences between pine species with different needle numbers because various combinations of these species do occur.

In this paper I demonstrate that the distributional patterns described by Storer and Usinger are accurate. Secondly, I present a hypothesis to explain the associations of pines that are found on the western slopes

of the central Sierra Nevada. Finally, I attempt to examine this hypothesis by a comparison of some of the morphological characteristics of species that either overlap extensively or replace each other abruptly over the elevational gradient.

ELEVATIONAL DISTRIBUTIONS

The elevational distribution of pines on transects of the western slopes of the Sierra Nevada in central California were determined by counting 100 individuals of the genus at stations separated from one another by 77 m altitude along State Highways 4, 88, and 108 (38°16–34'N, 120°0–55'W; Amador, Calaveras, Alpine, and Tuolumne Counties). Trees taller than 15 m were counted on 10-m-wide strips running along the contour of southeastern facing slopes at each station. Sampling was limited to southeastern slope aspects to reduce the variability in species abundance resulting from the different microclimates that exist at the same elevation but on different slope aspects. Only species of *Pinus* were counted and their relative proportions calculated at each station and plotted (Fig. 1a, b, c).

In this area of the Sierra Nevada only seven species of *Pinus* occur: four members of the subgenus *Diploxylon* and three species of the subgenus *Haploxylon*. *Pinus sabiniana* Dougl. (group *Macrocarpa*), *P. ponderosa* Laws., and *P. jeffreyi* Grev. and Balf. (the latter two species members of the group *Australis*) compose the sequence of 3-neededled *Diploxylon* pines while *P. contorta* Dougl. (group *Insignis*) is the 2-neededled *Diploxylon* species. *Pinus lambertiana* Dougl., *P. monticola* Dougl. (both members of the group *Strobi*) and *P. albicaulis* Engelm. (group *Cembrae*) make up the 5-neededled sequence of *Haploxylon* pines (taxa follow Shaw, 1914 and Mirov, 1967). For species of pines with three needles per fascicle abrupt replacements occur at approximately 840 m and 1740 m in this region. The latter replacement involves *P. ponderosa* and *P. jeffreyi*, which hybridize at the interfaces of their distributions (Mirov, 1967). In the region studied the zone of possible hybrids is small (approximately 25 m in elevational range) and falls between sampling sites. Identifications of canopy individuals of these two species are based upon gross characteristics of their barks and cones. For 5-neededled species abrupt replacements occur at approximately 1980 m and 2630 m (Fig. 1). For the four possible pairs of replacing species along the mountainsides, in only one instance do two species of *Pinus* with the same needle number occur together in the same sample. This overlap is for the high elevation, low relative abundance situation in which *P. albicaulis* replaces *P. monticola*. Thus the distributional pattern described by Storer and Usinger (1963) is verified.

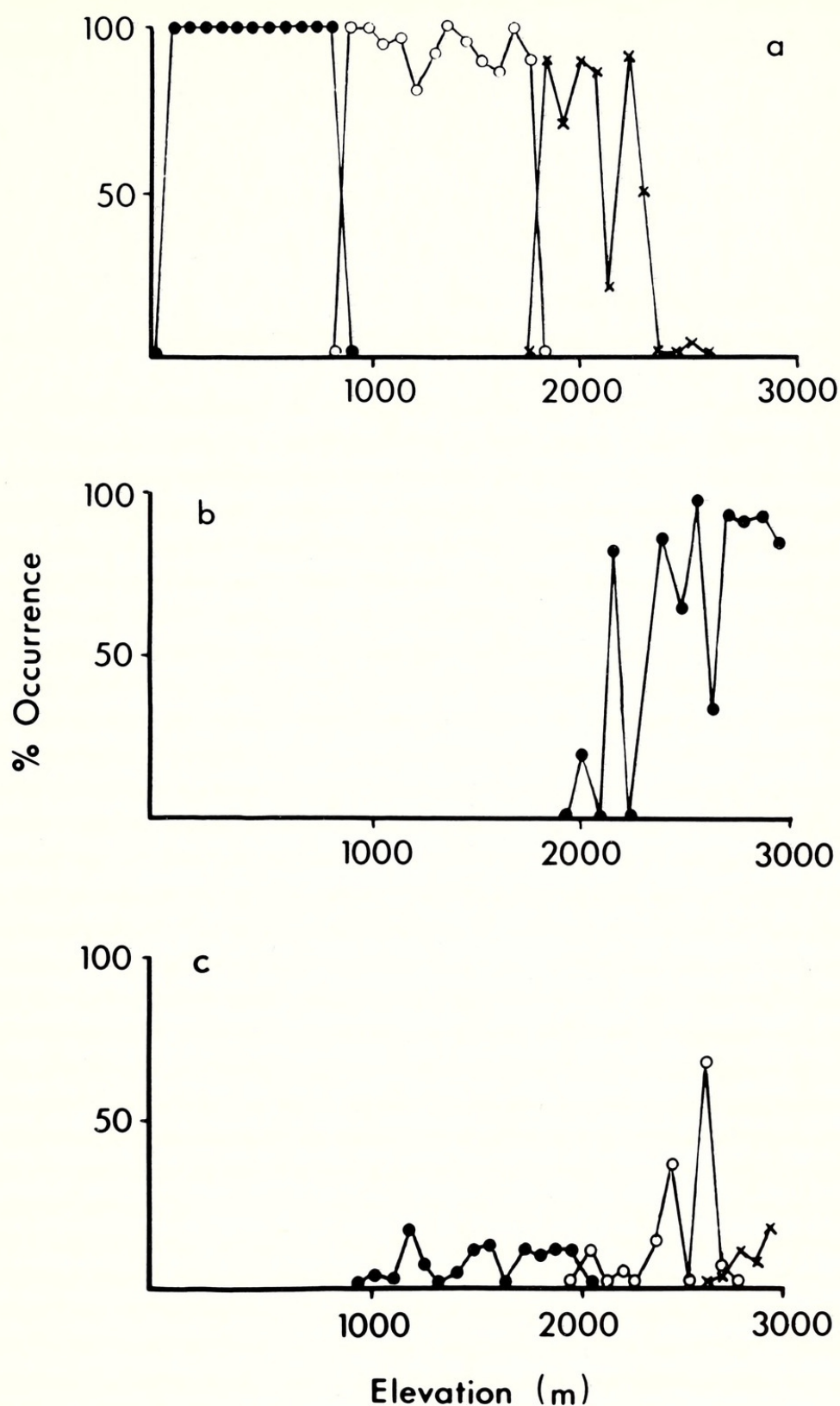


FIG 1. Percent occurrence of *Pinus* only for the seven species found on southeastern slope aspects on the western slope of the Sierra Nevada in central California. a. 3-needled pines. b. 2-needled pine. c. 5-needled pines.

THE HYPOTHESIS

A very precise pattern of replacements is observed among the larger individuals suggesting that their elevational distributions are determined by interspecific competition between seedlings and younger age classes. Seedlings of *Pinus* with different needle numbers per fascicle that are associated elevationally are often found growing together in clumps along with other species of conifers. Likewise, I have found seedlings of species with the same needle number associated in clumps at elevations at which one species replaces another abruptly. Hence the possibility for intense competition exists between seedlings growing in such close proximity within these clumps. Water would seem to be the important limiting factor in this relatively open-canopied community. It has been suggested that water is critical in the early life of pine seedlings (Pearson, 1930). Seedlings are dependent upon the moisture in the upper soil layers, where surface evaporation and transpiration rapidly deplete the available soil moisture (Stone and Jenkinson, 1971). For example, young ponderosa pines suffer intense intraspecific competition for available soil moisture (Weaver, 1961). Further, the smallest individuals of *Pinus* suffer more from decreases in moisture levels than do larger individuals (Turner, 1956; Weaver, 1961; Yeaton, 1978). Seedlings are probably most severely affected by environmental fluctuations because they are small and therefore do not have the benefit of the stabilizing effect provided by reserves accrued from growth in previous years. Hence, adaptive responses in water usage or habitat usage are most likely to be reflected in seedlings (Ledig et al., 1977).

For associated species, clumps of seedlings may be located upon soil patches with varying moisture levels over the course of the growing season. Species of *Pinus* with adaptations to reduce the effects of moisture stress would be expected to outcompete seedlings of species without these adaptations on patches that are relatively dry over the growing season. Adaptations to reduce the effects of drought might appear as a reduction in total needle surface area over which water may be lost, a decrease in the number of stomates to reduce transpirational water loss, or structural differences in needle anatomy to reduce epidermal water loss. In contrast, species of *Pinus* successful in competition on wetter patches may have greater total needle surface areas for increased photosynthetic surface area, increased numbers of stomates for higher rates of gas exchange during photosynthesis, and a reduced necessity for a specialized needle anatomy to reduce epidermal water loss. Their success on these wetter patches may be the result of an increased growth rate and their ability to store reserves to survive periods in which the characteristics of the patch are stressful. Coexistence of species at any one elevation may be maintained by use of patches with differing seasonal moisture regimes ranging from dry to relatively wet.

Species with the same needle number that replace one another abruptly elevationally are also subjected to a wide range of moisture availability. Species occurring at low elevations are faced with a hot dry summer while the species at the highest elevations are faced with the problem of a short growing season and a winter drought. Presumably the central species in each elevational sequence occupies the best available range of conditions for moisture and length of growing season and may outcompete the species above and below it as a result of increased growth rates (Yeaton et al., 1980).

NEEDLE NUMBER AND TOTAL NEEDLE LENGTH IN SEEDLINGS

The hypothesis suggests that 2-needled pines should occupy drier sites than associated 3- and 5-needled species and that 3-needled pines should use drier sites than their 5-needled associates because the total needle length per fascicle will increase from 3-needled to 5-needled fascicles. It also suggests that species with the same needle number that replace each other are more similar to one another than are species that form associations. However, these relationships may be complicated when the whole individual is considered due to differences in needle lengths and number of fascicles. The effect of these differences can be studied by measuring the total needle lengths in all fascicles of seedlings of each species and determining if the relationship observed for fascicles holds when the whole seedling is considered.

Needle width may complicate the needle number/needle length relationship. Haller (1962) has stated that needle width is unimportant in comparisons of species with different needle numbers and any width differences would not be great enough to affect these measurements. My analysis of needle widths agrees with Haller's statement. The surface area of a fascicle is approximately $10.28rl$ for a 2-needled species, $12.28rl$ for a 3-needled species and $16.28rl$ for a 5-needled species (where "r" is the radius and "l" is the length of the fascicle). These values result from viewing the fascicle as circular in cross-section. For all fascicles the outer surface area of the fascicle is $2\pi rl$. To this must be added $4rl$, $6rl$, or $10rl$ for the inner needle surfaces for 2-, 3-, and 5-needled species. Treating length of fascicle as a constant, to attain the surface area of a 5-needled species, a 3-needled associate must be 33 percent greater and a 2-needled species 58 percent greater in needle width. Similarly, a 2-needled species must be 19 percent greater in needle width to attain the same surface area as a 3-needled associate. Table 1 shows average measurements of needle width for specimens of the seven species of pines in this study. The measurements of needle width are very similar for all seven species.

The pair of associated species with the greatest difference in needle width is that of the 3-needled *Pinus jeffreyi* with the 5-needled *P. monticola* (Table 2). For these species the difference is 33 percent or, in other words, the surface areas per mm of needle length of fascicles

TABLE 1. ELEVATIONAL RANGE AND MEAN NEEDLE WIDTH (\pm S.E.) FOR THE SEVEN SPECIES OF *Pinus* ON THE WESTERN SLOPES OF THE SIERRA NEVADA. N = 10 for needle-width measurements.

Species	Needles per fascicle	Elevational range (m)	Needle width (mm)
<i>Pinus sabiniana</i>	3	100–915	0.95 ± 0.03
<i>Pinus ponderosa</i>	3	915–1740	0.88 ± 0.04
<i>Pinus jeffreyi</i>	3	1740–2670	0.81 ± 0.04
<i>Pinus lambertiana</i>	5	930–1980	0.70 ± 0.03
<i>Pinus monticola</i>	5	1980–2630	0.61 ± 0.02
<i>Pinus albicaulis</i>	5	2630–3000	0.84 ± 0.03
<i>Pinus contorta</i>	2	1930–3000	0.72 ± 0.03

are equal. For all other pairs of associated species the difference in needle width is smaller than that required for this parameter to have a significant effect on the surface area of species with different numbers of needles per fascicle. Hence, needle width is not a factor in the relationship of needle number per fascicle for associated and elevationally replacing species.

To study the effects of needle length, branching patterns, and spacing of needles along branches, the total needle lengths for seedlings of varying stem diameters were measured. Seedlings of the seven species of pines were found in areas adjacent to California State Highways 4 (through Ebbetts Pass), 88 (through Carson Pass) and 108 (through Sonora Pass). Seedlings were sampled in the centers of the distribution of each respective species. At least 25 seedlings of each species were counted. Seedlings were selected whose stems ranged from 0.5 to 30 mm in diameter as measured by calipers at a point 2.5 cm above the ground and whose diameters were fairly uniformly spaced from one another over this range. Individuals were chosen that had no apparent

TABLE 2. PERCENTAGE DIFFERENCES IN NEEDLE WIDTHS FOR ELEVATIONALLY ASSOCIATED PAIRS OF PINES. Percent difference needed for needle width to be important for measurement of needle surface area for associated species of *Pinus* calculated as (needle width of species with fewer needles per fascicle—needle width of associated species)/(needle width of species with greater number of needles per fascicle) \times 100. Negative percent indicates that needle width is greater for species with more needles per fascicle.

Pairs (needles per fascicle)	Expected % difference	Observed % difference
<i>P. albicaulis</i> (5)— <i>P. contorta</i> (2)	58	–14
<i>P. monticola</i> (5)— <i>P. contorta</i> (2)	58	18
<i>P. jeffreyi</i> (3)— <i>P. contorta</i> (2)	19	–11
<i>P. monticola</i> (5)— <i>P. jeffreyi</i> (3)	33	33
<i>P. lambertiana</i> (5)— <i>P. ponderosa</i> (3)	33	26

TABLE 3. THE RELATIONSHIP BETWEEN SEEDLING STEM DIAMETER AND TOTAL NEEDLE LENGTH FOR SEVEN SPECIES OF THE GENUS *Pinus* OCCURRING ON THE WESTERN SLOPES OF THE SIERRA NEVADA IN CENTRAL CALIFORNIA. Data fit a power curve, $y = cx^E$ where y = total needle length, c = a constant, x = seedling stem diameter, and E = exponent. " r^2 " is the coefficient of determination.

Species	Number sampled	Constant	Exponent	r^2
<i>P. sabiniana</i>	25	819	1.83	0.90
<i>P. ponderosa</i>	25	1298	1.76	0.98
<i>P. jeffreyi</i>	27	1187	1.69	0.90
<i>P. lambertiana</i>	25	1656	1.86	0.96
<i>P. monticola</i>	25	679	2.08	0.90
<i>P. albicaulis</i>	25	526	2.16	0.96
<i>P. contorta</i>	25	638	1.82	0.96

damage from grazing herbivores. For each seedling the diameter of each branch off the main stem was measured and all the fascicles of needles on that branch and its sub-branches counted. The length of a typical fascicle of needles on each branch was measured. This needle length was multiplied by the number of needles in the fascicle and that product multiplied by the number of fascicles counted on the branch. The total needle length for each branch on the seedling was then summed. A similar procedure was employed for fascicles growing out of the main stem between branches and these were added to the sum of the branches to give a total needle length per seedling.

The relationship between total needle length per seedling and the diameter of that seedling is best fitted by a power curve. For each species of pine studied, the total needle length per seedling is equal to

TABLE 4. PAIRWISE COMPARISONS OF ASSOCIATED PINE SPECIES AND ALTITUDINAL REPLACEMENTS. Values in parentheses are mean ratios of the square root of total needle length to stem diameter. Comparisons of the mean ratios were made using the median test.

Species pairs	χ^2	P
Altitudinal Replacements		
<i>P. sabiniana</i> (24.7)— <i>P. ponderosa</i> (28.1)	2.88	$0.05 < p < 0.10$
<i>P. ponderosa</i> (28.1)— <i>P. jeffreyi</i> (25.3)	2.77	$0.05 < p < 0.10$
<i>P. lambertiana</i> (35.9)— <i>P. monticola</i> (29.4)	5.12	$p < 0.05$
<i>P. monticola</i> (29.4)— <i>P. albicaulis</i> (27.7)	0	$p \cong 1.00$
Altitudinal Associates		
<i>P. contorta</i> (21.0)— <i>P. albicaulis</i> (27.7)	15.68	$p < 0.001$
<i>P. contorta</i> (21.0)— <i>P. jeffreyi</i> (25.3)	7.70	$p < 0.01$
<i>P. contorta</i> (21.0)— <i>P. monticola</i> (29.4)	11.52	$p < 0.001$
<i>P. jeffreyi</i> (25.3)— <i>P. monticola</i> (29.4)	7.70	$p < 0.01$
<i>P. ponderosa</i> (28.1)— <i>P. lambertiana</i> (35.9)	8.00	$p < 0.01$

a constant value times the seedling diameter approximately squared. All species fit this model well with correlation coefficients (r) of 0.95 or higher (Table 3).

These data can be used to answer several questions about the species that are either associated or replacing along the western slopes of the Sierra Nevada. Are species that are associated elevationally significantly different from one another in their total needle lengths? Are associated species different such that 5-needled pines have greater total needle lengths than their 3- or 2-needled associates? What relationships exist between total needle lengths for seedlings of species that replace abruptly over the elevational gradient? Are they more similar to one another than seedlings of species that form associations?

To answer these questions the ratio of the square root of total needle length to stem diameter was calculated for each seedling measured in the study. This ratio was used because the total needle length per seedling is approximately equal to the product of stem diameter squared and a species-specific constant (Table 3). Reduction of the data in this fashion reveals the sample value of this constant for each individual measured. Comparisons of these converted data were made using a Median test (Siegel, 1956) for sets of seedlings of elevationally associated or replacing pairs of species. All ratios of square root of total needle length to stem diameter for each species of 3- and 5-needled pine compared with the species replacing them higher on the mountainside have chi-square values with probabilities of occurrence greater than 0.01. Conversely, pairwise comparisons between pines that co-occur on the mountainside all have chi-square values whose probabilities of occurrence are less than 0.01 (Table 4). Furthermore, 5-needled pines attain significantly greater total needle lengths per individual than do their 2- or 3-needled counterparts. Thus, the species that replace one another elevationally have less different total needle lengths than do associated species.

The pattern of needle numbers in adult trees is a reflection of the total needle surface areas of their seedlings. This pattern for seedlings, in which species similar in total needle length per seedling replace one another elevationally and in which species dissimilar in total needle length overlap elevationally is consistent with the hypothesis that water availability for seedlings determines which species can occur together.

DISCUSSION

The data reported here are consistent with the hypothesis that competition between seedlings for soil moisture has led to the distributional patterns observed for the seven species of *Pinus* occupying the western slopes of the Sierra Nevada. Species that are morphologically similar to one another in characters reflecting water use are displaced over

the gradient, while species dissimilar in these characteristics overlap extensively over the same gradient. Additional evidence from the literature supports the hypothesis. Leaf anatomy is one area of possible evidence although morphological differences in their functional sense may not be clearly understood. Harlow (1947) has described the cross-sectional leaf anatomy for most species of North American pines. All *Diploxylon* (2- and 3-needled) species included in this study have well developed dermal regions, particularly in the hypodermal layer. The hypodermal layer is described as either biformed or multiformed with thick-walled cells. In contrast the dermal regions of the three species of *Haploxylon* (5-needled) pines are less well developed with no thickening of the hypodermal cell walls. Thickened cell walls in the dermal region of the *Diploxylon* species may be indicative of greater drought stresses. For example, those *Haploxylon* species of the group *Paracembra* (*Pinus monophylla* and *P. edulis*) occupying habitats at the edge of desert regions in the southwestern United States where moisture stress is high are described by Harlow (1947) as having a hypodermal layer two to four cells thick and the cells with thickened cell walls. It may be that the thickened cell walls and more complex development of the hypodermal layers in the *Diploxylon* species reflect adaptation to moisture stress to reduce epidermal water loss.

A second source of information on the relative water use of associated *Pinus* species is data for photosynthetic and transpiration rates. Unfortunately there is very little direct evidence on rates for associated species of pines. Miscellaneous evidence does exist for two sets of associated species, *P. ponderosa* and *P. lambertiana* in the Sierra Nevada of California and *P. banksiana*, *P. resinosa*, and *P. strobus* in the Great Lakes region of the United States and Canada. Snow (1924), studying *Pinus ponderosa* (3-needled) and *P. lambertiana* (5-needled), reported that shade was necessary for survivorship of *P. lambertiana* seedlings. In contrast, shade aided but was not necessary for survivorship of *P. ponderosa* seedlings. He concluded that *P. ponderosa* was more drought resistant than *P. lambertiana*. A similar observation about the drought resistance of *P. lambertiana* and *P. ponderosa* was made by Pharis (1966) with a suggestion that associations of these two species optimize water usage by tapping different subsurface zones of the soil.

More extensive work has been done with *Pinus strobus* and its 2- and 3-needled associates. Belyea (1925) reported that *P. strobus* (5-needled) is more susceptible to wind desiccation than its associate *P. resinosa* (long, 2-needled) and attributed the difference to the greater leaf surface area represented by the 5-needled species. Similar studies contrasting *P. strobus* with *P. resinosa*, *P. banksiana* (short, 2-needled), or *P. rigida* (3-needled) always place *P. strobus* on wetter sites than its 2- or 3-needled associates (Hutchinson, 1918; Cook et al., 1952). In a comparison of water loss in three of these species that

occur together in the vicinity of the Great Lakes, Walter and Kozlowski (1964) rank water loss as *P. strobus* > *P. resinosa* > *P. banksiana*. Brown and Curtis (1952), in a gradient analysis of the upland conifer-hardwood forests of northern Wisconsin, ranked these three species relative to the moisture-holding capacity of the soils. *P. banksiana* occurs on dry soils, *P. resinosa* on intermediate soils, and *P. strobus* on soils with greater moisture-holding capacity. While *P. resinosa* and *P. banksiana* are both 2-needled pines, *P. resinosa* has needles four times as long as *P. banksiana*.

Other authors have reported similar patterns in water usage for other pairs of associated species differing in needle number per fascicle [Larson (1927) for *P. monticola* and *P. contorta*; Coile (1933) for *P. taeda* and *P. echinata*; Pessin (1933) for *P. palustris* and *P. clausa*; Wright (1966, 1968, 1970) for *P. lambertiana* and *P. coulteri*]. In all cases the species with the greater needle number occupied what were described as relatively wetter sites.

Despite the observations for the seven species of *Pinus* on the western slope of the central Sierra Nevada reported above, no direct evidence for interspecific competition between seedlings of these species exists. Both Daubenmire (1943) and Haller (1959) have suggested that water stress and/or interspecific competition are critical in determining, at least in part, elevational ranges of species in western mountains. To test the hypothesis that interspecific competition is the organizing mechanism for these seven species of *Pinus*, long term field studies of seedling establishment, growth, and mortality as well as transplant experiments are in progress for the two elevationally replacing species *Pinus sabiniana* and *P. ponderosa*, and for the two elevationally associated species *P. ponderosa* and *P. lambertiana*. In addition, because most pairs of associated species comprise a *Haploxyylon* and a *Diploxyylon* species, further work on the comparative water requirements of these two subgenera is suggested, particularly with respect to differences in stomatal responses to increasing drought stress. Finally the distributional patterns observed in the central Sierra Nevada must be expanded to other sets of pines to see the generality of the patterns described here.

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