

ELEVATIONAL DISTRIBUTIONS OF *PINUS EDULIS*
AND *P. MONOPHYLLA* (PINACEAE) IN THE
NEW YORK MOUNTAINS, EASTERN
MOJAVE DESERT

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ABSTRACT

The elevational range over which sympatric populations of *Pinus edulis* and *P. monophylla* occur was measured on three north-facing slopes in the New York Mountains, eastern Mojave Desert. These two species have disjunct distributions over most of their geographic range, rarely occur together, and exhibit altitudinal zonation in the New York Mountains, where *P. edulis* occurs at higher elevations than *P. monophylla*. The elevation of contact varies locally. The highest ridge provides more run-off during the year, allowing *P. edulis* to exist at lower elevations than on a drier slope. The lowest and driest slope studied does not support *P. edulis* at all.

The two most abundant species of pinyon pine in the United States are *Pinus edulis* Engelm. and *P. monophylla* Torr. & Frem. They are morphologically similar and scarcely specifically distinct (Lanner, 1974; Roof, 1978), but are parapatric in distribution. While *P. edulis* ranges from Wyoming to the northern border of Chihuahua, Mexico, and west to southeastern California, *P. monophylla* is found in Idaho, western Utah, northwestern Arizona, Nevada, California, and Baja California (Critchfield and Little, 1966). They are sympatric in a few localities, the westernmost of which is the slopes of the New York Mountains in the Mojave Desert in southeastern California (Wolf, 1938; Griffin and Critchfield, 1972).

The simplest morphological character distinguishing these two species is needle number; *P. monophylla* usually possesses single needles whereas *P. edulis* has needles in fascicles of two or three (Lanner, 1974). Yet in the New York Mountains, individual trees are found with both 1- and 2-needled fascicles. Occasionally 3-needled fascicles are found. While these species are often found over the same elevational ranges, in the New York Mountains they are separated elevationally, with *P. edulis* occurring higher than *P. monophylla*.

There is some controversy over the correct identity of the trees in the New York Mountains. Using needle number, cone size, and resin canal number, Lanner (1974) concluded that *P. monophylla* is the only species found in this mountain range. However, he sampled only 24 trees and it is possible they were all from low elevations. Roof (1978)

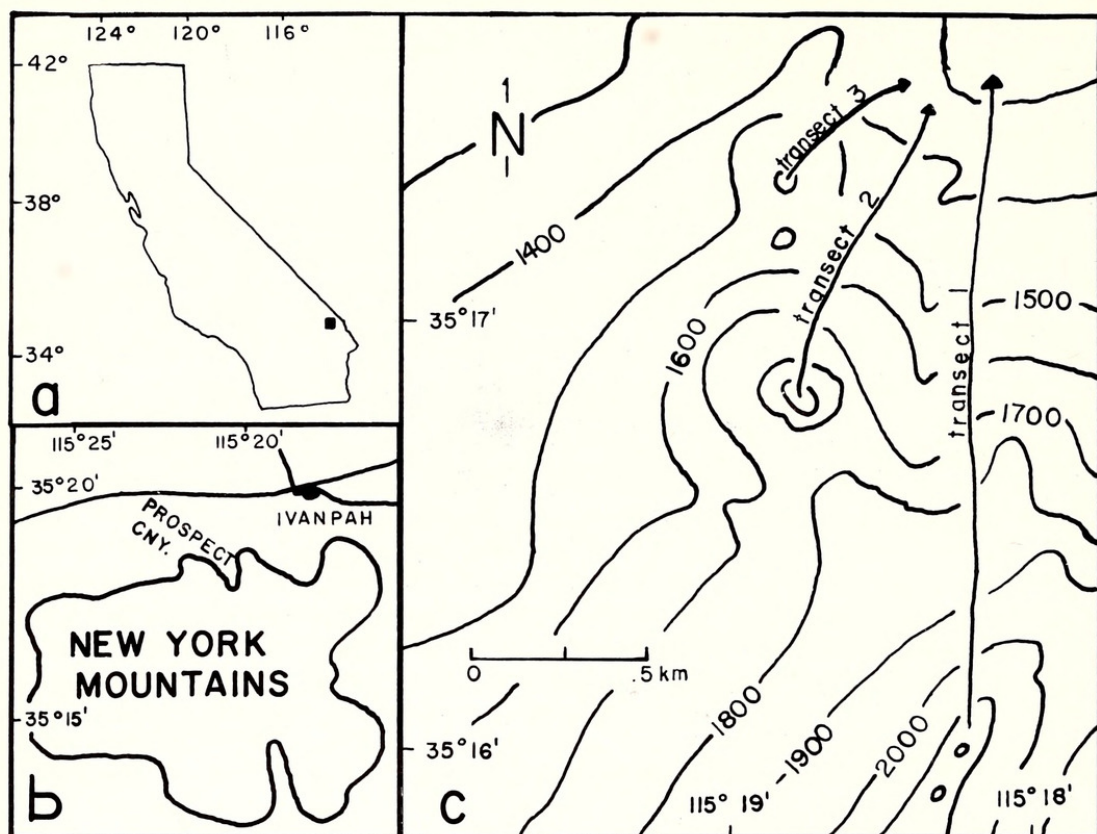


FIG. 1. Location of transects. a. Map of California, dark square shows location of New York Mountains. b. New York Mountain range. c. Topographic map with 100 m contours showing location of transects in "Prospect Canyon". Transect 1 is off the main summit ridge, transect 2 is intermediate and transect 3 is in the foothills.

claimed that *P. edulis* is the only pinyon species present based on tree color and form but not needle number.

The purpose of this paper is to document and interpret the distribution of *P. edulis* and *P. monophylla* in the New York Mountains. In this study we measured needle number per fascicle in a large number of trees from several locations. We surveyed a series of ridges from the main east-west crest north into the foothills of the range and determined the limits of the zone of overlap between the two pinyon species. We have attempted to identify the factors that affect the relative distribution of these taxa and to ascertain whether the population borders are stable or are changing over time.

METHODS

The data reported here were collected April 3–16, 1977. Three transects on the north side of the range were sampled near "Prospect Canyon", SSW of Ivanpah, CA (Fig. 1). One slope comes off the main summit ridge, one is located 2.0 km north of the summit in the foothills, and the third lies between the first two. Soil on all transects was rocky granitic sand. Elevations were determined by triangulation with

a Silva Explorer Type 3 compass and USGS topographical maps (Ivanpah, CA and Mid Hills, CA quadrangles) and a Jack Dfrost altimeter.

At 15–30 m increments in elevation, three to five trees were sampled (the greater the tree density, the more sampled) and the terminal 12–15 cm of one branch 1 m above the ground was taken from the tree. Sample trees at a given site were taken as far apart as possible to control for microclimatic effects and to enhance the chance of including a broad range of tree genotypes. Slope, aspect, soil type, and degree of exposure were recorded for each tree. The needles of each sample were subsequently examined and each fascicle classified as 1- or 2-neededled. No 3-neededled fascicles were found in any of our samples. As fascicles were counted, those with apparently only one needle were bent to encourage separation of needles. Samples contained 71–231 fascicles. We calculated the mean percent of 2-neededled fascicles at each site by averaging the percent of 2-neededled fascicles on each tree at that site. We then plotted this as the dependent variable against elevation for each of the transects. From a least-squares regression of these data we have determined the median elevation where 1- and 2-neededled fascicles occur in equal proportions. We then compared the curves describing the three transects.

RESULTS

Figure 2 shows the frequency of intermediate-type trees (with both 1- and 2-neededled fascicles occurring on the same tree) on the northern slopes of the New York Mountains. Nearly all intermediate-type trees exhibited less than 20 percent or more than 80 percent 2-neededled fascicles. No trees fell between 26 and 60 percent. Each tree can thus be classified operationally as either *P. edulis* or *P. monophylla* based on its predominant fascicle type.

Figure 3a shows the change in needle number per fascicle at each sample site along the elevational gradient of transect 1 and demonstrates the increasing proportion of *P. edulis* with increasing altitude. The fitted linear equation is $Y = -0.878 + (8.2 \times 10^{-4})X$ ($r = 0.51$, $p < 0.005$) where Y = the proportion of 2-neededled fascicles at each site and X = elevation. The elevation at which 50 percent of the fascicles per sampled site are 2-neededled ($X_{0.5}$, the turnover elevation) is 1680 m for transect 1.

Figure 3b shows a similar representation of the data for transect 2. Here $Y = -1.665 + (1.18 \times 10^{-3})X$ ($r = 0.69$, $p < 0.005$) with $X_{0.5} = 1834$ m. In transect 3 there is only one species present, so the data were not fitted to a line (Fig. 3c).

Thus transect 3 exhibits no species turnover and consisted only of *P. monophylla* while transect 2 shows a higher turnover elevation (1834 m) than transect 1 (1680 m).

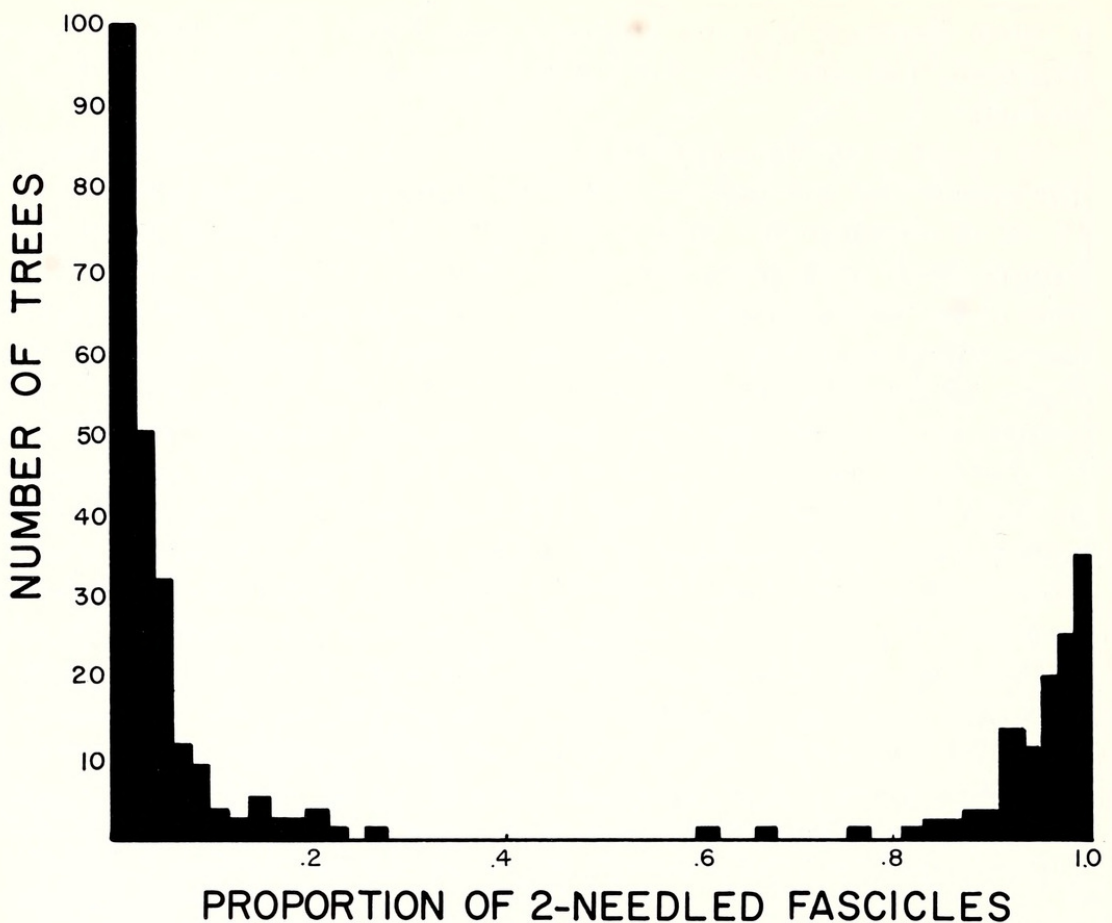


FIG. 2. Frequency distribution of intermediate-type trees in 2-percent units. All but seven of the 337 trees sampled in the New York Mountains have a proportion of 2-needled fascicles between 0 and 20 percent or between 80 and 100 percent. This allows an operational definition of *P. monophylla* as any tree with less than 50 percent 2-needled fascicles and *P. edulis* as any tree with greater than 50 percent 2-needled fascicles.

Figures 3a and 3b also show the elevations of the seven trees with 21–79 percent 2-needled fascicles. Five of these seven trees are located within 200 m of the calculated turnover point for their respective slopes. In addition, the proportion of 2-needled fascicles on each of these trees is compatible with the predictions made by the regression line—i.e., those lying below the turnover point have less than 50 percent 2-needled fascicles and those lying above the turnover point have greater than 50 percent 2-needled fascicles.

DISCUSSION

No conclusive data are presented here as to whether the intermediate-type trees are the products of convergence in response to similar edaphic conditions or to hybridization. The fact that intermediate individuals are found in isolated monospecific populations suggests that there is some developmental plasticity that affects needle number in

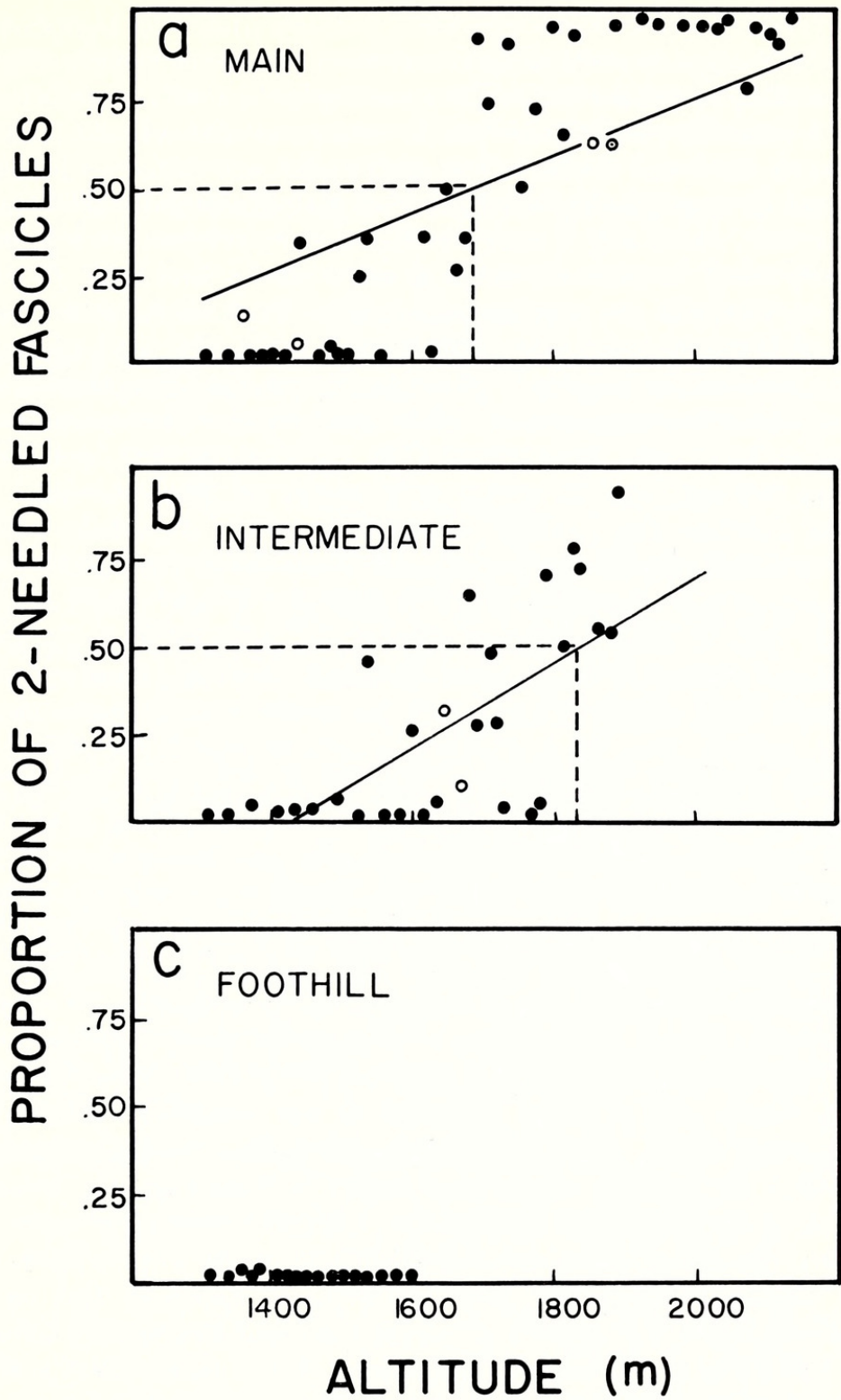


FIG. 3. Change in mean proportion per site of 2-needled fascicles with elevation on transects 1, 2, and 3. Open circles represent sites with one sampled tree that had 21–79 percent 2-needled fascicles. The dotted open circle represents a site with two such trees. a. Transect 1: *P. edulis* extends to low elevation. b. Transect 2: *P. edulis* found only at high elevations. c. Transect 3: *P. edulis* absent.

response to direct and immediate environmental pressure (Little, 1950, 1968). However, Lanner (1974) describes a slope that ranges over 400 m and several climatic zones. *Pinus monophylla* over this entire slope shows no variation in the number of needles per fascicle. In addition, much work has been attempted to answer the question of whether *P. edulis* and *P. monophylla* hybridize in nature (Lanner and Hutchison, 1972; Lanner, 1974) and it appears that such hybridization is possible.

As previously mentioned, there is some doubt that both *P. edulis* and *P. monophylla* are present in the New York Mountains. Lanner (1974), after examining needle morphology, cone size, and resin canal number, concluded that the 2-needled trees in the New York Mountains merely represented a form of *P. monophylla*. However, the discontinuous frequency distribution (Fig. 2) suggests that two distinct forms are present, and we retain both names for this material.

Figure 3 shows that, based on needle number, *P. edulis* replaces *P. monophylla* at higher elevations and the relative distribution of *P. monophylla* and *P. edulis* differs with location. *Pinus edulis* is absent from the lowest foothill slopes (transect 3), and on slopes near the main ridge (transect 2) the zone of transition between the two species occurs at a higher elevation than on the main summit slope (transect 1). This pattern may be a product of displacement competition—a process in which *P. monophylla* replaced *P. edulis* in lower, drier sites so that *P. edulis* became restricted to the high peaks of the main ridge in relictual stands. The sequence of events can be conceived as follows: *P. edulis* was once widely distributed at lower elevations in the Mojave Desert during pluvial Pleistocene climates (Wells and Berger, 1967). With glacial recession and climatic changes beginning about 20,000 years ago, *P. monophylla* began replacing *P. edulis* at lower elevations and on foothills. At present, *P. edulis* has been completely replaced on the foothill slopes, on all but the top of the intermediate slopes, and is being replaced on the uppermost main slope.

The causal factor of this altitudinal zonation is probably water availability. In general, water availability increases as one moves up the slopes of the New York Mountains. This may result from a number of factors, including more precipitation and lower evaporation rates due to cooler temperatures. Halvorson (1972) reported that narrow vegetational belts of *P. edulis*, *P. ponderosa*, and *Artemisia tridentata* on the north rim of the Grand Canyon are due to microclimatic effects that simulate an elevational moisture gradient even though there is no significant change in elevation. Likewise, species differences between sites at a given elevation are likely to be associated with microclimatic effects produced by topography, soil type, etc.

The altitudinal zonation exhibited by *P. edulis* and *P. monophylla* can then be interpreted as the superiority of *P. edulis* in cooler, wetter environments and the superiority of *P. monophylla* in hotter, drier environments. It is likely that the competitive dominance of each un-

der different moisture regimes prevents either from existing over a larger elevational range. Therefore, the elevation of contact is different on each slope due to the different levels of water availability. The highest ridge provides more run-off during the year, allowing *P. edulis* to extend to lower elevations than on either of the drier slopes. The lowest slope studied does not provide enough moisture to support *P. edulis* at all.

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