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Explanations of the Imbalanced Age Structure and Scattered Distribution of Ponderosa Pine within a High-Elevation Mixed Coniferous Forest

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ABSTRACT

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Many recent inventories have shown a marked drop in the amount of forest land dominated by ponderosa pine, with replacement by other species. I documented an imbalance in the size-class distribution of ponderosa pines at high elevations on the Paunsaugunt Plateau of southern Utah, due to a lack of individuals in smaller size classes. Germination and seedling survival experiments were conducted to investigate this reproductive failure. Fire-suppression policies of the 1900's, as well as the cooler and wetter recent climate, have probably made natural ponderosa pine regeneration difficult and have favored the more competitive, shade-tolerant spruce and fir. If these trends continue, this population of aged pines may be heading towards extinction. I would speculate that this phenomenon may occur among ponderosa pine populations growing at the upper elevational or northern latitudinal limit of the species.

INTRODUCTION

Many forest inventories show a marked decrease in area dominated by ponderosa pine (*Pinus ponderosa* Laws.), with concomitant replacement by other species (Cooper, 1960; Weaver, 1961; Schubert, 1974; Barrett, 1979; Eyre, 1980; Gruell et al., 1982). A paucity of ponderosa pine in smaller size-classes has been documented in many stands. Both of these changes may result from interactions of factors such as a change in climate, fire suppression policies, logging, or ranching.

This study intended to evaluate the relative importance of these factors in determining the imbalance in the size-class distribution of ponderosa pine trees at higher elevations on the Paunsaugunt Plateau, an isolated plateau of south-

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ern Utah. The primary goals were to elucidate the causes of their apparent failure to reproduce and to explain the limited and scattered distribution of old ponderosa pines growing among the high-elevation mixed coniferous forests.

MATERIALS AND METHODS

Study area

The Paunsaugunt Plateau is located within the Powell Ranger District of the Dixie National Forest and Bryce Canyon National Park. The east fork of the Sevier River and its tributaries have carved the uplifted Paunsaugunt Plateau into a series of canyons and slopes leading into a long, narrow central valley. The sides of the Plateau fall off in nearly vertical red sandstone cliffs to the lowlands below. The Paunsaugunt Plateau is approximately 49 km × 16 km, occupying a position midway between 37° and 38° N latitude, 16 km west of the 112th meridian. It slopes upward from about 2100 m in the north to 2870 m in the south.

Ponderosa pine is found near its lower elevational limit at the northern end of the Plateau where pinyon pine (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little) communities reach their upper limits (2100 m). From 2200 m to 2600 m ponderosa pine occurs in pure stands. It mixes with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at about 2200 m on north and east-facing slopes. Most of the higher elevations are covered with mixed coniferous forests including Douglas-fir, blue spruce (*Picea pungens* Engelm.), white fir (*Abies concolor* Lindl.), Engelmann spruce (*Picea engelmannii* Parre), limber pine (*Pinus flexilis* James), subalpine fir (*Abies lasiocarpa* Nutt.) and quaking aspen (*Populus tremuloides* Michx.). Bristlecone pine (*Pinus longaeva* D. K. Bailey) is common on exposed ridges with poor soils. Old individuals of ponderosa pine grow among the spruce and fir trees on the southern end of the Paunsaugunt Plateau.

Stand structure analysis

Stand structure analysis was performed to determine the size-class distribution of trees on the Paunsaugunt Plateau. Data were collected using U.S.D.A. Forest Service methods of timber inventory (Anonymous, 1970) including both variable-plot cruising and fixed-plot cruising. These methods produce a random sample of forest stands as described below.

Transects were randomly selected within stands, using aerial photographs to help define stand boundaries. Plot centers were chosen at random intervals along these transects.

In variable-plot cruising, a relaskop is used to define an infinite series of concentric plots (see Anonymous, 1970). Each tree sampled represents a given number of trees per ha. The sensitivity of this method increases for trees with a larger DBH, since they will be included in the sample at greater distances from the plot center. Fixed-plot cruising is simply sampling all trees within a circular plot of predetermined size.

Both fixed and variable-plot cruising were used at each plot center. A sample of 5249 trees covering 2316 ha was taken at mid-elevations (2380–2530 m), while 6433 trees were sampled covering 1736 ha at high elevations (2590–2775 m). Data collected were as follows: species; diameter at 1.37 m from the ground (DBH); height; and elevation. From these data, size-class distributions were developed. The distributions were compared using the *G*-test for goodness of fit (Sokal and Rohlf, 1981).

In addition, 200 mid-elevation and 200 high-elevation trees were randomly selected. Sizes were measured using a diameter tape and a clinometer. Ages were determined using core samples collected with an increment borer. Cores were sanded and the rings were counted.

Reproduction study

Three separate studies were performed to evaluate the apparent reproductive failure of ponderosa pine at high elevations on the Paunsaugunt Plateau. Seeds were collected by Forest Service crews from seven different areas. Germination tests were conducted at the Lucky Peak Nursery in Idaho. A correlation between elevation of seeds and germination percentage was calculated.

Survivorship after one, three and five growing seasons was recorded for randomly selected ponderosa pine seedlings that had been planted by Forest Service crews in clear-cut areas of the Paunsaungunt Plateau. Differences in survival of seedlings at mid versus high elevations were compared using paired *G*-tests.

One hundred 2-year-old ponderosa pine seedlings were planted at each of seven different areas within the intact high-elevation forest using a power auger. Survivorship was recorded after one growing season and results were compared using paired *G*-tests.

Fire history study

Fourteen fire-scarred ponderosa pine trees were analyzed using dendrochronological methods to develop a fire history of the Paunsaugunt Plateau (see Stein, 1988).

Study of meso-topographical and microsite conditions

Data were collected on seven physical characteristics (see Table 4) for plots surrounding each of 200 ponderosa pine trees and 200 random points within the high-elevation forest. A one-way ANOVA was performed for each variable to determine its importance in explaining the limited and scattered distribution of ponderosa pine at high elevations.

RESULTS AND DISCUSSION

Stand structure analysis

Stand structure analysis estimates the percentage of each size class of a population at a particular time. This structure is an expression of the population size and growth rate characterizing the population at a prior time and can be used, with caution, as a prediction of its future (Harper, 1977). Studies based on population structure at one point in time can provide valuable information on the stand dynamics (Blackburn and Tueller, 1970; Knowles and Grant, 1983).

Although evaluations of stand structure often are based only on diameter distribution (Smith, 1962; Leak, 1964), a more precise evaluation is sometimes possible using age (Hanley et al., 1975). Age-structure analysis was not attempted in this study because of the uncertainty of age determinations. Both missing rings and double rings, common in ponderosa pine in the study area,

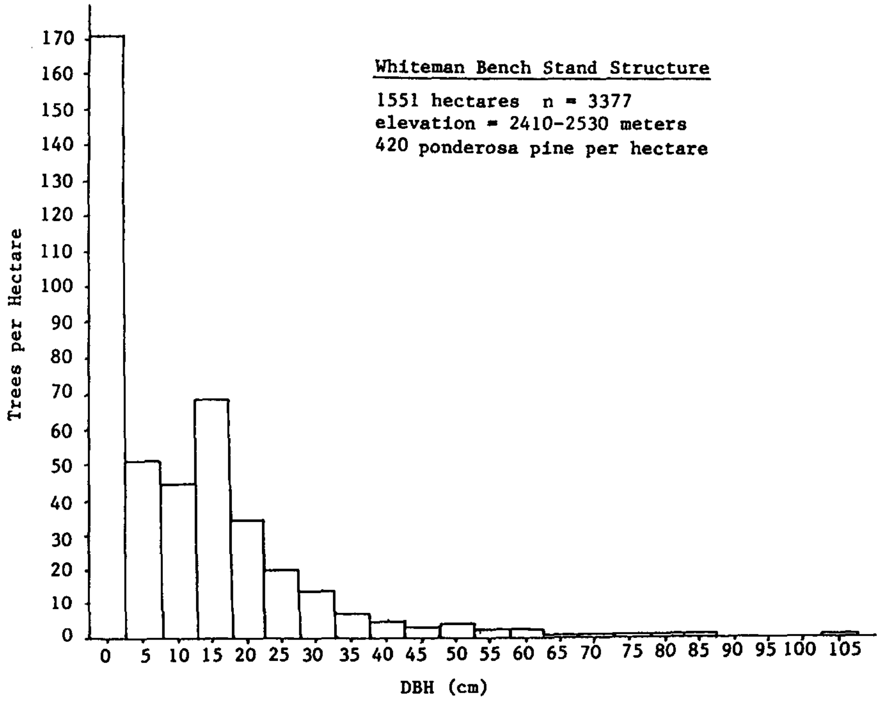

Fig. 1. Diameter structure of *Pinus ponderosa* on Whiteman Bench study area.

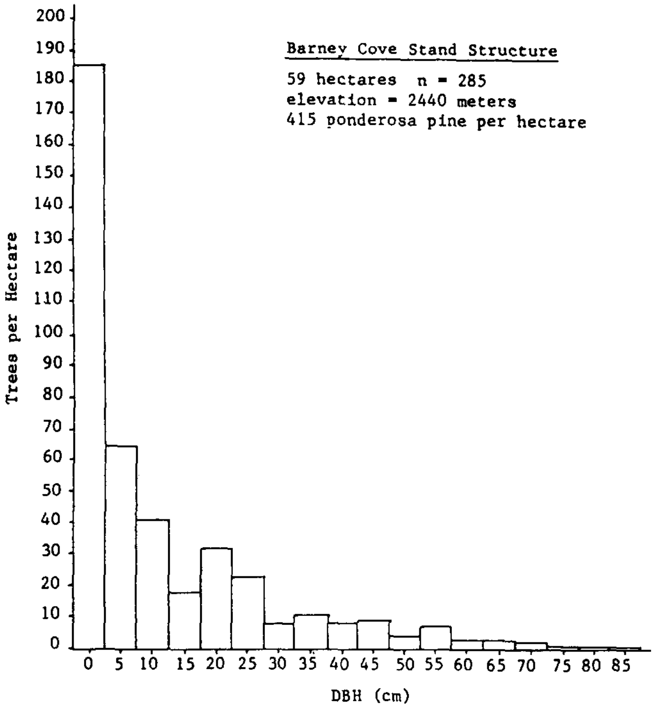

Fig. 2. Diameter of *Pinus ponderosa* on Barney Cove study area.

can cause errors in a direct count of rings. More importantly, tree cores were taken at DBH. This can introduce error due to the great variation in the number of years it takes individual trees to reach 1.37 m height, especially in the high-elevation stands studied. Knowles and Grant (1983) suggest that there are sound ecological reasons for emphasizing size distribution when analyzing forest stands.

The accepted definition of a balanced forest was proposed by the French forester De Liocourt in 1898 (Meyer and Stevenson, 1943). In an uneven-aged forest with a balanced distribution of diameter classes, the proportion of trees in each class remains fairly constant with time. The diameter distribution usually takes the form of a negative exponential curve (Figs. 1–3). When plotted on a semi-logarithmic scale this curve becomes a straight line.

Southwestern ponderosa pine forests can be described as all-aged forests composed of even-aged clumps (Cooper, 1960; Schubert, 1974). These small even-aged groups result from the fact that the best germination follows disturbance (especially fire), and because of the shade intolerance of ponderosa pine. However, when a large enough area is studied, the size distribution should follow De Liocourt's Law of a balanced forest.

For ease of presentation, the stand-structure data are grouped into 5-cm

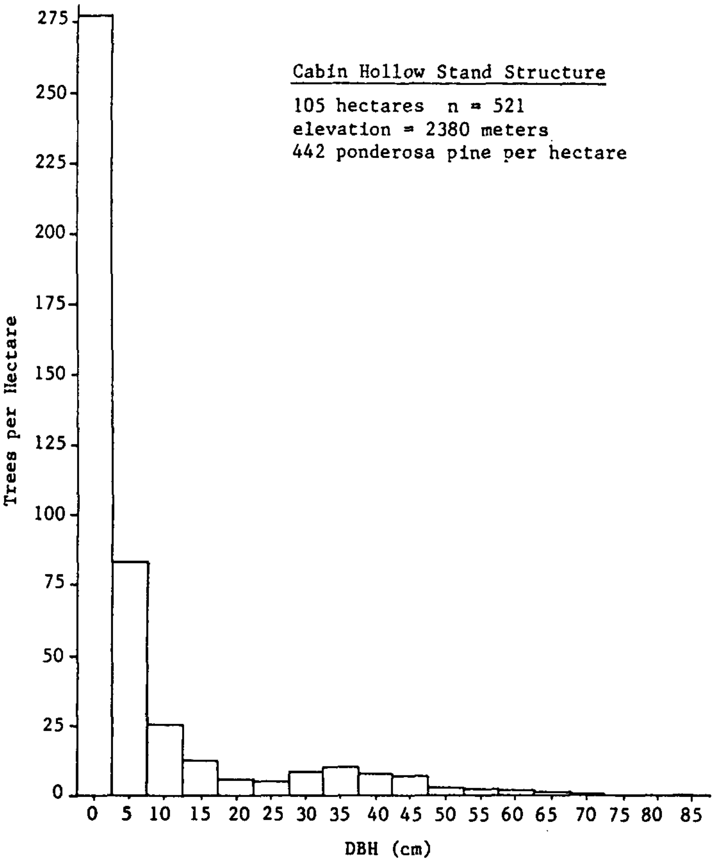

Fig. 3. Diameter structure of *Pinus ponderosa* on Cabin Hollow study area.

diameter classes. Calculation of the *G*-statistic showed that the distributions of diameters of the mid-elevation ponderosa pine stands (Figs. 1–3) were significantly different ($P<0.001$) from those at high elevations (Figs. 4–5).

Mid-elevation stands (Figs. 1–3) presented balanced distributions as defined by De Liocourt. Graphed on a semi-logarithmic scale this relationship is clearly linear for all three stands (Fig. 6). Such a stable size-distribution indicates that population sizes and distributions should remain relatively constant and may be classified as mature, steady-state stands (Rundel, 1971). There is at present sufficient reproduction to maintain the population of trees in the future.

In contrast, high-elevation stands (Figs. 4–5) did not show a balanced size distribution. These stands did not appear to be reproducing at a level to maintain a stable population, and may be termed senescent stands (Rundel, 1971). The high-elevation ponderosa pine stands, growing within the mixed conifer

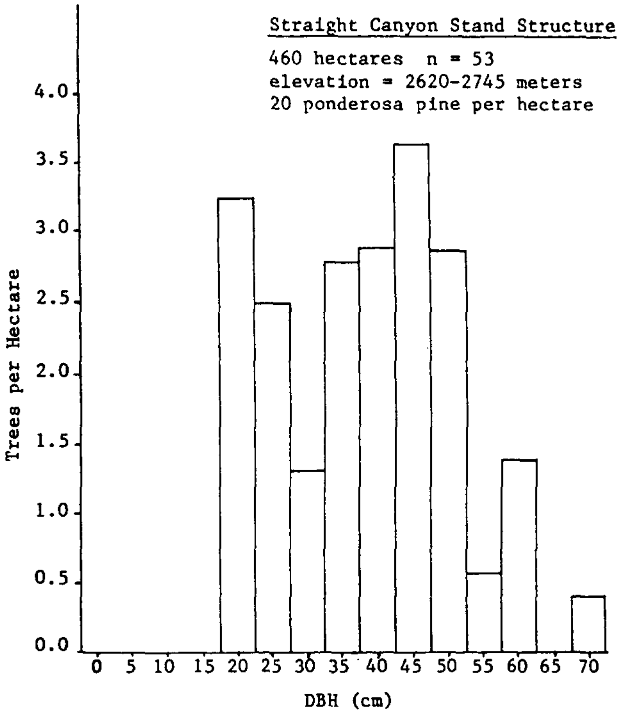

Fig. 4. Diameter structure of *Pinus ponderosa* on Straight Canyon study area.

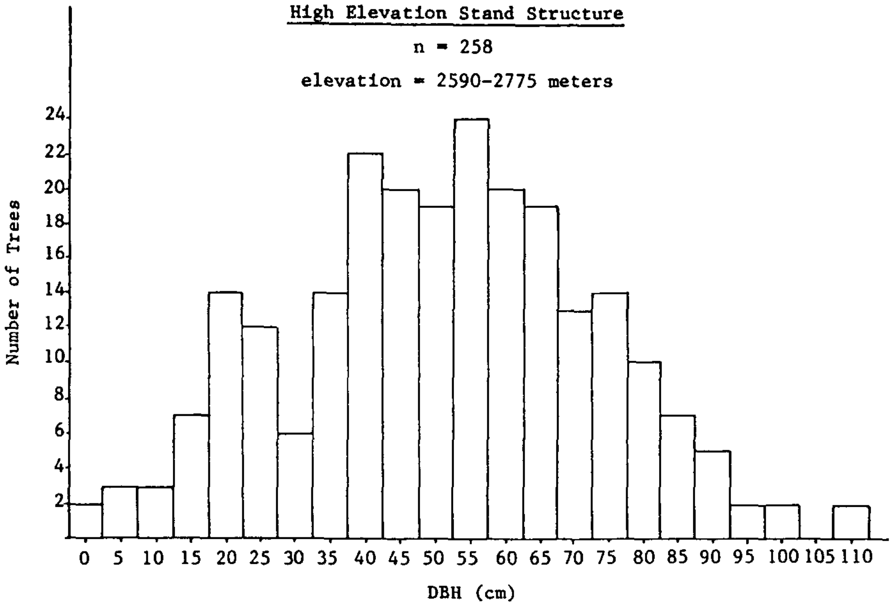

Fig. 5. Diameter structure of *Pinus ponderosa* on high-elevation study area.

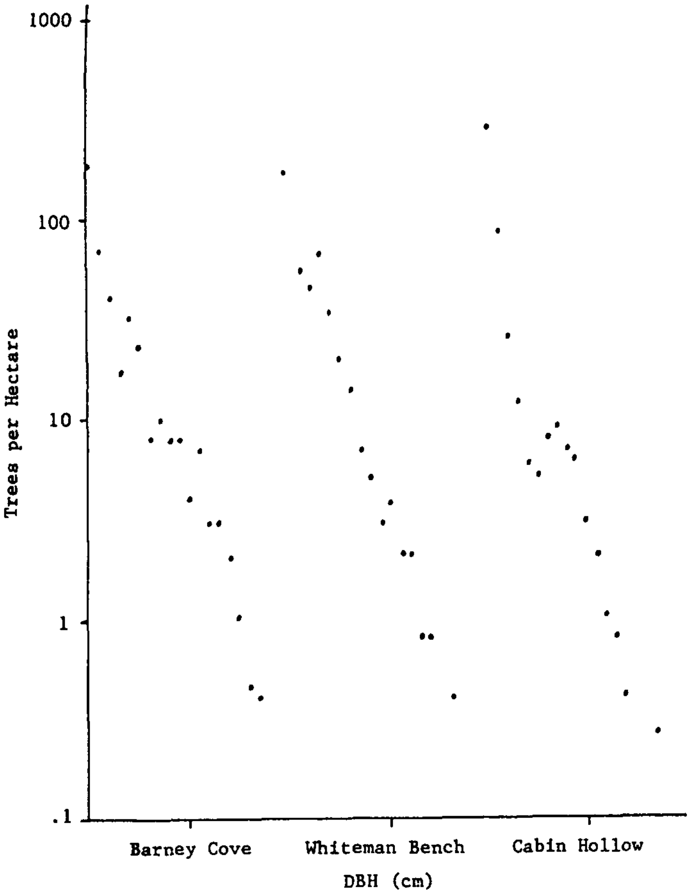

Fig. 6. Diameter structures of *Pinus ponderosa* on Barney Cove, Whiteman Bench, and Cabin Hollow study areas plotted on semi-logarithmic paper.

forest on the Paunsaugunt Plateau, may be heading towards extinction. However, some long-lived forest species have been known to maintain themselves with episodic reproduction (Harper, 1977).

Regeneration of ponderosa pine

The old ponderosa pine trees at high elevations produce cones which contain fully developed seeds. The apparent reproductive failure at high elevations may be due to nonviability of seeds or to lack of a proper environment for germination. A few natural ponderosa pine seedlings were observed in high-elevation clear-cuts and forest gaps. This suggested that the seeds are viable and that germination requirements are being met in at least a few cases.

Germination studies showed that high-elevation seeds are viable (Table 1).

TABLE 1

Germination percentages of *Pinus ponderosa* seeds planted at the Lucky Peak Nursery, Idaho

Area	Elevation (m)	Germination %
East Creek	2410	58
Ahlstrom Hollow	2410	60
Daves Hollow	2410	83
Mill Hollow	2440	77
Tropic Reservoir	2500	62
Whiteman Bench	2530	81
Badger Creek	2710	87

Correlation coefficient $r = 0.57$.

TABLE 2

Survival of 2-year-old *Pinus ponderosa* seedlings planted in clear-cuts

Elevation (m)	1st year			3rd and 5th year (pooled)		
	Alive	Total	% Alive	Alive	Total	% Alive
2410–2530	174	235	74.0	126	225	56.0
2590–2800	387	471	82.6	312	516	60.5

TABLE 3

Survival of 2-year-old *Pinus ponderosa* seedlings planted within the high-elevation coniferous forest

Location	Elevation (m)	Seedling survival		
		Alive	Total	% Alive
Coyote Hollow I	2560	22	100	22
Coyote Hollow II	2590	19	100	19
Coyote Hollow III	2620	25	100	25
Seiler Mill I	2650	24	100	24
Seiler Mill II	685	29	100	29
Seiler Mill III	2715	22	100	22
Seiler Mill IV	2745	18	100	18

Badger Creek (2710 m) was the highest site sampled and shows the highest germination percentage. Correlation suggests that germination percentage is weakly related to elevation ($P = 0.19$). Thus, high-elevation seeds appear to be at least as viable as mid-elevation seeds and reproductive failure at high elevations appears not to be due to seed inviability.

Seedlings planted in clear-cuts had high survivorship (Table 2). After one growing season, survivorship was less in mid-elevation clear-cuts than in high-elevation clear-cuts ($P < 0.05$). Results from the 3rd and 5th year pooled also showed greater survivorship in high-elevation clear-cuts than in mid-elevation clear-cuts, although statistically this was non-significant.

These results suggest that ponderosa pine seedlings can survive today at high elevations, even though very few natural seedlings were found. In clear-cuts, the seedlings benefit from increased solar radiation and temperatures, and decreased competition. Ponderosa pine seedlings do not exhibit light saturation (Tinus, 1970). My impression is that high-elevation clear-cuts have cooler temperatures and more organic soils than mid-elevation clear-cuts, so that desiccation is less of a problem.

Results of studies on seedlings planted within intact high-elevation coniferous forest stands are presented in Table 3. Survivorship after one growing season was <30% at all seven sites. Most of the live seedlings did not appear to be very healthy. Pine seedlings that germinate in dense shade seldom survive more than a few years, unless they outgrow the shade or the shade is removed (Pearson, 1950).

It appears that seeds from the high-elevation ponderosa pine stands are viable, and planted seedlings can survive and grow in high-elevation clear-cuts. I propose that reproductive failure may be due to climatic changes and fire suppression, which combine to make seedling establishment almost impossible. A cooler and perhaps wetter climate would encourage shade-tolerant trees (Douglas-fir, white fir, Engelmann spruce) that are present today and discourage natural wildfires. These species may have outcompeted the shade-intolerant ponderosa pine. In the past, periodic fires would have opened up and even fertilized areas within the forest which might have allowed reproduction of ponderosa pine seedlings. However, Forest Service policy for most of this century has encouraged fire suppression in this region.

Fire

Historical evidence indicates that fires have always been an ecological and evolutionary force in ponderosa pine forests (Weaver, 1951; Cooper, 1960). In particular, it has enhanced ponderosa reproduction. On the Paunsaugunt Plateau, fire frequencies estimated from individual trees vary from 19.5 to 47 years, and the composite fire intervals of three different areas range between 15.2 and 18.4 years before fire suppression (Stein, 1988). No fires were recorded after 1911, which corresponds with the initiation of fire-suppression policies. Before 1911, periodic ground fires may have helped recruit fire-dependent ponderosa pines at higher elevations where only scattered individuals remain today. The lack of fires since 1911 has likely made reproduction of ponderosa pine at high elevations very difficult, and favors the regeneration of shade-tolerant spruce and fir.

Climate

The climate of ponderosa pine forests in the Southwest is characterized as cool and subhumid (Schubert, 1974). The forests occur in a climatic zone between the relatively warm and dry piñon–juniper zone and the relatively cool and moist mixed conifer forests.

Climatic reconstructions derived using dendroclimatological methods suggest that there has been a general period of cooling and increased moisture over the past 380 years in the Intermountain West (Fritts, 1981). Mean annual temperatures between 1901 and 1970 were 0.44°C less than during the period 1602–1901, while annual precipitation was 10% greater.

In the past, a warmer and drier climate, coupled with periodic forest fires, may have allowed the establishment of an extensive ponderosa pine stand within the high-elevation mixed coniferous forest. The upper elevational limit of ponderosa pine may be moving downslope in response to the present cooling trend. Because low temperatures determine the upper altitudinal range of ponderosa pine (Pearson, 1920; Cochran and Berntsen, 1973), this cooling trend has probably reduced the growth and establishment of ponderosa pine and allowed spruce and fir to gain dominance. Once spruce and fir predominate in an area, the shade-intolerant ponderosa pine is unlikely to grow or reproduce without fire.

Lower temperatures and moister conditions probably are most critical during the transition from seed to seedling. Southwestern ponderosa pine seeds do not germinate until the soil temperature reaches 12.8°C (Schubert, 1970). If the climate is getting cooler, a delay in germination would result, decreasing the length of the first and most important growing season of the germinating seedling. Initial root development is an important factor in the survival of ponderosa pine seedlings (Larson, 1967). A well-developed root system helps seedlings resist drought and frost-heaving.

Ranching

During the 1800's, severe overgrazing by livestock in the West damaged ponderosa pine reproduction in some areas. However, unless grazing is very heavy, there is little effect on natural regeneration (Hill, 1917; Progulske, 1974; Currie et al., 1978), especially in dense stands of timber (Clary, 1975). Madany and West (1983) reported that heavy grazing by livestock can actually promote the establishment of tree seedlings due to the reduction of the herbaceous ground cover. Reports on the impact of grazing on seedling establishment are not consistent due to the interactions of many variables.

The Paunsaugunt Plateau has been grazed by domestic livestock since Panguitch Valley was settled in 1866 (Rathburn, 1971). Large numbers of sheep and cattle used the area from early spring to late fall. Grazing was extremely heavy until about 1920, but was reduced when Forest Service guidelines were enforced.

The extremely heavy grazing in the late 1800's and the early 1900's probably reduced the reproduction of trees in the valley bottoms. The effects of grazing on regeneration of ponderosa pine seedlings in the high-elevation areas was probably minimal because these areas are distant from water, and slopes are steep and long. However, grazing may play a minor role in explaining the lack of ponderosa pine reproduction at higher elevations.

Heavy grazing can reduce the frequency, rate of spread, and intensity of fire because of fuel reduction. There was no change in fire frequency during the heavily grazed years on the Paunsaugunt Plateau (Stein, 1988). This supports the contention that grazing had a minimal ecological impact on the high-elevation mixed conifer forest.

Logging

Heavy cutting of mature ponderosa pine, coupled with fire suppression over the past 70 years, has favored regeneration of Douglas-fir over ponderosa pine in western Montana (Gruell et al., 1982). This pattern may recur in other western forests due to the difficulty that ponderosa pine has in regenerating in the absence of fire. Logging may have had a minor role in the reproductive failure of ponderosa pine at high elevations on the Paunsaugunt Plateau, although the cutting on the Dixie National Forest over the past 70 years has been much lighter than the cutting program described by Gruell et al. (1982).

Distribution analysis of high-elevation ponderosa pine

The four most important factors affecting the distribution of ponderosa pine are: temperature (both air and soil); available moisture; competition from shade-tolerant trees; and fire. Low temperatures generally determine the upper altitudinal range, primarily by limiting growth processes (Bates, 1924; Pearson, 1931). Available moisture is most important in determining the lower altitudinal range (Schubert, 1974). Fire is most important for ponderosa pine regeneration in mixed coniferous forests which include ponderosa pine, such as the high-elevation forests of the Paunsaugunt Plateau.

Less moisture was available at ponderosa pine sites than at random sites (Table 4). Ponderosa pine trees are better adapted to deal with moisture stress than are spruce and fir trees (Schubert, 1974). This is especially so in the seedling stage, due to a rapidly developing taproot and long laterals. Ponderosa pine sites had rockier soils and higher positions on slopes than random sites

TABLE 4

Results of ANOVA comparisons of 7 meso-topographic and microsite conditions at ponderosa pine (PP) sites versus random sites

Condition	PP* sites		Random sites			
	$\bar{X}$	s	$\bar{X}$	s	F	P
Physical characteristics						
Aspect: north = 0, south = 180	58.5	39.1	47.1	50.4	3.68	0.057
Slope (%)	20.3	15.5	25.8	18.0	6.16	0.014
Soil temperature (°C)	10.2	1.2	4.4	0.2	528.17	<0.001
Soil texture: 0–30 (very rocky)	23.6	5.3	20.2	7.5	15.94	<0.001
Moisture availability: 0–100 (very moist)	52.7	9.7	64.9	12.8	65.39	<0.001
Light: 0–30 (very light)	17.3	4.8	13.1	6.4	31.59	<0.001
Position on slope: 0–10 (high)	7.4	2.4	6.2	3.2	11.11	<0.001

(Table 4). Both these factors act to decrease available moisture. One might expect steeper slopes on ponderosa pine sites because these would drain moisture quickly, but this was not the case in this study (Table 4).

Root growth in ponderosa pine responds more to soil temperature than to air temperature (Schubert, 1974). Root growth does not normally start until the soil temperature exceeds 5°C (Larson, 1967). Significantly higher soil temperatures were recorded at ponderosa pine sites than in surrounding random locations (Table 4).

Ponderosa pine trees generally benefit from all the light they can receive (Tinus, 1970). Significantly greater amounts of light were recorded on ponderosa sites versus random sites (Table 4). The increased radiation in openings in the dense forest raises temperature and promotes local air circulation. This increases evapo-transpiration, decreasing available moisture and favoring ponderosa pine over spruce and fir.

Ponderosa pine occurs more often at higher elevations on southern aspects than on northern (Schubert, 1974) and is replaced by more shade-tolerant species on northern exposures. Although the ponderosa pine plots of this study were found on more southerly aspects than the random plots, there was not a significant difference (Table 4).

SUMMARY AND CONCLUSIONS

Stand structure analysis demonstrated a marked difference between mid-elevation ponderosa pine stands and the high-elevation stands on the Paunsaugunt Plateau. The high-elevation stands did not show a balanced distribution due to a lack of individuals in smaller size-classes; a continuation of this trend would render these stands liable to extinction.

The failure of natural regeneration of ponderosa pine at high elevations is probably due to a general period of climatic cooling and increased moisture as well as the exclusion of fire for the past 75 years. Both the changing climate and fire exclusion have favored the shade-tolerant spruce and fir trees. Ponderosa pine is shade-intolerant, and in the absence of periodic fires, both seed germination and seedling establishment diminish as more shade-tolerant trees establish.

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