CHANGES IN MORPHOLOGICAL CHARACTERISTICS OF PINUS ENGELMANNII OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO

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ABSTRACT

Needle number per fascicle has been used to distinguish two varieties of pine (*Pinus engelmannii* Carr., and *P. engelmannii* var. *blancoi*). This character, along with needle length and the number of rows and number of stomates per mm of row, was studied in pines growing over an elevational gradient in Durango, Mexico. Differences in needle number per fascicle were found to represent clinal variation within the species: a gradual increase in needle number occurred with altitude and age. Seeds from 5-needled pines, grown for 21 months in the laboratory under dry conditions, confirmed this by producing predominantly 3-needled seedlings.

INTRODUCTION

In the genus *Pinus* there are many examples that exhibit variation in needle number over environmental gradients. *Pinus monophylla* is described as having predominantly 1, but sometimes 2 needles per fascicle (Shaw 1909). Recently Trombulak and Cody (1980) reported an increase in needle number per fascicle for *P. monophylla* with increase in elevation in the New York Mountains of California. This suggests clinal variation of the character along a moisture and temperature gradient. Dodge (1963) reported an increase in needle number per fascicle from the high elevational or northern *P. ponderosa* var. *scopulorum* to the mid-elevational *P. arizonica* Engelm. in the mountains of southeastern Arizona. He used this result along with other characteristics to conclude that *P. arizonica* Engelm. is a variety of *P. ponderosa, P. ponderosa* var. *arizonica*. Haller (1965) made a similar claim for *P. ponderosa* var. *scopulorum, P. arizonica,* even *P. durengensis,* and described a clinal increase in needle number per fascicle with decreasing latitude in the Sierra Madre Occidental of northwestern Mexico.

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In this study we examine some of the characteristics of *Pinus engelmannii* over an elevational gradient in the Sierra Madre Occidental of Durango, Mexico. Shaw (1914) reduced this species to synonymy under *P. ponderosa*. Martinez (1948) reconsidered Shaw's work, rejected this designation, and recognized two varieties: the typical form in Mexico, *P. engelmannii* Carr., and *P. engelmannii* var. *blancoi*. He assigned Shaw's *P. engelmannii* to the latter variety. Martinez distinguished the two varieties of *P. engelmannii* on the basis of needle numbers per fascicle; *P. engelmannii* var. *engelmannii* Carr. is described as having 3 or 4 needles and sometimes 5, whereas *P. engelmannii* var. *blancoi* exhibits 3 (very rarely 4 or 5). Other characteristics are described as being relatively similar or exhibiting great overlaps. The geographical ranges of the two varieties overlap greatly as well. Both are sympatric throughout the Sierra Madre Occidental, particularly in the states of Durango and Chihuahua (Martinez 1948, Mirov 1967). Foresters in this region identify individuals at high elevations as var. *engelmannii* and those at low elevations as var. *blancoi*. Our question is a straightforward one: Are there two distinct varieties of this species or do the characteristics of *P. engelmannii* vary clinally in response to environmental changes over an environmental gradient?

Study Sites and Methods

Ascending the eastern slopes of the Sierra Madre Occidental in Durango, Mexico, gradual changes in the plant associations are observed beginning with those species typical of warm Chihuahuan desert to those associated with mixed grassland, chaparral, and broad-sclerophyll forest and ending finally in open ponderosa-pine like forests (Oosting 1956). A series of four study sites was established over the 230 m elevational range of *Pinus engelmannii* along Mexico Highway 40. The sites were evenly distributed (77 m elevational intervals), beginning beside the Rio Mimbres at the lower edge of the distribution of *P. engelmannii* and ending at Los Cumbres, its upper limit (Table 1).

At each site 10 adult individuals (defined as having trunk diameters greater than 16 cm at base) and 10 juveniles (trunk diameters less than 5 cm at base and less than 1 m in height) were selected randomly. For each individual 10 fascicles were picked randomly and needle length and needle number per fascicle were determined. Average needle number per fascicle and average needle length were calculated for each individual. From one needle on each tree the number of stomate rows was counted, and from one row on this needle the number of stomates per mm of row was determined. Means and standard errors for each parameter were then calculated for adult and juvenile classes at each site. Student's t-test was used to determine statistical significance of differences in means of adults and juveniles within a site and within

TABLE 1. CHARACTERISTICS OF STUDY SITES ALONG AN ELEVATIONAL GRADIENT ON THE EASTERN SLOPES OF THE SIERRA MADRE OCCIDENTAL IN DURANGO, MEXICO.

Elevation (m)	Site	Aspect	Predominant vegetation
2177	Rio Mimbres	West-facing	Open chaparral with scattered *Pinus* and *Quercus*
2254	Santa Barbara	Flat	Pastureland with scattered *Pinus*
2331	Unnamed	South-facing	Chaparral and open scrubland with *Quercus* and some *Pinus*
2408	Los Cumbres	Flat or north-facing	Open woodland with *Pinus* and *Quercus*

classes between sites. Due to the large number of tests performed, we decided to accept $p < 0.01$ as our level for rejecting the null hypothesis of no difference between means.

A sample of seeds was gathered from 5-needled members of the Los Cumbres population and grown in 3-inch diameter pots under bright sunlight and dry conditions in Claremont, California, from August 1978 to May 1980. The number of needles per fascicle in the secondary bundles were counted and each individual was categorized as exhibiting solely 3, 4, or 5 needles per fascicle, or some combinations of 3, 4, and 5 needles per fascicle.

RESULTS

The means and standard errors of the four parameters measured are given in Table 2 for each age class and site.

TABLE 2. MEANS AND STANDARD ERRORS FOR NEEDLE NUMBER, LENGTH, AND STOMATES FROM ADULT AND JUVENILE *Pinus engelmannii* OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO.

Elevation (m)	Class	Needle number	Needle length (cm)	No. of rows of stomates	No. of stomates per mm of row
2177	Adult	3.11 ± 0.04	25.75 ± 0.93	21.90 ± 1.31	13.00 ± 0.02
	Juvenile	2.85 ± 0.09	22.39 ± 1.23	19.10 ± 1.09	12.30 ± 0.69
2254	Adult	3.42 ± 0.16	27.97 ± 0.69	23.50 ± 1.18	13.10 ± 0.28
	Juvenile	3.02 ± 0.05	20.29 ± 1.26	19.20 ± 0.94	12.50 ± 0.31
2331	Adult	3.74 ± 0.14	22.65 ± 0.95	17.80 ± 1.18	12.10 ± 0.53
	Juvenile	3.40 ± 0.12	19.28 ± 0.89	18.10 ± 1.22	11.80 ± 0.39
2408	Adult	4.14 ± 0.17	25.71 ± 0.80	18.60 ± 0.86	12.30 ± 0.50
	Juvenile	3.27 ± 0.11	18.71 ± 0.80	18.20 ± 0.51	11.80 ± 0.42

TABLE 3. COMPARISON OF MEAN VALUES USING STUDENT'S T-TEST FOR NEEDLE NUMBER PER FASCICLE OF *Pinus engelmannii* WITHIN AGE CLASSES AND BETWEEN SITES OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO. Values in table are t's. * $p < 0.01$. Diagonal line from A to B separates juveniles (left) from adults (right).

	Elevation (m)	A	2177	2254	2331	2408	
Juveniles	2177			1.87	4.21*	5.81*	Adults
	2254		1.79		1.48	3.05*	
	2331		3.69*	2.08		1.78	
	2408		2.98*	3.03*	0.81		
						B	

Both adult and juvenile trees exhibit significant differences in needle number per fascicle with altitude (Table 3). Adult needle number increases from predominantly 3 needles per fascicle at 2177 m to more than 4 needles per fascicle at 2408 m (Fig. 1). Although the increase is consistent, adjacent sites are not far enough apart to produce statistically significant differences. However, sites 140 m or more apart do exhibit significant differences. For juveniles a similar pattern exists, except that maximum needle number per fascicle occurs at 2331 m (Fig. 1). Comparing age classes, the greatest difference in needle number per fascicle occurs at the highest site (2408 m), where adults have significantly more needles per fascicle than do juveniles (Table 4). Adults also tend to have more needles per fascicle at the lower sites but the differences are not significant.

Needle lengths of adults are significantly shorter at 2331 m than at the other three elevations (Table 5). The longest needles are at the 2254 m site (Santa Barbara). For juveniles, needle lengths decrease slightly with increased altitude, but the differences are not significant. Within elevational sites, adult needle length is 11–37% greater than that of juveniles.

For adults, the number of rows of stomates is significantly greater

TABLE 4. COMPARISON OF MEAN VALUES USING STUDENT'S T-TEST FOR NEEDLE CHARACTERS OF *Pinus engelmannii* BETWEEN ADULTS AND JUVENILES WITHIN SITES OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO. Values in table are t's. * $p < 0.01$.

Elevation (m)	Needle number	Needle length	No. of rows of stomates	No. of stomates/ mm of row
2177	2.70	2.18	0.40	0.92
2254	2.39	5.34*	0.18	1.45
2331	1.84	2.59	2.86	0.46
2408	4.24*	6.20*	1.64	0.77

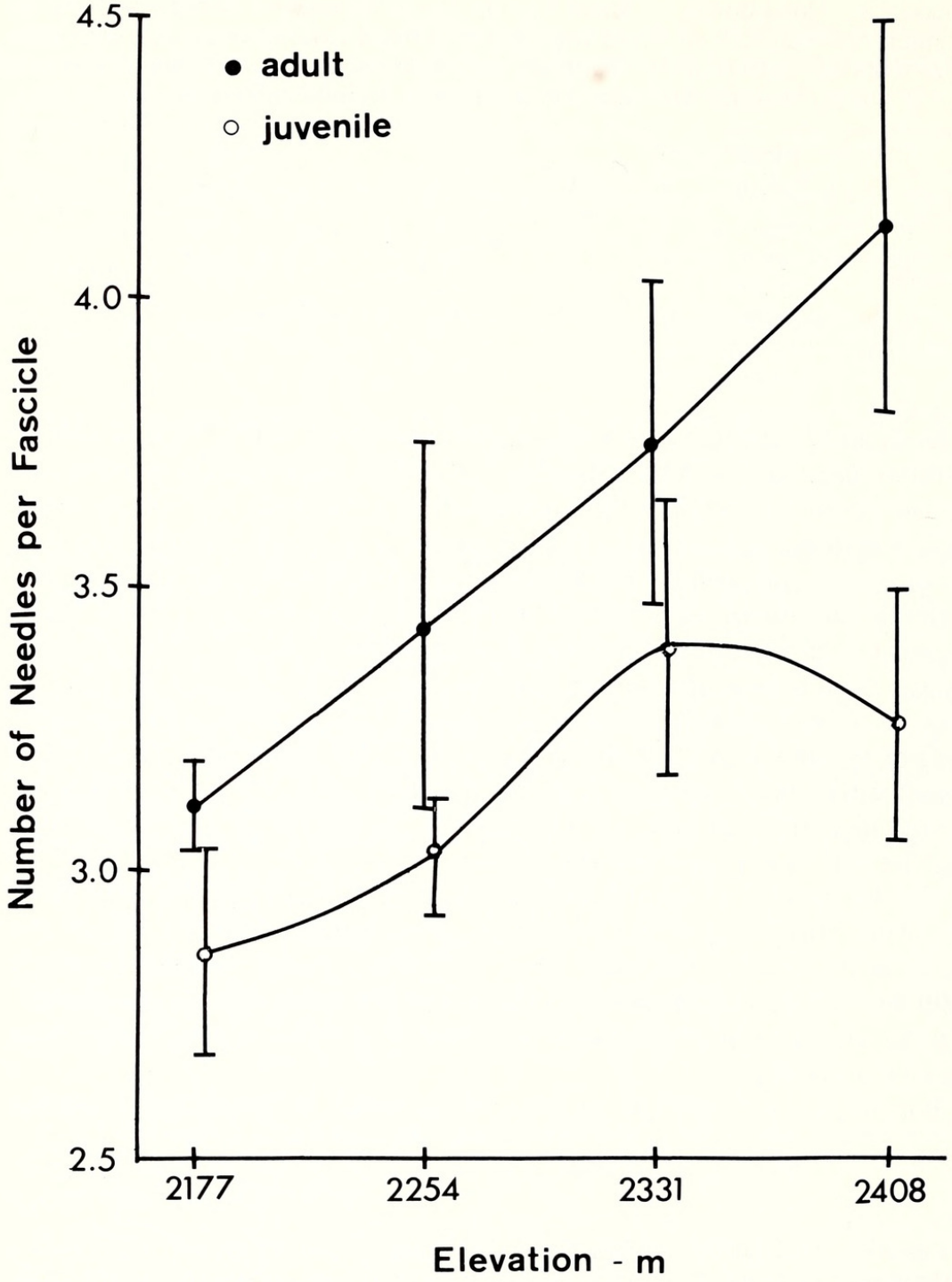

FIG. 1. Average number of needles per fascicle in adult and juvenile *Pinus engelmannii* over an altitudinal gradient. Error bars represent 2 × standard error.

at 2254 m than either of the two higher sites. With juveniles, no significant differences in this character are found between sites. Comparison of adult and juvenile pines also reveals no significant difference in number of stomate rows at any elevational site. Likewise the number of stomates per mm of row did not differ significantly, either

TABLE 5. COMPARISON OF MEAN VALUES USING STUDENT'S T-TEST FOR NEEDLE LENGTH OF *Pinus engelmannii* WITHIN AGE CLASSES AND BETWEEN SITES OVER AN ELEVATIONAL GRADIENT IN DURANGO, MEXICO. Values in tables are t's. * $p < 0.01$. Diagonal line from A to B separates juveniles (left) from adults (right).

	Elevation (m)	A	2177	2254	2331	2408	
Juveniles	2177			1.92	2.33	0.03	Adults
	2254		1.19		4.54*	2.15	
	2331		2.04	0.65		2.47	
	2408		2.51	1.06	0.48		
						B	

between adults and juveniles at any site, or with altitude for a given age class.

Seedlings of *Pinus engelmannii* Carr. grown from the seed of 5-needled individuals of the 2408 m population under hot, dry conditions predominantly have 3 needles per fascicle; of fifty plants only one had 5-needled fascicles and even then, only in some fascicles (Table 6).

DISCUSSION

The major character distinguishing *Pinus engelmannii* var. *engelmannii* from *P. engelmannii* var. *blancoi* is needle number per fascicle. Our measurements indicate that this character varies clinally with elevation from the Rio Mimbres (2177 m) to Los Cumbres (2408 m), and that both adults and juveniles exhibit significant increases with increasing elevation. Needle number increases with elevation more markedly in adults than in juveniles, so that at the highest site (2408 m) a significant difference between age classes occurs. These differences appear to be a response to changing moisture levels experienced over the mountainside; where more soil moisture is present, needle number per fascicle is greater.

TABLE 6. INDIVIDUAL NEEDLE COUNTS AND % OCCURRENCE FOR SECONDARY FASCICLES ON SEEDLINGS OF 5-NEEDLED *P. engelmannii* ADULTS IN THE LOS CUMBRES POPULATION (2408 M) GROWN UNDER DRY CONDITIONS AT CLAREMONT, CALIFORNIA.

Needle number in fascicles	Number of individuals	% occurrence of individuals
3 only	33	66
4 only	9	18
5 only	0	0
3, 4	7	14
3, 5	1	2
4, 5	0	0

Since *P. engelmannii* occupies the lower and middle slopes of the Sierra Madre, it experiences quite dry and hot conditions at desert edge but encounters increasing levels of precipitation and cooler temperatures with increasing elevation. Juveniles of *Pinus engelmannii* appear to suffer more from drought stress than do adults. This is presumably because juvenile root systems have not developed sufficient size or depth to protect them during dry periods (Ledig, Clark, and Drew 1977; Yeaton 1978). In contrast, adult trees have larger root systems that potentially have access to soil moisture sources unavailable to juveniles. Juveniles may respond to drought stress during development by maintaining lower needle numbers per fascicle and shorter needle length, thereby reducing their relative transpirational surface area. Adult trees respond to increased water availability by producing more and longer needles per fascicle, hence increasing their photosynthetic surface area. The results of growing seedlings from seeds of 5-needled individuals support our contention that differences in needle number reflect developmental responses on the part of the individual.

The pattern of increasing precipitation and lower temperatures with increasing elevation is typical of, at least, the lower and middle elevations of all mountain ranges (e.g., MacArthur 1972). It should be noted that in high mountain ranges a point is reached at which rising, cooling air is no longer saturated with moisture and the amount of precipitation begins to decrease with increasing elevation. This means that on very high mountains the highest levels of precipitation will be found at intermediate elevations. This fact explains Dodge's (1963) observation that needle number per fascicle in *P. ponderosa* decreases with increasing elevation in the high mountains of southeastern Arizona. It also explains another interesting and apparently similar situation seen in *P. hartwegii,* a timberline species that has an elevational range of over 1000 m and is restricted to the higher elevations of the Transverse Range in Mexico. This species shows a gradual decrease in needle number per fascicle with increasing elevation, as the species ranges into zones with decreased precipitation and increased winter drought stresses. For example, on Tláloc Mountain, in the state of México, needle number per fascicle for adults of *P. hartwegii* decreases from an average of 3.52 at 3230 m to an average of 3.0 at 3530 m (R. I. Yeaton, unpubl. data). Juveniles from the same elevational range decrease from an average of 3.11 to 2.99 needles per fascicle. These observations are rather similar to those reported here for *P. engelmannii*; increased precipitation is again associated with increased needle number per fascicle.

This study indicates that the two varieties of *Pinus engelmannii* represent the extremes of clinal variation within the species. We now pose a second question that is not as simple to answer. In regions of the northern hemisphere such as Mexico, where there is a wide range of environmental conditions imposed upon members of the genus *Pi-*

nus, how do the characters used traditionally to distinguish varieties and species (e.g., needle number per fascicle, needle length, internal needle structure, bark and cone characteristics, and even phytochemistry), respond developmentally to diverse environmental conditions? It seems to us that they may vary a great deal and in their variation contribute much confusion to the taxonomy and the understanding of the evolutionary history of this genus.

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LITERATURE CITED

DODGE, R. 1963. Investigations into the ecological relationships of Ponderosa pine in southeast Arizona. Ph.D. dissertation, Univ. Arizona.

HALLER, J. R. 1965. The role of 2-needle fascicles in the adaptation and evolution of ponderosa pine. Brittonia 17:354–382.

LEDIG, F. T., J. G. CLARK, and A. P. DREW. 1977. The effects of temperature treatment on photosynthesis of pitch pine from northern and southern latitudes. Bot. Gaz. (Crawfordsville) 138:7–12.

MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, NY.

MARTINEZ, M. 1948. Los pinos mexicanos. Ediciones Botas, Mexico City.

MIROV, N. T. 1967. The genus *Pinus*. Ronald Press, NY.

OOSTING, H. J. 1956. The study of plant communities. W. H. Freeman Co., San Francisco.

SHAW, G. R. 1909. The pines of Mexico. Arnold Arboretum Publ. 1:1–29. J. R. Ruiter and Co., Boston.

———. 1914. The genus *Pinus*. Arnold Arboretum Publ. 5:1–96. Riverside Press, Cambridge.

TROMBULAK, S. C. and M. L. CODY. 1980. Elevational distributions of *Pinus edulis* and *P. monophylla* (Pinaceae) in the New York Mountains, eastern Mojave Desert. Madroño 27:61–67.

YEATON, R. I. 1978. Competition and spacing in plant communities: differential mortality of white pine (*Pinus strobus* L.) in a New England woodlot. Amer. Midl. Naturalist 100:285–293.

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