

Stand dynamics and regeneration patterns of a pinyon pine forest in east central Mexico

Gerardo Segura^{a*} and Laura C. Snook^b

^aCollege of Forest Resources, AR-10, University of Washington, Seattle, WA 98195, U.S.A.

^bYale School of Forestry and Environmental Studies, New Haven, CT 05611, U.S.A.

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ABSTRACT

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Stand development of a pinyon pine forest (*Pinus cembroides* subsp. *cembroides* Zucc.) at the southern edge of its range was analyzed using size and age distributions. Frequencies by size class closely approximate a negative exponential distribution, suggesting a balanced and continuous multi-aged condition. Age distributions, however, showed that trees colonized the stand following discrete disturbance events. Significant differences in the relationship between size (e.g. diameter) and age occurred among individuals in the same stand. Stand structure and regeneration patterns were strongly influenced by natural and human disturbances, particularly a large fire that destroyed most of the forest in 1938.

Topographic variations appeared to create differences in microclimates and soils, and caused different patterns of regeneration, growth and disturbance. Gullies with favorable microclimates and productive soils encouraged dense pine regeneration, growth, and fuel build-up following disturbances. Devastating fires, like the one that occurred in 1938, appear to remove most of the vegetation cover and renew the erosion processes in the gullies. On uplands between gullies, slower growth and fuel build-up make fires less frequent and intense, and occasional pines survive fires and reseed the area.

INTRODUCTION

Pinyon pine forests occupy extensive areas in the rain shadows of the eastern and western Sierra Madre mountain ranges in Mexico. These forests represent a transition zone between xeric and relatively mesic forest communities at higher elevations (Rzedowsky, 1978).

* Present address: Centro de Ecología, Universidad Nacional Autónoma de México. Apdo. Postal 70-275. 04510, México, D.F., México.

Pinyon pine forests in Mexico have been used for centuries for pine nut harvesting, fuelwood extraction, and grazing. Because of their tolerance to adverse environmental conditions and their capacity to establish on poor soils (Robert, 1977; Passini, 1985), pinyon pines have been used for reforestation of arid and eroded zones (Robert, 1977). However, very little is known about the dynamics and regeneration patterns of natural pinyon pine forests and virtually no plans have been proposed for their management in Mexico.

Pinyon and other pine forests in Mexico are greatly influenced by natural and human-caused disturbances such as fire, insect damage, pine nut harvesting, clearing, and grazing (Rzedowsky, 1978; Cuanalo, 1979; Passini, 1982). The role of disturbances in determining the structure, composition, and spatial variation of these forest communities, however, has usually been underestimated.

Differences in disturbance and stand development patterns within a single forest stand may result from microclimatic and topographic variations. These differences have been observed in pinyon-juniper communities of the south-west United States (Jameson, 1987) and other temperate coniferous forests (Romme and Knight, 1981). Drainage bottoms, deep and narrow gullies, and other micro-topographic irregularities caused by massive erosion movements are common in many Mexican pinyon pine forests and probably determine disturbance regimes and stand development patterns.

The objectives of this study were (1) to determine the stand development patterns of a pinyon pine forest at the most southern boundary of its range; (2) to evaluate the effect of fire and other natural and human disturbances on the regeneration and development of this forest; and (3) to examine differences in stand development and disturbance regimes resulting from micro-topographic irregularities.

METHODS

Study area

The study was conducted in a pinyon pine forest on a southeast slope within an extensive highland basin between Puebla and Veracruz, Mexico, about 40 km west of Perote, Veracruz (latitude, 19°25'N, longitude, 97°34'W) (Fig. 1). This 180 ha forest occurs at an elevation that ranges from 2300 to 2500 m.

The region is in the rain-shadow of the eastern Sierra Madre mountain range. The climate is temperate with warm and rainy summers and is the most humid of the semiarid climates of Mexico (García, 1973). Annual precipitation is 577 mm, and mean annual temperature is 17.6°C (Geréz, 1982).

Soils are shallow and often extremely eroded, with an irregular hardpan at depths from 15 cm to 100 cm. They are sandy loams to loamy sands, well drained, relatively alkaline (pH between 7.1 and 8.5), with a high percentage

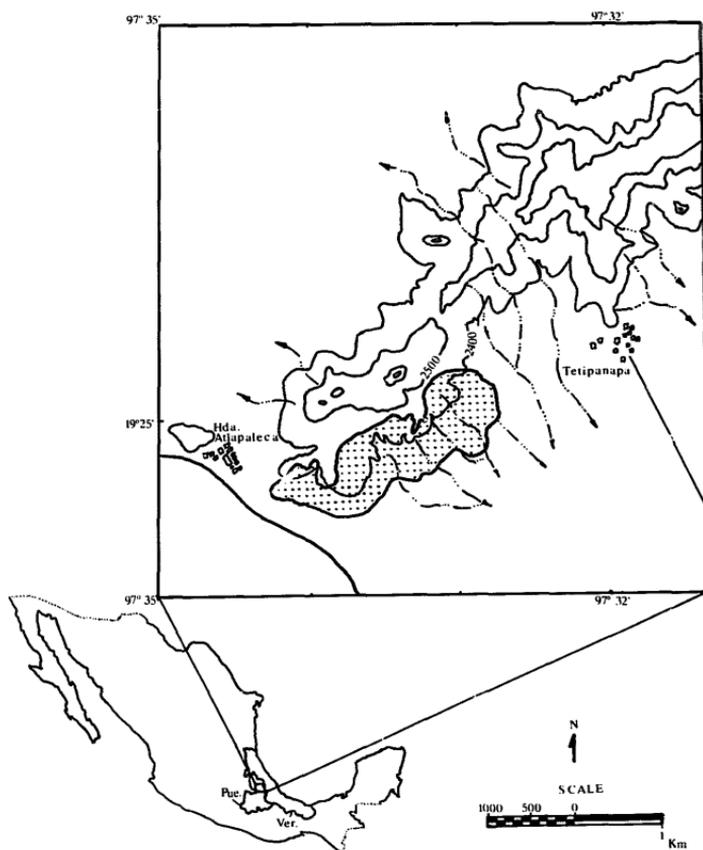


Fig. 1. Location of study area. (Stippled area represents study area).

of calcium (24–34%), and low in organic matter (4% in A horizon).

Narrow and deep (3–20 m) gulches with steep sides (45–90°) are conspicuous in most of the stand and constitute approximately 5% of the stand area (Fig. 2). These sites are drainage courses of small, ephemeral streams during the rainy season (May–September), when heavy storms of short duration may occur.

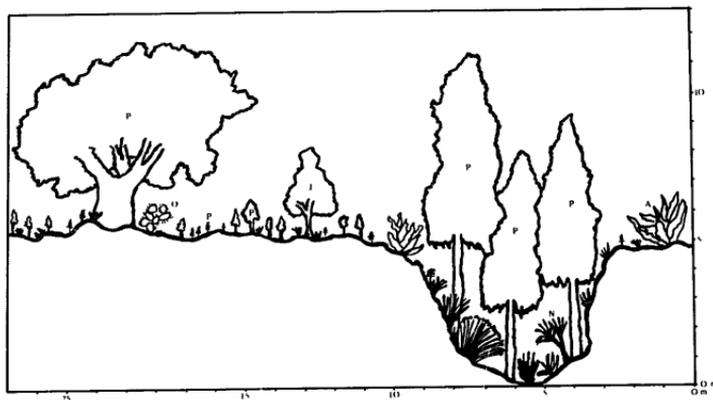


Fig. 2. Profile of the vegetation showing micro-topography and differences in forest structure between uplands and gullies. (P = *Pinus cembroides* subsp. *cembroides*, J = *Juniperus deppeana*, N = *Nolina parviflora*, O = *Opuntia* spp., A = *Agave* spp.).

The vegetation is typical of pinyon pine forests described by Miranda and Hernández-X. (1963) where pinyon pine is the dominant species. Dominant trees range in height from 6 to 15 m; density is about 870 stems/ha (> 1 cm dbh); and basal area is about 10 m²/ha. *Juniperus deppeana* (Stend.), and occasionally *Quercus microphylla* (Nec), *Amelanchier denticulata* (H.B.K.) C. Koch.), and *Pinus pseudostrobus* (Lindl.) var. *oaxacana* ([Mirov.] Harrison), are also present in the overstory. Common understory species are *Nolina parviflora* ([H.B.K.] Hemsl.), *Yucca periculosa* (Baker.), *Dasylirion acrotriche* (Zucc.), *Agave* spp. and *Opuntia* spp. Ground cover is discontinuous and consists mainly of grasses. *Tillandsia usneoides* (Linn.) is commonly found as a conspicuous epiphyte on the bark of stems and branches of large trees.

Human activities are common in the region since pre-colonial times (Geréz, 1982). Large forested areas have been converted to agricultural lands of low productivity, and forests remain only on hills with steep slopes and poor soils. Periodic human disturbances such as fire, pine nut harvesting, grazing, and selective cuttings still occur in the study area (Geréz, 1982).

Measurements of forest structure

The study area was stratified into a larger, upland area and a smaller area of intervening gullies. Twenty 400 m² plots (20 x 20 m) were systematically distributed over a 12 ha area considered to be representative of the upland

area of the stand. Five plots were set out 50 m apart along each of four transects running across the slope at a constant elevation. The transects were located 50 m apart to cover the altitudinal range of the forest. No plots fell within gullies, which were sampled separately (see below).

Diameter at breast height (dbh) of all trees and heights of all shrubs and trees, including seedlings and saplings, were measured in every plot. Seedlings were arbitrarily defined as < 0.10 m tall; and saplings were > 0.01 m but < 1.5 m tall.

Ages of 204 pines were sampled systematically over the whole range of tree sizes including seedlings and saplings. Age was determined from increment cores (for large trees) or stem sections (for seedlings and saplings). Increment cores were taken at 1.4 m, and stem sections were taken at ground level. Trees were sampled systematically according to size categories and the number of samples per size category was proportional to the density of trees in each category.

Stem sections and cores were sanded and annual rings were counted using a binocular microscope. A cross-dating technique (Fritts, 1976) was used to identify missing rings and determine actual tree ages. In order to estimate tree age at ground level from trees from which cores were taken, it was assumed that it takes approximately 5 years for a pinyon pine seedling to reach breast height. This assumption was based on field observations and analysis of growth patterns of seedlings and saplings growing in the open.

A separate sampling method was used to determine patterns of stand and tree growth in gullies. Three pairs of plots of 250 m² were systematically distributed along each of three different gullies and in the adjacent uplands. Tree diameters, heights and ages were measured as in the rest of the upland plots.

Annual ring widths from increment cores from 10 representative dominant trees on each plot were measured to analyze growth on both gully and upland plots. Measurements were made to the nearest 0.025 mm using a binocular microscope with movable stage and dial micrometer.

Spatial pattern

Distances to the nearest neighbor and to the nearest neighbor of the same size class were measured on 245 pines covering the range of tree sizes over the 20 upland plots. Spatial distribution of trees was described using a plant-to-plant distance technique (Clark and Evans, 1954), which determines departure from random distribution (Pielou, 1977). Pooled mean nearest neighbor distance (r_A) was compared with mean distance expected from a hypothetical randomly distributed population (r_E) having the same density as the observed population (ρ). The ratio of observed to expected mean distances (R) is used as an index to measure departure from random distribution. When $R = 1.0$, the population is randomly distributed. When the population is aggregated, $R < 1.0$; and when regular $R > 1.0$ (Clark and Evans, 1954).

Statistical significance of departure of r_A from r_E was evaluated using the statistic:

$$C = r_A - r_E / (Q) r_E$$

(a standard variate of the normal curve) where r_E = standard error of mean distance to nearest neighbor of a randomly distributed population with density equal to that of the observed population (Q) (Clark and Evans, 1954).

Stand history

Because downed logs and woody debris left after fires or other disturbances are usually removed for fuelwood, little evidence of past disturbances was available. Local residents contributed with important information on the recent disturbance history of the forest. Dates of past fires were confirmed by examining partial sections (wedges) cut from scarred trees. The occurrence of scarred trees and charcoal fragments in the upper soil profile were also used to estimate the extent and intensity of recent fires. The number and degree of deterioration of available blown-down trees was used to evaluate the frequency of windthrows.

RESULTS

Forest structure

Both diameter and height distributions of the pinyon pines resembled a negative exponential distribution ("reverse J shaped" distribution) (Fig. 3). The diameter distribution (Fig. 3A) shows a dramatic and relatively constant decline in frequencies for the first few diameter classes (< 20 cm dbh). More than 90% of the trees were in diameter classes less than 20 cm, with the majority of these corresponding to the seedlings and saplings size classes. Diameter classes larger than 20 cm show relatively constant frequencies up to 60 cm. Only a few larger individuals were found.

The height distribution (Fig. 3B), also showed a drastic decrease in frequencies above the lowest categories. Almost 60% of all individuals were less than 6 m tall. A few taller individuals were up to 20 m tall.

Unlike tree size, ages (Fig. 4) did not follow a negative exponential distribution. At least two major age groups were distinguished in the age distribution of trees taller than 1.5 m (Fig. 4A): a relatively young cohort represented by trees that invaded the stand between 1938 and 1970; and the remnants of one or more older generations represented by a few individuals that became established prior to 1900. Over 90% of these trees invaded after 1938 while only a few large individuals remain of those which became established prior to 1930. The majority of these large trees had fire scars and were probably survivors of a fire that destroyed most of the stand in 1938.

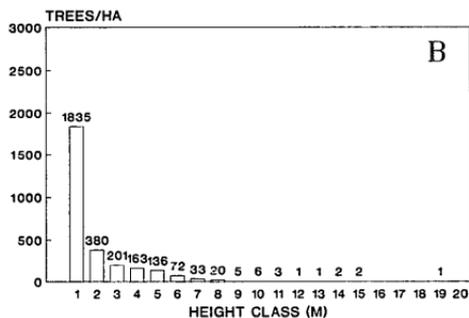
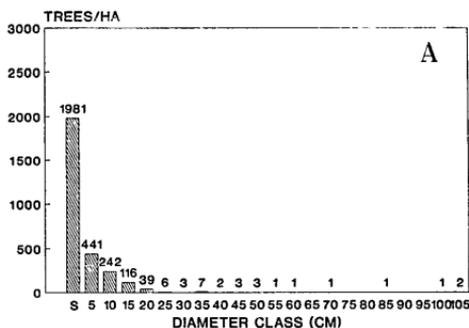


Fig. 3. Diameter (A) and height (B) class frequency diagrams for *P. cembroides* subsp. *cembroides*. (Diameter class S = seedlings and saplings.)

Over 90% of the trees less than 1.5 m tall were between 11 and 31 years old (Fig. 4B). Very few of these trees had become established after 1980 and most of them were individuals that had been suppressed for a long time under the canopy of large trees.

A linear regression model testing the relationship of diameters and ages of pinyon pines taller than 1.5 m (not including seedlings and saplings) showed a significant correlation ($r^2 = 0.56$, $P < 0.001$). A size-age scattergram, however, indicates that considerable variation existed for trees over 30 cm in diameter (Fig. 5). Diameter variability appeared to increase with age. Analysis

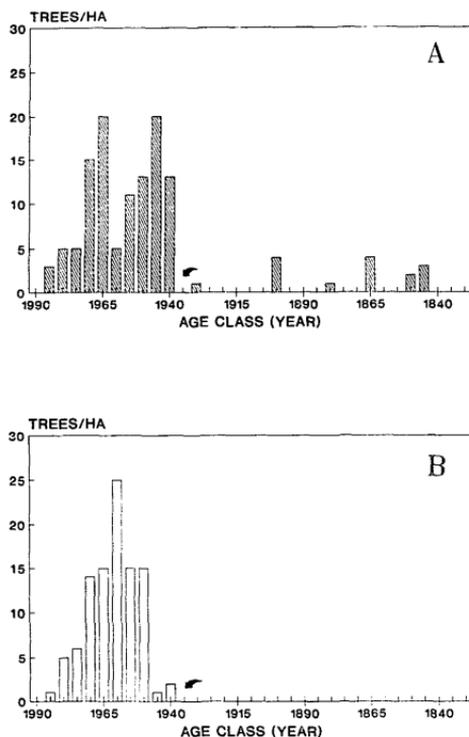


Fig. 4. Age class frequency diagram of *P. cembroides* subsp. *cembroides* for individuals > 1.5 m tall (A); and seedlings and sapling (< 1.5 m tall) (B). (Arrow indicates the date of the 1938 fire.)

of residual variance from the regression suggests the relationship between diameters and ages is not constant for the whole range of diameters (test for non-constant variance; $S = 60.925$, $P < 0.001$; Cook and Weisberg, 1983).

Spatial distribution

The mean distance to nearest neighbor yielded an index of dispersion for the total population significantly less than 1 ($P < 0.0001$) indicating a tendency towards an aggregated pattern (Table 1). This pattern may reflect clumped

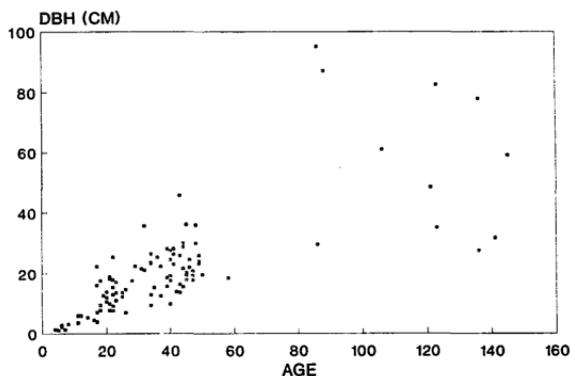


Fig. 5. Relationship of breast height diameter to age of *P. cembroides* subsp. *cembroides* for individuals taller than 1.5 m.

TABLE 1

Dispersion index (R) of *Pinus cembroides* subsp. *cembroides* for the total sampled population

	N	r_A	R	C	P
Total population	301	0.815	0.8115	6.0330	<0.0001

(N = number of sampled individuals; r_A = mean distance to nearest neighbor for the total population; C = standard variate of the normal curve; P = probability value of greater differences between r_B and r_A).

survival following the 1938 fire as well as clumped regeneration associated with windthrow events and differences in microsite characteristics.

A different distribution pattern of mean distances to nearest neighbor was observed for individuals of specific size classes (distances to neighbors of the same size class) (Tables 2 and 3). A tendency going from aggregation towards regularity was observed for progressively larger individuals up to 20 cm in diameter (Tables 2 and 3). While trees < 1.5 m tall were aggregated ($R < 1$) (Table 2); individuals that belonged to diameter classes of 1–10 and 11–20 cm were regularly spaced ($R > 1$) (Table 3). Trees in classes over 20 cm, however, tended to be randomly distributed ($R = 1$) (Table 3). These larger trees were both dominant trees of the cohort that invaded after 1938 and older individuals that survived the 1938 fire.

TABLE 2

Dispersion index (R) of *Pinus cembroides* subsp. *cembroides* for specific size classes (individuals between 0 and 1.5 m tall)

Size Class height (m)	N	$r_{A(ghc)}$	R	C	P
0.00–0.50	72	1.2350	0.8618	2.2449	0.0073
0.51–1.00	27	2.1981	0.6237	3.7416	0.0001
1.01–1.50	18	1.8917	0.5181	3.9115	<0.0001

(N = number of sampled individuals; $r_{A(ghc)}$ = mean distance to nearest neighbor of the same height class; C = standard variate of the normal curve; P = probability value of greater differences between r_E and r_A)

TABLE 3

Dispersion index (R) of *Pinus cembroides* subsp. *cembroides* for specific size classes (individuals larger than 1 cm dbh)

Size Class dbh (cm)	N	$r_{A(sdc)}$	R	C	P
1–10	98	3.0228	1.6775	12.9390	<0.0001
11–20	41	5.8048	1.3173	3.8874	0.0001
21–30	24	10.3375	1.1324	1.2411	0.1075
31–40	3	12.5333	0.7415	0.8566	0.1877
41–50	8	11.4750	0.7257	1.4840	0.0694
> 50	10	17.2300	1.2183	1.3209	0.0934

(N = number of sampled individuals; $r_{A(sdc)}$ = mean distance to nearest neighbor of the same diameter class; C = standard variate of the normal curve; P = probability value of greater differences between r_E and r_A)

Forest structure and growth in relation to micro-topography

Dramatic differences in forest structure were observed between gullies and uplands (Fig. 2). Density of pinyon pines (> 1 cm dbh) was substantially greater in gullies (818 stems/ha) than in uplands (344 stems/ha). Basal area, however, was not significantly different between plot means ($P < 0.5$).

Both uplands and gullies showed major tree recruitment following the 1938 fire (Fig. 6). A narrower age distribution occurred within gullies, indicating most stems invaded during a relatively short period (15–20 years) (Fig. 6A). On uplands adjacent to gullies (Fig. 6B), as in the rest of the upland plots (Fig.

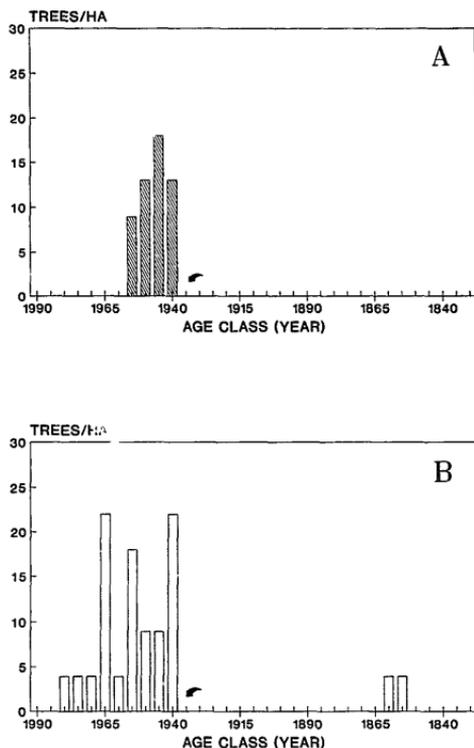


Fig. 6. Age class frequency diagram for *P. cembroides* subsp. *cembroides* from gullies (A) and uplands (B). (Arrow indicates the date of the 1938 fire.)

4), trees invaded over a longer period. Two major establishment periods occurred: one beginning in 1938 and another in the mid 1960s. A few older individuals were found in uplands, but not in gullies.

Diameters on both types of sites (Fig. 7) approximate a negative exponential distribution. However, only about 40% of all stems belonged to the smallest size class in gullies (Fig. 7A), while nearly 90% belonged to this class in uplands. A dramatic decline in tree numbers occurred from the smallest to the next largest diameter class in uplands (Fig. 7B) while tree number changes on

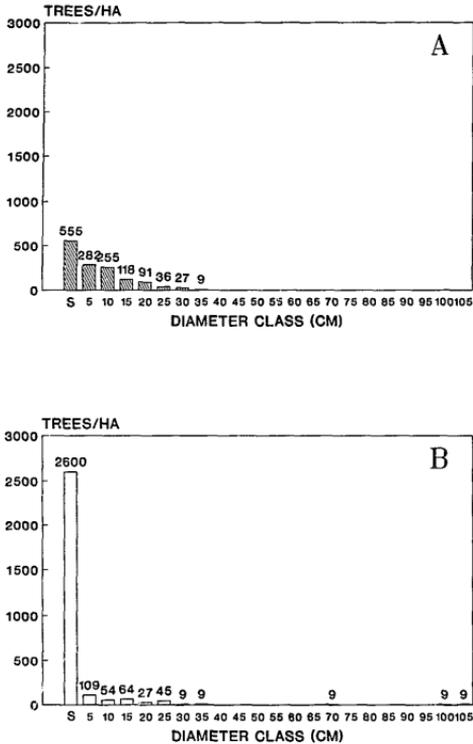


Fig. 7. Diameter class frequency diagram for *P. cembroides* subsp. *cembroides* from gullies (A) and uplands (B). (Diameter class S = seedlings and saplings.)

gullies were more uniform (Fig. 7A). A few trees of large diameters and large gaps in the diameter distribution were also common on uplands. Gullies had a more continuous range of tree sizes but no trees larger than 35 cm dbh.

More short trees (0–1 m tall) were found on uplands than on gullies (Fig. 8). In gullies tree heights were continuously distributed over most range of heights (Fig. 8A), whereas no trees between 10 and 13 m tall were found on uplands (Fig. 8B). The few, individuals taller than 13 m on uplands were all over 130 years old. Within gullies, however, no trees were found which became

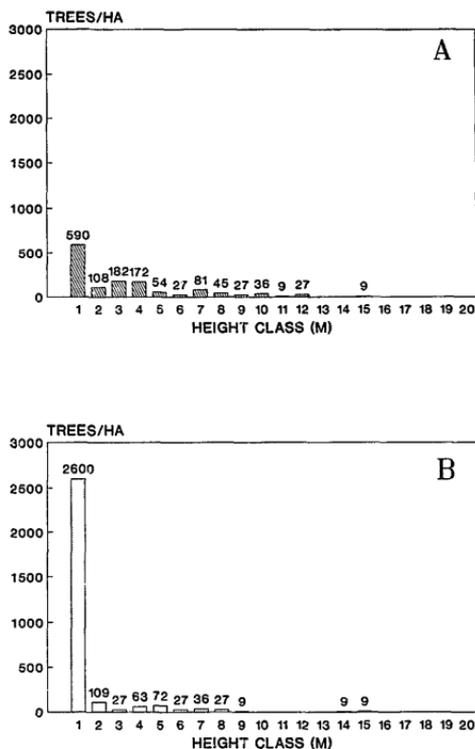


Fig. 8. Height class frequency diagram for *P. cembroides* subsp. *cembroides* from gullies (A) and uplands (B).

established before 1938; all trees taller than 8 m belonged to the cohort that invaded the stand after 1938.

Dominant trees in gullies were significantly taller ($P < 0.001$) and had smaller diameters, while trees growing in uplands tended to be shorter but with larger diameters (Fig. 9). The relationship between height and diameter (ht/dbh ratio) also was significantly different between the two sites ($P < 0.05$).

Figure 10 shows mean cumulative radial increment (at 1.4 m) over time for dominant trees which invaded after 1938 for two upland and two gully plots.

Trees in gullies appear to have grown more vigorously than trees in uplands. Both gully and upland trees show a similar rate of diameter growth until the early 1950s. After this period, upland trees show a drastic decline in growth while gully trees continue growing at the same rate until 1970.

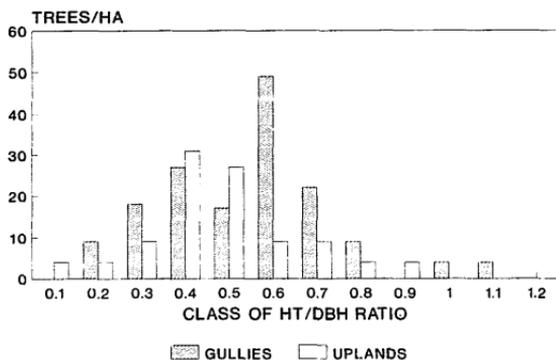


Fig. 9. Height/diameter ratio frequency diagram showing the difference between gullies and uplands.

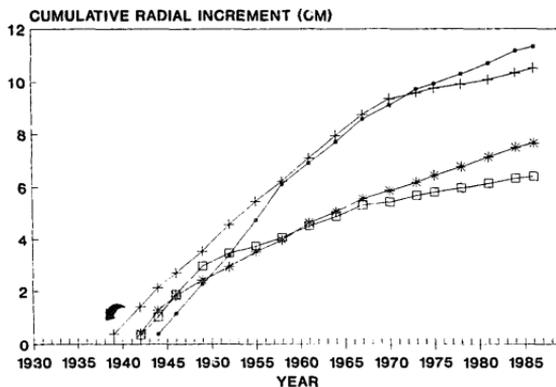


Fig. 10. Relationship of mean cumulative radial increment and age of dominant trees of *P. cembroides* subsp. *cembroides* from two gully and two upland plots. (Arrow indicates the date of the 1938 fire.)

Disturbance history

Over 70% of all pinyon pines > 30 cm dbh had basal fire scars in upland area while no scarred trees were found in gullies. Aging stem sections and wedges of scarred trees dated an extensive fire to 1938. Other more localized fires also occurred between 1938 and 1940, and in 1960. The stand was subjected to intensive goat grazing after 1938 and small fires were usually set deliberately by farmers to encourage grass sprouting. Grazing animals and fire, however, were excluded and, except for the harvest of pine nuts, the stand has been free of human disturbances since the early 1960s.

Many charcoal fragments were observed in the upper soil profile along gullies, whereas only a few pieces were found in upland soils. The greater accumulation of charcoal in gullies may have been caused both by erosive transport from uphill sites and by more wood being burned in gullies during intense fires. Windthrow was also relatively frequent in upland areas. Large trees on shallow soils on sites exposed to strong winds most frequently suffer windthrow.

DISCUSSION

Forest structure

Age and size distributions provided important information for understanding the dynamics of this pinyon pine forest. Because of large differences in growth rates and size/age relationships, size distributions alone were insufficient for the interpretation of stand development patterns.

Size distributions (Fig. 3), showing a high frequency of small stems and a few large individuals, give the impression of a balanced multi-age condition in which recruitment and mortality rates tend to be constant. Although the age distribution (Fig. 4) shows the stand is dominated by a young population, trees did not invade the stand in a continuous manner, but in discrete intervals following disturbance events. Similar age structures have been reported for other temperate forest ecosystems (Hough and Forbes, 1943; Oliver and Stephens, 1977; Lorimer, 1980; Oliver, 1981; Larson and Oliver, 1982; Stewart, 1986; Harcombe, 1986) but have not previously been noted in pinyon pine forests.

Most trees invaded the stand in a wave that began after the 1938 fire. Intensive grazing and smaller scale, human-caused fires between 1950 and 1960 probably caused high tree mortality, particularly among smaller size classes, and reduced recruitment of stems during this period. The absence of disturbances after 1960 has allowed the stand to reoccupy the available growing space and gradually exclude the recruitment of new stems.

Spatial distribution

The aggregated pattern observed in seedlings and saplings (Table 2) may reflect seed dispersal patterns and the spatial distribution of favorable microsites following the 1938 fire. The relative shade tolerance of pinyon pine (Tueller and Clark, 1975), and the fact that this species has a heavy and wingless seed, probably encouraged the establishment of dense clumps of seedlings under the canopy of parent trees that survived the fire. In some pinyon pine forests of the southwest United States, successful establishment of seedlings under the canopy of "nurse trees" (Emerson, 1932) appears to be associated with low canopy density which does not reduce light intensities below tolerance levels (Mecuwig and Bassett, 1983). Tree canopies also protect young seedlings from high temperatures and favor the accumulation of needles on the forest floor. These conditions increase soil moisture retention considerably favoring the survival of seedlings. High numbers of pinyon pine seedlings beneath canopies compared to more open sites has been reported elsewhere for pinyon-juniper communities (Sudworth, 1917; Emerson, 1932; Meagher, 1943; Johnsen, 1962; Everett et al., 1986) and may be associated with soil wettability, which decreases outward from the trees to openings (Scholl, 1971).

As tree clumps continue to grow, intense competition probably leads to high mortality rates and the regular spacing observed among larger trees (diameter classes of 1-10 and 11-20, Table 3). Tress and Klopatek (1987) suggested that mortality of pinyon pine is high and growth rates slow in the smaller size classes. As trees become dominant, however, their growth rate tends to increase and their probability of mortality decreases. The differentiation and assertion of dominance appears to occur before the dominant trees reach 20 cm in diameter in our study area.

Forest development in relation to micro-topography.

Strikingly different patterns of development occurred between gullies and uplands. After the 1938 fire, growing space was quickly reoccupied in gullies, where relatively mesic conditions and good soils favor rapid colonization and growth. Trees were taller and stem density was higher in these sites. Crown closure and a stage of stem exclusion (Oliver and Larson, 1990) was reached in approximately 20 years after which the recruitment of new trees was mainly limited by low light intensity.

In contrast, uplands, which are more xeric sites where soils are shallow and environmental conditions more stressful, the reoccupation of the site after the 1938 fire was much slower. Diameter growth was slow, and spacing between dominant trees tended to be wide. Crown closure had not occurred after 50 years and may never occur. Maximum density in these sites is probably limited by soil moisture and nutrient deficiencies rather than by light.

Uplands and gullies had different recent histories of disturbance as a result of the differences in stand structure, fuel accumulation, density of understory vegetation, and topography. A closed canopy and much denser herbaceous and shrub vegetation probably made gullies more susceptible to catastrophic fires. The higher productivity of these sites result in higher fuel accumulation which increases the intensity and frequency of fires. Because gullies are usually narrow, crowns of dominant trees overlap with each other and with the herbaceous vegetation on adjacent slopes (Fig. 2). Consequently, small fires starting in gullies or adjacent uplands can easily become crown fires in gullies and consume most of the vegetation.

The spread of fires from gullies to uplands would be slowed by a more open forest structure and less fuel accumulation. Catastrophic fires could only occur in uplands if the accumulation of fuel was sufficient to permit its spread. Even under these circumstances, fire behavior would be influenced by the pattern of forest structure, fuel accumulation and its distribution. On uplands, substantial litter accumulation occurs under dominant tree crowns. These areas alternate with litter-free areas where soils are partially or totally exposed. Such conditions probably limit the spread of fires to clumps of trees where fuel accumulation has occurred, leaving isolated trees or small groups of trees more protected.

The shape and vertical stratification of crowns may also have an important effect on the spread of fires in uplands. Trees that branch near the ground and large trees surrounded by smaller understory trees, are probably more vulnerable to surface fires. In contrast, isolated trees with high branches are less likely to suffer a crown fire.

Apparent differences in fire behavior, frequency, and intensity between gully and uplands support Jamson's (1987) hypothesis that pinyon-juniper stands developing under mesic conditions are more susceptible to fires than stands developing under xeric conditions. An opposite pattern of fire behavior and stand development in relation to topographic gradients has been suggested for other moist temperate forests (Habeck, 1970, 1976; Quirk and Sykes, 1971; Loope and Gruell, 1973; Romme and Knight, 1981). In these forests, the oldest stands occur along drainage bottoms and valleys because fires and other disturbances are infrequent and stand reestablishment following disturbances is rapid.

The present study suggests a different hypothesis for xeric environments. Although mesic conditions within gullies favor a rapid rate of stand development, microclimatic conditions are not sufficiently humid to limit the occurrence of fires. A higher accumulation of fuel and a continuous crown cover make these sites susceptible to high intensity fires. This self-perpetuating process will prevent the stands from arriving at older stages of development. These patterns of repeated intense burning of the vegetation cover will also tend to induce a permanent condition of soil instability, favoring erosion processes responsible for the formation of gullies.

Management considerations

Pine nut harvesting, grazing and firewood cutting are the most common uses of pinyon pine forests in this region. To maintain forests with characteristics to maximize these uses, it is important to control fire and grazing. These disturbances can lead to the destruction of the forest and cause severe erosion problems that can reduce site productivity.

Stands reach the stage of crown closure within gullies approximately 20 years after fire, occupying most of the available growing space. Accumulation of fuel and close contact between crowns and vegetation on surrounding slopes then increase the risks of a new fire. Before this phase of increased fire danger is reached, control of stand density by thinning intermediate and codominant trees could significantly reduce the risks of fire dispersion.

In uplands where the herbaceous and overstory vegetation is less dense and irregularly distributed, soils are more exposed. Overcutting or overgrazing in these sites destabilize soils and favor erosion. Elimination of old and large trees which have become susceptible to windthrow, insects and diseases, and which usually produce fewer cones per unit of crown area would, however, mimic the occurrence of natural, smaller scale disturbances. Under the crown of these large trees, small trees and a high accumulation of seeds should ensure reoccupation of the liberated growing space and reduce risks of surface erosion. As the stand continues to develop, thinning of trees with less vigorous crowns may substantially encourage the development of larger canopies among remaining individuals. Large crown surface areas in young and vigorous trees tend to produce the largest amounts of seeds.

Regeneration of pinyon pines occurs primarily after large disturbances. Harvesting of pine nuts after the stands have been established and are reaching a stem exclusion stage will probably have a minor effect on the patterns of regeneration and the structure of the population. After small or large scale disturbances the availability of regularly spaced seed source and the leaving of seeds on the ground will be essential to ensure rapid and successful regeneration of pines. During this period of stand development the proper control of grazing and fire will also determine the success of regeneration.

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