Pollock & Suckling 1997

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Presettlement Conditions of Ponderosa Pine Forests in the American Southwest

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Table of Contents

Cover photos. Coconino National Forest, AZ. Note high stand desity, age class diversity, ground cover, and downed logs.
Unknown, Circa 1910

INTRODUCTION

The structure, composition, and ecological processes in Southwestern ponderosa pine (Pinus ponderosa) forests have been dramatically altered from conditions existing prior to European settlement. Southwestern ponderosa pine forests occupy about eight million acres, primarily in the 11 National Forests of Arizona and New Mexico (Pearson 1950). Extensive logging and grazing over the past century has dramatically decreased the biological integrity of these forests, rapidly degrading desired ecosystem attributes such as biodiversity, productivity, stability, and resilience. Additionally, the ability of these forests to provide essential ecological goods and services such as high quality timber, grazing forage, endangered species habitat, clean water, erosion control, water storage, and recreational opportunities has been seriously compromised.

Because of the problems created by current management strategies, Federal agencies have recently called for new strategies to steer Southwestern forested ecosystems towards presettlement or natural conditions (Reynolds et al. 1992, 1996; Johnson 1995; USDI 1995). Although there is now an expressed desire to return to presettlement conditions, there has been little effort to assess existing studies or to collect new data to determine what those conditions were. As a result, plans attempting to recreate certain attributes of presettlement forests are not developed from a solid scientific foundation (e.g. Reynolds et al. 1992). Many descriptions of presettlement conditions are not supported by scientific evidence and frequently contradict existing data (e.g. Reynolds et al. 1992, 1996; Johnson 1995; Boyce 1996).

not in 2011

If Southwestern forests are going to be managed so as to recreate presettlement conditions, there is the requisite step of first determining what those conditions were (Covington and Moore 1994a; Kaufmann et al. 1994). The goal of this paper is to critically evaluate available data providing insights into the structure, composition, and successional processes of Southwestern ponderosa pine forests. Specifically, using existing data whenever possible and inference when necessary, we determine the likely density and size distributions, spatial structure, regeneration and mortality patterns, successional processes, and fire regimes in presettlement forests. We don't anticipate that this paper will quell the scientific debate over the nature of presettlement conditions, but we do hope it will place the debate on a more factual foundation.

Open stand of Ponderosa pine, Apache-Sitgreaves National Forest, AZ.

by Mearns, 1887. Library of Congress

OBSERVATIONS OF EARLY EXPLORERS

"Open and park-like" is a phrase frequently used to describe presettlement forests by today's managers. While such descriptions were used by early explorers and foresters, they also spoke of "dense, shady" forests (e.g. Beale 1858). Additionally, the term "open and park-like" was used by European-American explorers and foresters some 100 years ago to contrast Southwestern forests with Eastern Seaboard and Pacific Northwest forests, where dense, wet, deciduous and coniferous forests dominated. By comparison, the Southwest's forests were open and park-like. It is important to realize that the meaning of such terms can change with time. Today, land managers are using such qualitative terms to justify managing forests at certain tree densities that they feel represent open and park-like conditions (e.g. Reynolds et al. 1992; Johnson 1995). Unfortunately there is no way to assess whether open and park-like means the same thing to different people separated in time by almost a century. The same problems are also true for qualitative terms such as dense, shady, or heavily timbered, which also appear in the early literature. For this reason, we do not place much emphasis on qualitative, descriptive information in our assessment of presettlement conditions. However, some of the descriptions of early reports are included here, along with interpretation, in order to give the reader some perspective in understanding the early descriptions of presettlement forests.

The Beale Expedition of 1858

Beale, while crossing the Mogollon Plateau, produced a frequently quoted description "proving" the scarcity of trees in presettlement forests:

> "We came to a glorious forest of lofty pines, through which we have traveled ten miles. The country was beautifully undulating, and although we usually associate the idea of barrenness with the pine regions, it was not so in this instance, every foot being covered with the finest grass, and beautiful broad grassy vales extended in every direction. The forest was perfectly open and unencumbered with brush wood, so that the traveling was excellent."

Smith (1991) has determined that this description was written on Beale's second day in the ponderosa pine forest of the Coconino National Forest, at an elevation of 6,100 feet, where sparse pines intermingle with juniper grasslands. However, two days later, he would ascend to 7,400 feet, the heart of pine country. Here the forest was:

> "black with heavy timber...a heavy forest of pine...in the highest sense, sylvan."

Elsewhere in his journal he describes forests as "heavily timbered with pine," "thick growth of pine," "heavy growth of pine timber, "thick forest of pine covers the mountain," etc. He also describes some areas as "open forest of tall pine," "fine open forest," "open forest and mountain valley," but such descriptions are much less common. Though the quote from his description of a low elevation, open forest is continually presented by some as "the state of the forest," his complete journal contains references to dense, heavy or heavily timbered forests three times as often as references to open forests. The descriptions of dense forests however, are not often cited in current literature, leaving the uncritical reader with the sense that Beale's description of one sparsely forested area is representative of most of the Southwestern ponderosa pine region. In fact, what makes this particular journal entry remarkable, is that it is a relatively unique description of the landscape through which he was traveling. Beale made no mention of such a forest continuing for days on end. When he did mention forests he often mentioned how heavily timbered they were, or simply observed that timber was abundant. In fact, in his journal, Beale states that he avoided much of the ponderosa pine country because traveling was much quicker in the open, treeless areas of the lower elevations.

The Lang and Stewart Survey of 1909

The first timber survey of the Kaibab National Forest on the north rim of the Grand Canyon was conducted in 1909 (Lang and Stewart 1910). In their report Lang and Stewart subjectively described ponderosa pine as growing "mostly in open park-like stands or even isolated in character." Quantifying 500 acres of representative ponderosa pine stands, however, they found tree densities up to 152 trees/acre. From this survey then, a quantitative sense for what the early foresters meant by "open and park-like" can be estimated. Lang and Stewart also warned that forest conditions are extremely variable, and that great care should be taken not to confound conditions in one area with those in another. Their photographs are a good indication of such variation. Ponderosa pine forests at lower elevations mixing into piñon and juniper are very open, while those at higher elevations are much denser.

Other Early Expeditions

Dutton's (1882) description of the Kaibab Plateau as having a "succession of parks and glades, dreamy avenues of grass and flowers winding between sylvan walls," corresponds well with the assessment of Lang and Stewart. It also matches descriptions of the White

Mountains in eastern Arizona: "dense forests alternating between well watered glades" (Rothrock 1873) and "large prairies enclosed all around by dark woods" (Molhaussen 1858). All these accounts convey the impression of dense forests interspersed with grass-covered openings or parks.

It is hard to draw any quantitative conclusions from these descriptions. However they do help to illustrate the general nature of the forests. Unlike forests of the Pacific Northwest or the Eastern Seaboard, Southwest forests did not have a continuous canopy of trees. They were much more open. It is clear from the descriptions that there were open, treeless parks between stands of trees. However, it is less clear that the forest stands themselves were "open and park-like." To better understand the pattern of forests and parks in the landscape and to assess the densities of the forest stands themselves, it is necessary to rely on quantitative data.

THE SPATIAL STRUCTURE OF PONDEROSA PINE FORESTS

Quantitative evidence supports the hypothesis that presettlement ponderosa pine forests had three major spatial scales of tree-grassland patterns in ponderosa pine forests: between stands, between groups, and within groups (Lang and Stewart 1910; Woolsey 1911, Pearson 1950). At the landscape scale, large stands of trees occupying thousands of acres were found adjacent to large treeless areas also occupying thousands of acres. We refer to this scale as landscape patterns. Within a large stand of trees, or the forest proper, there was also a pattern of tree and grass openings occurring at a mesoscale. We refer to this scale as stand-level patterns. Within a stand there were dense clusters of trees grouped together. We refer to this finer scale level as group pattern. Each of these scales of pattern are discussed below.

Landscape Patterns

In the presettlement landscape, treeless areas were common and early surveys in various Forest Reserves (FR) and National Forests (NF) indicate that they occupied 32% of the Lincoln FR, 18% of the San Francisco Mountains FR, 15% of the Coconino & Tusayan NF, 5% of the Black Mesa FR, 26% of the Gila River FR, of the landscape (Plummer and Goswell 1904; Lieberg et al. 1904; Plummer 1905; Rixon 1905; Woolsey 1911). These treeless areas included ridges and ravines as well as parks. Lang and Stewart (1910) described such treeless areas as

> "irregular areas entirely free of growth-parks, broad canyon bottoms, dry southern exposures, and in many cases ridges, the latter especially near the upper limits of the forest."

Therefore the percentages cited above exceed the area of grassland parks, but suffice to give a rough approximation of their aerial extent. Woolsey (1911) describes Garland Prairie in the Coconino National Forest as 16,800 acres of open land, and mentions a timber sale area of 9,250 acres in Tusayan (Kaibab) National Forest that contained 71% forest and 29% open land. Lieberg et al. (1904) described the ponderosa pine region in the San Francisco Mountains as follows,

> "The stands surround and enclose many areas entirely devoid of arborescent growth - so-called parks. These parks are of varying extent, from a mere glade of five acres up to tracts embracing 14,000 acres."

The general sense of these early foresters was that the parks were maintained by fire, drought and wet soil conditions in the bottoms of swales. Aspen, spruce, and fir were observed invading some of the parks at higher elevations in the mixed-conifer zone (Greenamyre 1913), but in the ponderosa pine zone, these early reports (cited above) contain no mention of pine trees invading these areas.

Stand-Level Patterns

Within ponderosa pine stands, presettlement forest cover has been described as ranging from 17% (Covington and Sackett 1986) to 25% (White 1985) to rarely reaching 30% and usually not over 25% (Pearson 1923:38) to 33% (Pearson 1950:120; Madany and West 1984). Caution should be used in applying these estimates to wider areas, as four of the five are from a single ponderosa pine-bunchgrass forest growing on silty-clay loams (Fort Valley Experimental Forest, near Flagstaff), while the fifth is from Utah. Clearly, based on stand density measurements, a wider range of canopy conditions existed (e.g. Woolsey 1911; Madany and West 1983). Pearson (1950) described typical openings in ponderosa pine forests as ranging from 100–150 feet wide (approximately 0.25–0.5 acre openings). In general, at the low elevation end of the ponderosa pine forest, where trees were sparse, canopy coverage was considerably lower, while at the higher elevation end of the forest, where ponderosa pine grades into a mixed conifer forest, the canopy coverage was higher. In the middle of its range, these canopy estimates, combined with tree group size and canopy opening estimates (Pearson 1950; Cooper 1960; White 1985), suggest that the typical acre of ponderosa pine forest contained one to several groups of trees, along with a scattering of individual trees. Adjacent to these open forest stands were non-forested parks ranging in size from a few to thousands of acres.

Table 1. Age and spatial structure of Ponderosa pine forests (White 1985).

Group	No. Trees	Group Area Acres	Group Density trees/acre	Age (yr)	Min Age	Max	Range
1	26	0.37	440	156	128	173	45
2	20	0.42	284	382	335	404	69
3	44	0.72	378	189	128	309	181
4	15	0.15	652	157	127	180	53
5	3	0.05	366	246	175	329	154
6	8	0.15	348	151	121	163	42
7	14	0.15	534	354	284	402	118
8	10	0.20	306	263	231	289	58
9	30	0.27	704	160	134	181	47
10	10	0.35	180	340	138	406	268
11	20	0.35	358	169	125	293	168
12	3	0.05	366	360	342	378	36
13	19	0.42	282	156	135	168	33
14	6	0.07	457	178	145	271	126
15	4	0.10	272	310	238	373	135
16	4	0.15	153	141	109	173	64
Mean	14.8	0.25	379.9	232.0	180.9	280.8	99.8
min	3.0	0.05	153.1	141.0			33.0
max	44.0	0.72	704.0	382.0			268.0
SD	11.4	0.18	150.8	88.9	79.1	95.5	67.6

Group Pattern And Age Structure

It is well known that trees in presettlement ponderosa pine forests were non-randomly distributed, forming discrete groups of trees in a grassland matrix (Woolsey 1911; Cooper 1960; White 1985). Based on White's study, the number of trees in these groups ranged in size from 3–44 trees and occupied areas ranging from 0.05–0.72 acres. The age of trees in these groups was quite variable. The average stand age ranged from 141–382 years, while within groups, the range varied from as little as 33 years to as much as 268 years. On average, the age range within a group was 100 years (Table 1). Unfortunately, White's (1985) study reconstructed a presettlement forest from tree ring analyses, and did not include stumps and snags. It also did not include some very large trees because they were too large to core. Nevertheless, these are the best data available on group pattern and age structure.

It has often been stated that ponderosa pine stands are composed of even-aged groups, but there is little data supporting this assertion.

It has often been stated that ponderosa pine stands are composed of even-aged groups, but there is little data supporting this assertion. Most authors making this claim cite no papers, provide no data, or inappropriately cite previous papers (e.g. Reynolds et al. 1992; Schubert 1974). Many of the early foresters (e.g. Lang and Stewart 1910; Pearson 1950) made this assertion with no supporting data, but modern foresters often cite their work.

Cooper (1960) actually collected data which suggested (to him) that tree groups were even aged, and his work is often cited as evidence for an even-aged structure. However, a close examination of his methodology reveals that he actually did not directly collect age data on his stands. Instead Cooper used stand densities obtained from surveyors who themselves had used aerial photographs combined with on the ground spot checks to determine diameter and the Keen tree class of individual trees. Cooper then cored 107 trees and stratified them according to the Keen tree class system, a system which classifies trees into 16 classes based on four broad age groups and four broad vigor classes (based on the size and health of the crown). From these 107 cores Cooper developed 16 hand drawn age-tree class curves (which by his own accounts were too scattered to permit a least-squares regression).

Based on these curves, Cooper classified trees from the timber surveyor's inventories into age classes. Needless to say, this technique, which was quite sophisticated for its time, has several places where errors could occur. There is error in the original estimate of the Keen tree class and diameters, and there is error in Cooper's age-tree class curves. No confidence intervals were assigned to his estimates, but they undoubtedly would be quite large. Since Cooper did not provide any of the original data in his manuscript (i.e. the timber surveys or the age-Keen tree class curves), we are left with his interpretation of the data, which only conformed with current thinking.

Considering that more recent, sophisticated studies support the idea that groups are uneven-aged (White 1985) along with this critique of Coopers methods, we consider it valid to question whether even-aged groups of ponderosa pine ever occurred under natural conditions. This view is supported by a later reassesment by Cooper, suggesting that even age stands were likely rare (Cooper 1992).

TREE DENSITIES AND DIAMETER DISTRIBUTIONS

One of the most frequently debated questions among academics and forest managers is the actual density of presettlement ponderosa pine forests. Like many other parameters in these forests, tree densities varied as a function of the environment and past history. At the low elevational end of their range, ponderosa pine forests consist of scattered pockets of trees rising above a canopy of scrubby trees such as juniper and piñon pine (Plummer and Goswell 1904). In general, densities of ponderosa pine increase as precipitation increases at higher elevations, and then again decreases as colder, wetter conditions began to favor other conifer species such as Douglas fir, true firs, and spruce (Brown 1994). Additionally, tree density varies as a function of scale. Landscape-level measurements produce low tree density estimates, whereas within group measurements produce high tree density estimates. However, most studies of tree densities examined forests at the stand-level. Table 2 provides a list of all known estimates of presettlement tree densities at the stand-level. Not all of these estimates included all size classes. In particular the smaller size classes were usually absent, so these data are not directly comparable. A summary of the more extensive of these studies is provided below, followed by a brief discussion of studies which examined tree densities at the landscape or group scale. Unless otherwise specified, references to tree density refer to the stand-level.

One of the few thorough surveys of a forest where all tree sizes were tabulated was performed by Lang and Stewart (1910) in their survey of the Kaibab National Forest. In their study they describe in detail the diameter

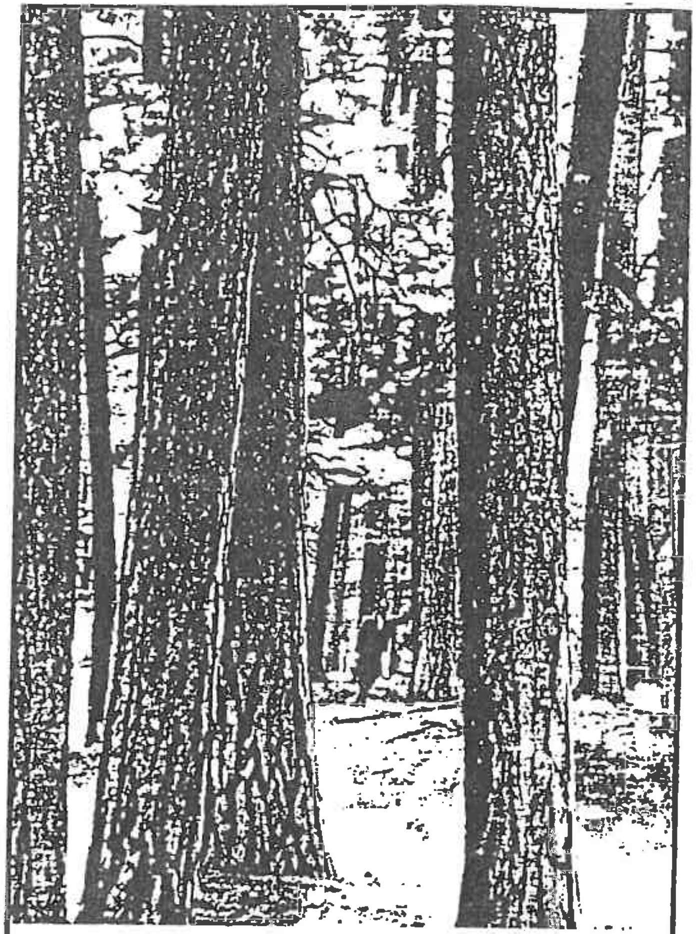
Table 2. Tree Densities in Southwestern Ponderosa Pine forests.

Location	Area acres	Density stems/ac	stems/ac dbh >12"	stems/ac dbh >18"	Author	Notes
Prescott NF	128	27.7	10.2	4.4	1	dbh>4"
Coconino NF	1888	16	13.2	8.3	1	dbh>6", malpais flats
Tusayan (S. Kaibab) NF	5920	10.7	7.9	5.3	1	dbh>6", volcanic cinders, dry soils
Carson NF	10	57	51.2	38.8	1	dbh>4", max stand
Carson NF	10	37.7	28	20.4	1	dbh>4", max stand
Tusayan NF	2	35.5	34.5	ND	1	dbh>16", max stand
Alamo (Lincoln) NF	10	46.5	39.4	22.4	1	dbh>4", max stand
Zuni (Cibola) NF	10	22.9	15.7	10.7	1	dbh>4", max stand
Jemez (Santa Fe) NF	10	35.6	30.1	20.4	1	dbh>4", max stand
Coconino NF	10	34.5	32.4	20	1	dbh>4", max stand
Datil F(N. half of Gila) NF	10	23.7	18.7	14.4	1	dbh>4", max stand
Sitgreaves NF	10	31	21.2	13.2	1	dbh>4", max stand
Apache NF	10	29.1	29.1	18.8	1	dbh>12", max stand
Datil F(N. half of Gila) NF	ND	115.8	ND	ND	1	dbh>6"
Datil F(N. half of Gila) NF	ND	130.8	ND	ND	1	dbh>6"
Coconino/Tusayan NF	8	29.8	20.7	12.7	1	dbh>4". Avg conditions in good soil
Coconino NF	336	10.3	ND	ND	1	dbh >10"
ND	ND	137.4	38	3.4	1	dbh >4"
ND	ND	150	46.2	7.2	1	dbh >4"
Apache NF	500	26.3	12.7	7.1	2	Pipo in mixed forest, avg conditions
Apache NF	500	69	27.5	14.6	2	All spp in mixed forest, avg conditions
Ft. Valley Expmtl. Forest	160	21.8	19.5	14.3	3	dbh> 9"
Kaibab NF	500	91.5	23.5	12.1	4	dbh>4" Pipo in Pipo forest, avg conditions
Kaibab NF	500	152.3	25.1	13.1	4	dbh>4"All spp. in Pipo forest, avg conditions
Kaibab NF	128	54.4	9.4	3.4	4	dbh>4"Pipo in mixed forest, avg conditions
Kaibab NF	128	185.6	23.4	9	4	dbh>4"All spp in mixed forest, avg conditions
Coconino NF	43.4	22.8	ND	ND	5	No small trees, basalt & cinder soils
Kaibab NF	10	55.9	ND	ND	5	No small trees, limestone soils
Kaibab NF	ND	40-55	ND	ND	6	1940 trees>6" dbh
White Mountains, A-S NF	<2.5	41	ND	ND	7	Basalt soils
White Mountains, A-S NF	<2.5	45	ND	ND	7	Basalt soils
White Mountains, A-S NF	<2.5	51.5	ND	ND	7	Basalt soils
White Mountains, A-S NF	<2.5	54	ND	ND	7	Basalt soils
White Mountains, A-S NF	<2.5	317	ND	ND	7	Only trees<14"dbh, basalt soils
Zion NP	ND	129	ND	ND	8	limestone soils
Ft. Valley Expmtl. Forest	18	14.9	ND	ND	9	No small trees, lava soils

1=Woolsey 1911, 2=Greenamyre 1913, 3=Pearson 1950, 4=Lang and Stewart 1910, 5=Covington and Moore 1991, 6=Rasmussen 1941, 7=Cooper 1960, 8=Madany and West 1984, 9=White 1985.

distribution of 500 acres of ponderosa pine forest (Table 3 and Figure 1). The data show that the majority of trees in these unmanaged forests were found in the smaller size classes, and that in general, the number of individuals decreased as tree size increased. Indeed, 70 % (107 out of 152 trees/acre) of the trees in their plots were less than 6" dbh (diameter breast height) in a ponderosa pine dominated forest, while trees > 6" dbh averaged 45 trees/acre. The histogram (Figure 1) shows a fairly even distribution of trees in the 7" 23" dbh classes, and then a relatively rapid decline in tree size classes > 24" dbh. However trees > 24" dbh still average just under five trees/acre and constituted approximately 40% of all trees > 18" dbh, indicating that very large trees were well represented in presettlement forests. One caveat with these data is that they were collected in the early 20th century, and thus may not truly represent presettlement conditions. While timber harvesting in the area was minimal, the history of livestock grazing and fire suppression are not well documented. If they occurred, grazing and fire suppression probably affected regeneration patterns.

Cooper (1960), measured tree densities (<14" dbh) of 317 trees/acre in Malay Gap, a relatively undisturbed ponderosa pine forest. He reported approximately 20 trees/acre in size classes > 16" dbh, which approximates the total tree density at around 337 trees/acre (ignoring trees = 15" dbh). Cooper also estimated the number of trees in each age class at four stands near Maverick. Trees established before 1900 ranged from 41–54 trees/acre with trees > 16" dbh averaging 26 trees/acre. Because these stands are not pristine, estimates of the number of trees in smaller age classes (< 60 yr) cannot be assumed to be equal to presettlement conditions, and thus are not included in this analysis.



Coconino National Forest, AZ. Note various age classes, herbaceous ground cover, and downed logs.

Unknown, Circa 1910

Woolsey (1911) tabulated densities for a number of stands in many National Forests of the Southwest (Table 2), most of which were for trees > 4" or > 6" dbh. His stand densities ranged from 11–150 trees per acre and varied as a function of soil type. Eleven trees/acre (> 6"dbh) was typical of dry soils derived from volcanic cinders, 16 trees/acre (> 6"dbh) was typical of malpais flats and 30 tree/acre (> 4" dbh) was typical of what he termed "good soils." He found 150 trees/acre (> 4" dbh) in a fully stocked blackjack stand. Woolsey didn't quantify the density of smaller trees, but described in general terms the quality of reproduction in Coconino and Kaibab National Forests. He surveyed 1,258,240 acres, of which 85% was forested, the remainder being parkland. Of the forested areas Woolsey rated 26% as having good reproduction, 32% as having fair reproduction and 42% as having poor reproduction. Good meant seedlings stock the ground, fair meant seedlings are scattered but dense in some places, and poor meant seedlings were entirely lacking or very incomplete. These descriptions can't be converted into quantitative data, but it clearly suggests that total stand densities were much higher in many of the places he surveyed when small trees were taken into account.

Figure 1. Size distribution of trees ≥ 6" DBH in 500 acres of Pondersosa pine forest. Trees < 6" DBH = 107 trees/acre. From Lang & Stewart (1910).

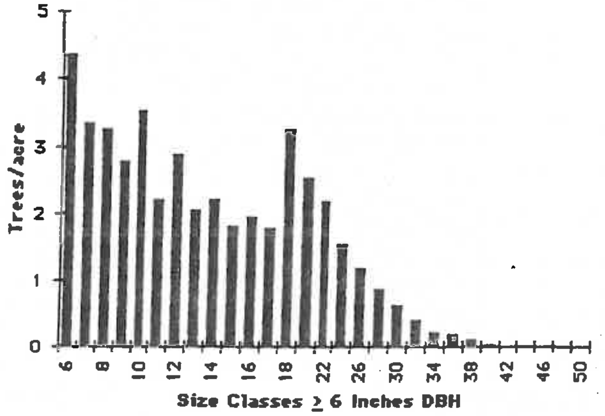


Table 3. Presettlement tree densities in Ponderosa pine forests of the Kaibab Plateau (Lang and Stewart 1909). Average of 500 acres.

	Tree Density/acre				
dbh (inches)	P. pine	D Fir	Balsam	Spruce	Total
<3 feet tall	28.9	2.9	18.0	4.3	54.0
3'-6"dbh	22.2	3.0	21.8	6.0	53.0
6	3.6	0.2	0.5	0.2	4.4
7	3.1	0.0	0.1	0.1	3.3
8	2.7	0.1	0.4	0.1	3.3
9	2.5	0.1	0.1	0.1	2.8
10	3.1	0.1	0.2	0.1	3.5
11	2.0	0.0	0.1	0.1	2.2
12	2.5	0.1	0.2	0.1	2.9
13	1.9	0.1	0.1	0.0	2.1
14	1.9	0.1	0.2	0.1	2.2
15	1.7	0.0	0.1	0.0	1.8
16	1.7	0.1	0.1	0.1	2.0
17	1.7	0.0	0.1	0.0	1.8
18	3.0	0.0	0.1	0.1	3.3
20	2.3	0.0	0.1	0.0	2.5
22	2.0	0.0	0.1	0.1	2.2
24	1.4	0.0	0.1	0.0	1.5
26	1.1	0.0	0.1	0.0	1.2
28	0.8	0.0	0.0	0.0	0.9
30	0.6	0.0	0.0	0.0	0.6
32	0.4	0.0	0.0	0.0	0.4
34	0.2	0.0	0.0	0.0	0.2
36	0.2	0.0	0.0	0.0	0.2
38	0.1	0.0	0.0	0.0	0.1
40	0.0	0.0	0.0	0.0	0.0
42	0.0	0.0	0.0	0.0	0.0
44	0.0	0.0	0.0	0.0	0.0
46	0.0	0.0	0.0	0.0	0.0
48	0.0	0.0	0.0	0.0	0.0
50	0.0	0.0	0.0	0.0	0.0
Totals	91.5	7.0	42.4	11.5	152.4

Greenamyre (1913) surveyed a mixed-conifer forest in what is now Apache-Sitgreaves National Forest. He measured the diameter of all trees > 4" dbh in five separate plots that totaled 500 acres (0.3% of the total area). His results are presented in Table 4 and Figure 2. Ponderosa pine densities averaged 26.3 trees/acre, with a mean dbh of 14.0" while all conifers averaged 68.7 trees/acre with a mean dbh of 12.8". There were 7.9 ponderosa pines/acre > 18" dbh and 16.2 conifers/acre > 18" dbh. Approximately half of both these larger pines and all conifers were > 24" dbh. No estimates of seedlings < 4" dbh were provided, but observations were made that regeneration of all coniferous species was occurring. Greenamyre did determine age-diameter and age-height relationships in the stand which suggests that for ponderosa pine and Douglas fir, the dominant species in the stand, a dbh of 4" corresponds to an age of approximately 45 years and a height of 16–18 feet. Based on size and age distributions observed in other stands (e.g. Table 2), it is likely that at a minimum, this forest had conifer densities greater than 200 trees/acre, and quite likely had considerably higher densities. Additionally, Greenamyre noted that there was significant numbers of aspen interspersed amongst the conifers, but he did not quantify their abundance.

White (1985), analyzed tree cores in an 18 acre ponderosa pine stand nine miles northwest of Flagstaff, as part of a study to determine the age structure of tree clusters. His results can be used to calculate a presettlement stand density of 14.9 trees/acre. Because this was an historical analysis and only examined extant trees that were established prior to 1875, White was not able to determine the number of trees that existed in the presettlement stand but have subsequently perished. As such, the 14.9 trees/acre constitutes a very conservative estimate of presettlement conditions.

Covington and Moore (1992), using methods similar to White (1985), examined five acres of ponderosa pine forest 25 miles south of Flagstaff, and determined that the presettlement tree density (trees established prior to 1867) was approximately 22.8 trees/acre. The same caveats applied to White's (1985) study apply to this study as well. Trees alive in 1867 but that have since perished were not included in the estimate. Thus, 22.8 trees/acre is another conservative figure. Covington and Moore (1992) also reexamined some of the plots sampled by Lang and Stewart (1910) in the Kaibab plateau. They determined that these sites had a density of 55.9 trees/acre, which roughly corresponds to Lang and Stewart's estimates for trees > 6" dbh (45 trees/acre). Since Lang and Stewart demonstrated that 70% of the trees were < 6" dbh, we infer that modern assessments underestimate presettlement tree densities because they are unable to count small trees that existed but subsequently perished.

The early surveys of Forest Reserves provide additional, coarse-scale data on average tree diameters, on a township-by-township basis, but provide little in

Figure 2. Size distribution of trees > 4" dbh in 500 acres of mixed-conifer forest. From Greenamyre (1913).

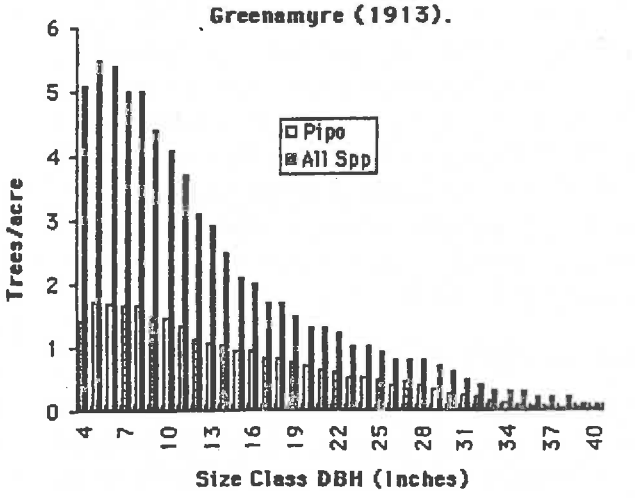


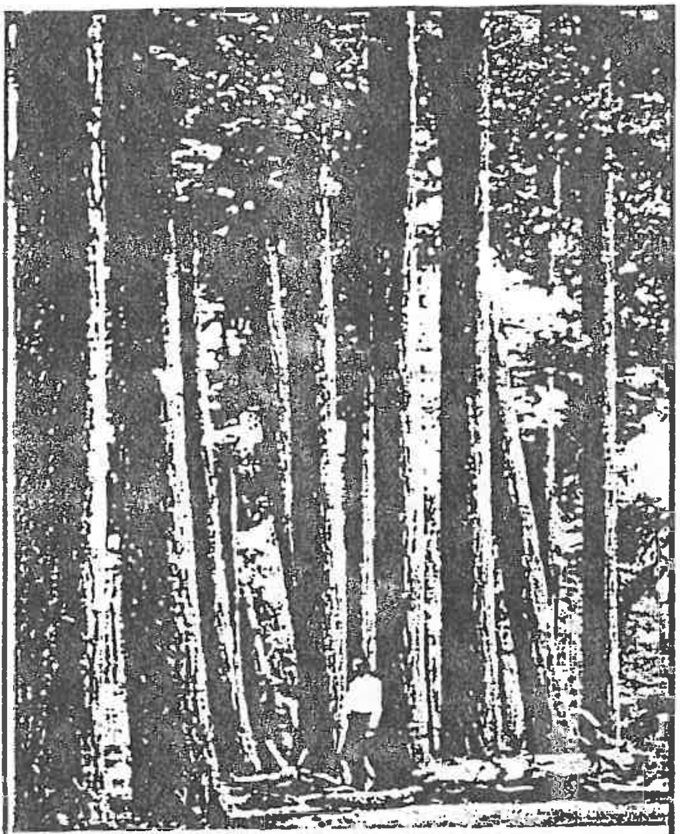
Table 4. Size distribution of Ponderosa pine and all coniferous species (>4"dbh) in 500 acres of mixed-conifer forest (Apache-Sitgreaves NF). Adapted from Greenamyre (1913).

dbh (in)	Ponderosa Pine	All Species
4	1	5
5	2	6
6	2	5
7	2	5
8	2	5
9	1	4
10	1	4
11	1	4
12	1	3
13	1	3
14	1	3
15	1	2
16	1	2
17	1	2
18	1	2
19	1	2
20	1	1
21	1	1
22	1	1
23	1	1
24	1	1
25	0	1
26	0	1
27	0	1
28	0	1
29	0	1
30	0	1
31	0	1
32	0	0
33	0	0
34	0	0
35	0	0
36	0	0
37	0	0
38	0	0
39	0	0
40	0	0
Total no. trees/acre	26	69
No. trees/acre, dbh>12"	14	31
No. trees/acre, dbh>18"	8	16
No. trees/acre, dbh>24"	4	8
Avg dbh	14	13
Avg dbh, trees 12"	20	20

the way of information on stand densities. In Black Mesa Forest Reserve, tree diameters averaged 17.5 inches, with the average in each township ranging from 12–26" dbh. In the San Francisco Mountains Forest Reserve, trees averaged 18" dbh overall and ranged from averages of 15–22" dbh in each township. Average diameter in the Gila River Forest Reserve was 19.3 inches, whereas in the sparsely forested Lincoln Reserve, the average diameter was just 9.5 inches.

Landscape-Level Tree Densities

Estimates of landscape scale tree densities can be calculated from some of the early surveys of the Forest Reserves (Plummer and Goswell 1904, Lieberg et al. 1904; Plummer 1905; Rixon 1905; Woolsey 1911). These studies don't directly provide actual density numbers, but do provide total estimates of board feet and average tree diameters for areas encompassing hundreds of thousands of acres. These areas include ponderosa pine forests, woodlands of piñon and juniper, subalpine forests, grasslands, and other non-timbered areas. Thus the numbers derived are a measure of tree densities that include areas outside of the ponderosa pine belt. Using the dbh-volume tables provided by Woolsey (1911), the total number of ponderosa pine trees can be estimated at this landscape-level. For the entire Lincoln FR ponderosa pine density = 10.7 trees/acre, Black Mesa FR ponderosa pine density = 9.2 trees/acre, San Francisco FR ponderosa pine density = 14.6 trees/acre, and Gila River FR ponderosa pine density = 5.3 trees/acre. Ponderosa pine makes up approximately half the total timber volume of the Lincoln and Gila FR's, suggesting that total tree densities were considerably higher. Ponderosa pine makes up virtually all of the timber volume in San Francisco FR, while it makes up approximately 85% if the volume in Black Mesa FR. If much of the areas covered by woodlands and grasslands at low elevation sites that are climatically unsuitable for the growth of ponderosa pine are removed from the calculations, then densities increase as follows: Lincoln FR ponderosa pine density = 19.4 trees/acre, Black Mesa FR 10.7 trees/acre, San Francisco FR density = 14.6 trees/acre (no difference), and Gila River FR density = 7.4 trees/acre. Again, these numbers do not include other timber species, but do give a better approximation of landscape-level densities of ponderosa pine in areas within and above its growing range. Eliminating areas above the growing range of ponderosa pine would further improve the landscape density estimates, but this is not possible to determine from the data. Instead one is left with a conservative and admittedly somewhat speculative estimate of landscape densities which suggest that at a minimum, pine densities of merchantable trees (i.e. probably > 6" dbh in Lincoln FR and > 12" dbh in the other FR's) were in the range of 7–20 trees/acre. If density estimates of smaller trees and other timber species are taken into account (e.g. Lang and Stewart 1910), the total densities increase considerably, upwards towards 30–100 trees/acre and possibly even higher. It needs to be reemphasized that these numbers are somewhat speculative estimates, subject to considerable, unquantifiable error, but they provide the only known landscape-level estimates of presettlement tree densities. The primary purpose of this section is simply to illustrate that estimates of tree density will vary as a function of scale (see following paragraph) and to provide minimum tree densities estimates at coarse scales.



Coconino National Forest, AZ. Note the high stand density, and downed logs.

Unknown, Circa 1910

Group Tree Densities

We are aware of only one study that estimated within group tree densities. White (1985) estimated within group densities at an 18 acre site in the Fort Valley Experimental Forest. He measured within-group ponderosa pine densities averaging 380 trees/acre and ranging from 153–704 trees/acre. These estimates did not include small trees (see description of his study above). The size of these groups ranged from 0.05–0.7 acres, and therefore these density estimates should not be extrapolated to larger areas.

Conclusions

From these studies we conclude that there was considerable variation in the density of presettlement forests stands. The total density of trees was rarely measured, so that many of these studies represent minimum densities. Based on these measures, it appears that the range of trees > 12" dbh varied from less than 1 tree/acre to upwards of 51 trees per acre, with more typical stand densities being in the range of 10 30 trees/acre, depending on the soil type. Densities of trees > 18" dbh range from less than one tree/acre to 38 trees per acre, with more typical stand densities being in the range of 5–15 large trees/acre. Even in presettlement forests, it appears that most trees were found in the smaller (< 6" dbh) size classes, so that typical total forest stand densities were probably in the range of 100–200 trees/acre. More ecologically important than the total density of all trees is the size distribution of these trees. In the presettlement forest, there were many large trees (> 18" dbh and very large trees > 24" dbh). In many forests these large trees have been harvested and subsequently replaced by high numbers of small trees.

TREE HEIGHT

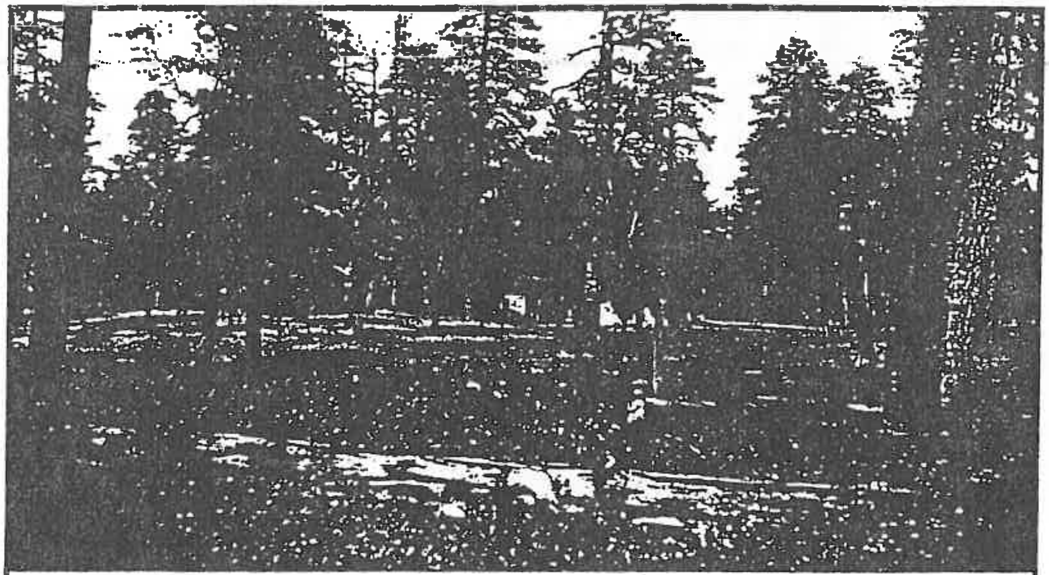
Tree heights were not precisely measured in the early surveys, but averages over large areas such as entire townships were often provided (Table 5). From these coarse scale surveys, one can see that there was a wide range of variation in tree heights. For example, pines (> 12" dbh) in the 84 townships of the Black Mesa Forest Reserve averaged 90 feet, whereas pines (>12" dbh) in the 30 townships of the Lincoln Reserve, near the lower limits of the ponderosa pine zone, averaged only 44 feet in height. A number of townships in the Black Mesa Reserve were quite productive, consisting of trees that averaged 115-125 feet in height. However, in the majority of townships, ponderosa pine (> 12" dbh) averaged between 80–100 feet. Average heights over many square miles do not convey a detailed picture of the variation in heights within stands. Unlike dbh measurements, there are no direct measurements of tree heights from the early surveys. Given the absence of detailed, stand specific data, one can only speculate as to the spatial distribution of tree heights in ponderosa pine forests during

Table 5. Average tree heights (ft) and average dbh (inches) of Forest Reserves near the turn of the century.

Data calculated from Pummer 1904; Lieberg et al. 1904; Plummer and Goswell 1904; Rixon 1905.

Forest Reserve	Black Mesa		San Francisco		Gila River		Lincoln	
	Height	dbh	Height	dbh	Height	dbh	Height	dbh
mean	90.2	17.5	82.4	18.0	86.5	19.3	43.7	9.5
maximum	125.0	26.0	95.0	22.0	na	na	60.0	12.0
minimum	60.0	12.0	75.0	15.0	na	na	30.0	7.0
Std Deviation	14.8	2.1	5.6	1.8	na	na	6.4	1.4
No. of townships (n)	84	84	27	27	101	101	30	30

presettlement times. However it is safe to say that many forests contained numerous trees well in excess of 100 feet high. It is unfortunate that so little is known about the historical distribution of tree heights, because tree height is important ecologically, especially as it relates to shade cover for both seedlings and understory herbs and seed dispersal. The quality, quantity, and timing of light striking the forest floor varies as a function of canopy height and density, but the effects of such variation in ponderosa pine forests has not been well studied. Additionally, telemetry studies consistently link owls and goshawks with the tallest available trees (AGFD 1993; Beier 1994). In general, the height of a forest determines the overall forest volume (not board feet, but space occupied by the forest) and thus influences the amount of habitat available to forest dependent species. An important contribution to our understanding of the structure of presettlement forests would be to measure the spatial distribution of tree heights at remnant pristine sites, and to relate three dimensional forest structure to specific ecological functions.



Small opening in dense ponderosa pine forest. White Mountains, AZ. Note fire scars, and large number of snags.

Mearns, August 1887. Library of Congress

FIRE IN PRESETTLEMENT FORESTS

There is overwhelming evidence in the scientific literature that prior to European settlement, fires were a widespread and frequent phenomenon in ponderosa pine forests. The role of fire in presettlement forests has been discussed frequently, and excellent reviews can be found elsewhere (Swetnam 1990; Harrington and Sackett 1992; Covington and Moore 1992, 1994a; Swetnam and Baisan 1994). Here we briefly summarize the main features of presettlement fire regimes. Historically, fire regimes in the Southwest occurred at intervals averaging approximately two to ten years, with maximum fire free intervals ranging from 8 to 26 years, depending on the location (Swetnam 1990; and references cited therein). In general, fires occurred less frequently at higher elevation (wetter) forests. Fire frequencies have declined dramatically since European settlement. Figure 3 illustrates the number of fires per decade on Langstroth Mesa in the Gila Wilderness (data adapted from Swetnam and Dietrich 1985). The dramatic decrease in fire frequency by the turn of the century is typical of most forests throughout the Southwest. Grazing by livestock and active fire suppression virtually eliminated the frequent ground fires that historically occurred. The fires in the ponderosa pine forests consumed only the understory vegetation (including seedlings) and occasionally killed larger trees by burning through old fire scars or from torching. Trees > 6" dbh were generally immune to presettlement fires. High fire frequencies kept the understory clear of dead and fallen wood. Live trees and snags, when they fell, were soon consumed by fires. This meant that in general, presettlement ponderosa pine forests were devoid of the accumulations of large woody debris that form a common and important structural component of moister forests typical of other regions of the western United States (e.g. the Pacific Northwest). In the absence of fire, organic material decomposes quite

Grazing by livestock and active fire suppression virtually eliminated the frequent ground fires that historically occurred. High fire frequencies kept the understory clear of dead and fallen wood.

Table 6 Annual percent mortality of trees killed by different agents in an intact ponderosa pine stand from 1925–1940. Mortality is measured as a percentage of trees standing in 1925. Unclassified is primarily root rot and stem rust. Stand size is 160 acres (Pearson 1950).

	Percent of 1925 stand killed, by diameter group (inches)				Percent of total 15 year mortality
Killing Agent	12–20	21–30	31+	12+	
Lightning	0.03	0.09	0.42	0.10	30.6
Wind	0.03	0.09	0.12	0.07	20.4
Bark Beetles	0.05	0.13	0.18	0.11	32.7
Mistletoe	0.02	0.01	0.03	0.02	6.1
Unclassified	0.03	0.02	0.09	0.03	10.2
Total	0.17	0.35	0.84	0.33	100

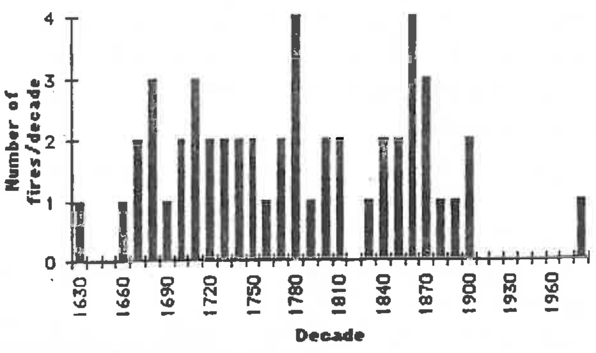
slowly in the arid southwest environment. Therefore, by consuming down wood, needles and twigs, fires also help to improve soil conditions by releasing nitrogen and other nutrients (Covington and Sackett 1986, 1990).

Analysis of historical climate records and fires return intervals suggests that fire regimes exhibit cyclic behavior on a regional scale. Fire scar chronologies throughout the Southwest demonstrate that there were particular years where fires were much more common. Conversely, there were other years when there was a low probability of fire on a regional basis. Swetnam (1990) observed that these low fire years were correlated to El Nino Southern Oscillation (ENSO) events. Severe ENSO years result in heavy rainfall in the Southwest and a reduced probability of fire. There were also fewer fires during periods of particularly wet years such as during the 1830's–1840's, which was apparently one of the wettest periods in the last 200 years.

ADULT MORTALITY

The principle causes of adult tree death in presettlement ponderosa pine forests were wind, lightning, mistletoe, and bark beetles (Pearson 1950). The reports of early foresters (Plummer and Goswell 1904; Lieberg et al. 1904; Plummer 1905; Rixon 1905; Lang and Stewart 1910; Woolsey 1911; Pearson 1950) suggest the following generalizations. Death of adult trees by fire in ponderosa pine forests was an uncommon event. Mortality-inflicting crown fires in ponderosa pine forests were rare and ground fires did not kill mature trees. Wind and lightning normally destroyed individual trees at widely spaced intervals. Large pines struck by lightning usually died within a few years, whereas younger trees recovered. Bark beetle attacks were common, but sporadic. Spatial patterns of bark beetle attacks in presettlement forests was not well documented, but qualitative observations suggest that they generally did not destroy entire stands. Mistletoe was observed attacking entire stands of trees, but whether this led to the simultaneous death of many trees is unclear. The rate of death after mistletoe infection is largely a function of initial tree vigor, and rates of mistletoe spread are fairly slow, so that trees in a stand are not all simultaneously infected (Hawksworth and Geils 1990; Hawksworth et al. 1989). Additionally, the brooms formed by mistletoe are highly flammable, and evidence suggests that fires served to prune infected branches off of trees, thus reducing the degree of infection and prolonging the life of trees (Alexander and Hawksworth 1975). Never the less, it is likely that in some instances, mistletoe infections and bark beetles did result in the death of a number of trees in close proximity over a relatively short time frame (e.g. years to decades). Data from Pearson (1950) provides an example of the relative importance of the four primary agents of mortality in relatively pristine ponderosa pine forests (Table 6). The data show that lightning and bark beetles each accounted for about 30% of stand mortality over a 15 year period, wind accounted for 20%, mistletoe accounted for 6%, while unclassified (primarily root rot and rust) accounted for the remaining 10% of the mortality. Lang and Stewart (1910) provide additional mortality figures in their survey of the Kaibab Plateau. They noted the number of board feet found in dead trees in the 30 townships (1080 mi^2) in which they subsampled 5% of the total area. Of an estimated 1,362,130 million board feet trees measured, which included only ponderosa pine > 18" dbh and all other species > 14" dbh, 2.2 % of the volume was from dead trees (these estimates only included solid, merchantable snags). Approximately half of this dead volume was the result of "bugs," which we presume to mean bark beetles. Their data also illustrates how much variation in large tree mortality there was between townships. In these townships the volume of large snags ranged from less than 0.5 % to more than 10% of the total volume, while the number of "bug killed" trees ranged from 0% to just over 10% of the total volume.

Figure 3. Fire frequency/decade in Langstroth Mesa, Gila Wilderness, NM. Apapted from Swetnam and Dietrich (1985).



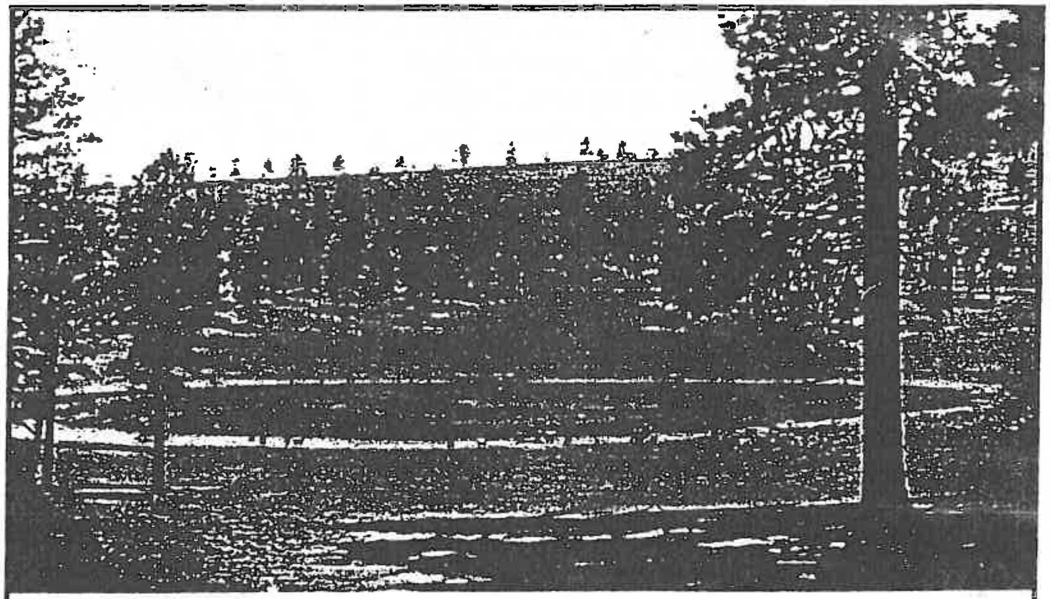
No data was provided on the size of the snags. Other historical surveys of townships have noted that the percent of trees that are snags typically ranges from 1–5%, although occasionally forests may consist of up to 10% snags (Plummer and Goswell 1904; Lieberg et al. 1904; Plummer 1905). None of these surveys mentioned the percent of snags attributable to the various snag forming agents (e.g. bark beetles, mistletoe, lightning etc.).

SEEDLING MORTALITY

Early observation of regeneration patterns, combined with more modern reconstructions of tree ages by analyzing tree cores, suggest that in presettlement ponderosa pine forests, regeneration was sporadic in both time and space. In general, high numbers of seedlings were (and still are) produced when there was a good cone year followed by an unusually wet spring. Unless this sequence of events was followed by a few more years of wetter than average summer weather, most of the seedlings did not survive.

One analysis of the historical record suggests that years favorable for seedling establishment occurred in pulses. Over a 300 year record (1575–1875), large numbers of trees established between the years 1810–1840, while almost no trees established between 1740–1790 (White 1985). In most other years establishment was quite low. Overall, 60% of the years had no tree establishment. More recently, the first 18 years of this century other than 1914, were not particularly conducive to high seedling establishment, while wetter than normal spring conditions in 1919 (in combination with overgrazing and fire suppression) allowed enormous numbers of seedlings to establish. The next 25 years following 1919, with the exception of 1929, were not particularly favorable to seedling regeneration (Pearson 1950).

Even with favorable climatic conditions, the successful establishment of a seedling was heavily dependent on microsite conditions. Soil moisture, light availability, overstory and understory competition, and susceptibility to fire are important factors determining microsite suitability. There can be little doubt that in presettlement forests, the most important of these microsite factors influencing seedling mortality was the presence of competing understory vegetation. The presence of ground cover, particularly grasses, was identified early and often as a major cause for pine seedling mortality (Woolsey 1911; Pearson 1942; Larson and Schubert 1969; Elliot and White 1987; Riegel et al. 1992). Certain grasses such as Arizona fescue (Festuca arizonica) begin their growth earlier in the season than do pine seedlings. This allows them to bring in much of the soil moisture. In general, established grasses are able to out compete pine seedlings for soil moisture. It is only when seedlings develop roots deeper than the relatively shallow grass roots that they are able to reliably obtain moisture. In addition, grasses also inhibit seedling development by shading (some grasses can grow as tall as three feet). Grasses are also known to release phytotoxic substances that inhibit the germination and growth of pine seedlings (Jameson 1968). Finally, grasses produce fuel which carry ground fires capable of destroying seedlings. These multiple effects made it extremely unlikely that pine seedlings could establish where there was understory vegetation.


Very open stand of ponderosa pine forest surrounding Crater Lake, Coconino National Forest, AZ.

Mearns, June 1887. Library of Congress

There has been some question in recent years as to whether grasses by themselves are capable of causing ponderosa pine seedling mortality or preventing seedling establishment in the absence of fire. Several studies comparing relatively pristine and degraded understories of ponderosa pine forests have demonstrated that even in the absence of fire, very little pine regeneration occurs where there is an intact understory of grasses. Madany and West (1983, 1984), in their study of nongrazed and grazed ponderosa pine forests in relict mesas of Zion National Park, observed that almost all the ponderosa pine on pristine mesas were between 100–360 years of age. There were several regeneration groves of approximately 60 years, which date back to the 1919 regeneration year that was widespread throughout the Southwest. Trees less than 100 years old had an average density of 16 trees/acres on these mesas. Conversely, a similar plateau that had been grazed had considerable regeneration, and trees less than 100 years old averaged 102 trees/acre. The nongrazed mesas had not burned since the 1891, so fire did not play a roll in seedling mortality, in this case. In a similar study, Rummell (1951) compared an isolated plateau in eastern Washington which had never been grazed by livestock and had not been burned since 1898, with a plateau that had been grazed but not logged. His data showed that the size distribution of trees > 4" dbh was similar, but that the grazed plateau had more than 2,000 ponderosa pine seedlings/acre < 4" dbh, while there were no ponderosa pine seedlings < 4" dbh on the nongrazed plateau. Both these studies emphasized the "unbelievably lush" character of the understory grasses. They also both concluded that such grass covers were typical of presettlement ponderosa pine forests and that the presence of such a grass cover limited ponderosa pine regeneration, even in the absence of fire. Where understory vegetation was not continuous, fire was likely an important agent of pine seedling mortality (see Swetnam and Baisan 1994).

Ground cover was absent underneath and often on the north side of relatively dense patches of mature ponderosa pine in an area heavily grazed for 30–40 years (Pearson 1923). Pearson's research suggests that pine seedlings did establish themselves on the edge of these grass-free environments, where competition from trees and understory vegetation was at a minimum, when climatic conditions were favorable. Ponderosa pine seedlings establish best in the presence of other trees and was thought to be related to seed rain, protection from temperature extremes, and protection from direct sunlight. Therefore successful establishment in presettlement forests required the presence of some mature trees nearby, but not too close. Pearson (1923) estimated that good regeneration occurred when seedlings were approximately 25 feet from a live tree crown.

We hypothesize that seedlings could also become established in microsites where a snag fell and was subsequently consumed by fire. Such fires burn hot enough to destroy ground cover and any shallow tree roots in the area surrounding the snag fall. This would provide a competition-free environment in close proximity to standing trees. Such a site would eventually be recolonized by understory vegetation, but there would be a window of opportunity for the establishment of seedlings, should the correct set of climatic conditions prevail (White 1985).

It appears then that there was a relatively narrow set of circumstances that allowed ponderosa pine seedlings to become established. Seedlings could establish near an existing group of trees, especially after a mature tree died, or shortly after a live tree or snag fell and was subsequently consumed by fire, but only if the right set of climatic conditions prevailed. Faced with such obstacles, it is easy to understand why there was not a continuous canopy in presettlement ponderosa pine forests and why successful regeneration was a rare event. Even in modern times, when fires have largely been suppressed (at least temporarily) and extensive grazing has dramatically reduced competition from grasses, widespread, successful regeneration of ponderosa pine in the first half of this century has been limited to just a few years due to the lack of favorable climatic conditions (Pearson 1950). In addition, the widespread regeneration early in this century (circa 1919) limited regeneration in subsequent years because of dense canopies.

SUCCESSIONAL PROCESSES

Succession, the change in plant species composition over time, is a normal process in many plant communities. In many forests, a catastrophic event such as a fire, insect outbreak, severe windstorm, or logging, often destroys most of the dominant trees. This sets the stage for a series of vegetational changes that will eventually lead to a forest (climax) that will retain a relatively constant composition until another catastrophic event destroys the stand and the process of succession begins again. Such a model has been applied to predict expected changes in forest structure for many forests in North America (e.g. Cooper 1923; Shugart et al. 1973; Spies and Franklin 1988).

Ponderosa pine forests are somewhat unique in that such a successional model likely does not apply, at least in the presettlement forests, before logging, grazing, and fire suppression commenced. Ponderosa pine forests were subject to repeated fires at intervals ranging from 2–10 years (Swetnam 1990; and references therein). Such fires, rather than being a catastrophic disturbance, became an integral part of the forest ecosystem that helped to give these forests their characteristic open structure. Early reports of forest conditions suggest that insect outbreaks and stand-destroying windstorms were

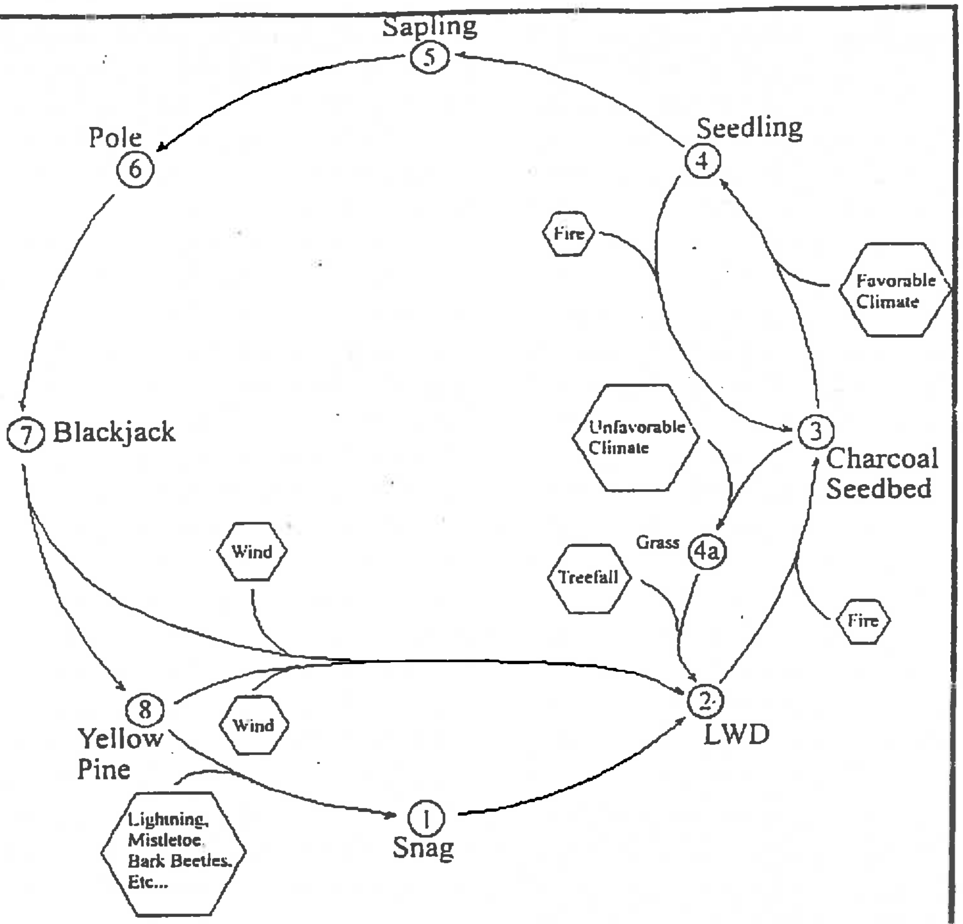


Figure 4. Individual-based successional model for Southwestern ponderosa pine forests with a grass understory. Circled numbers are successional stages, while hexagons indicate important processes driving succession.

also relatively rare (Plummer and Goswell 1904; Lieberg et al. 1904; Plummer 1905; Rixon 1905; Lang and Stewart 1910; Woolsey 1911; Greenamyre 1913). Mistletoe outbreaks probably destroyed some groups of trees, but over a long period of time. In short, there were very few stand replacement mechanisms. Therefore, rather than occurring on the scale of stands or groups of trees, it is likely that much of the succession in presettlement ponderosa pine forests occurred on a tree by tree basis. This contrasts with current models of succession in ponderosa pine forests that assume succession occurs at the scale of stands (Moir and Dieterich 1988; Reynolds et al. 1992; Boyce 1996).

Support for an individual-based successional model comes from the observations of early foresters who commented on the rates and agents of regeneration and mortality in pristine ponderosa pine forests (Plummer and Goswell 1904; Lieberg et al. 1904; Plummer 1905; Rixon 1905; Lang and Stewart 1910; Woolsey 1911; Greenamyre 1913). Their observations indicate that in general, the death of mature trees was an individual event, and that regeneration was sporadic in both time and space. Support for this model also comes from modern studies which demonstrate that groups of presettlement trees were uneven-aged (e.g. White 1985).

An Individual-based Successional Model

Based on our interpretation of the ecological literature cited in this paper, we propose the following model to explain succession in presettlement ponderosa pine/ grassland forests (Figure 4). This model occurs at the scale of individual trees (microsites), rather than at the stand scale. This model assumes that fires occur at regular intervals, that there is an abundant grass understory, and that there is no grazing or logging.

The model begins with the death of a large tree. Therefore the first stage in our model is the formation of a snag. When the tree dies it opens up above (light) and below ground resources (nutrients, water) that are quickly co-opted by adjacent trees and understory vegetation. If the tree died slowly, then this process occurs over a longer period of time. If climatic conditions are favorable, seedlings might also become established at this time. In stage two, the tree falls to the ground, in some state of decay. This stage can occur at more than one time, since parts of the snag may break off at different times. If a tree has been killed by windthrow, then the process begins at this stage. In stage three, the tree is consumed by fire. The volume of wood creates a very hot fire, destroying all understory vegetation, including the roots. This creates a nutrient- rich microsite, free of vegetation and seeds, and possibly containing some organic matter from the unburned remains of the decaying snag. In short, an ideal but ephemeral ponderosa pine seedbed is created.

In the next stage (four) the site becomes occupied either by ponderosa pine or recolonized by grasses and forbs. Understory vegetation begins to recolonize the site right away, from both encroachment by adjoining grasses and deposition of seeds from forbs and grasses. However, the establishment of ponderosa pine requires a suite of fortuitous climatic circumstances (described previously). If ponderosa pine seedlings do become established, they still must compete with the encroaching understory vegetation for a number of years. Ideally, seedlings are able to develop root systems deeper than the understory vegetation before the competition becomes too severe, thus enabling them to tap into resources (e.g. water) unavailable to the herbaceous plants. Seedlings must also contend with the threat of fire. Understory vegetation, litter from overstory trees, and the seedlings themselves are all sources of flammable material that fuel seedling-destroying ground fires. Thus seedbeds created by fallen, burned snags offer seedlings another advantage in that they clear out flammable material, thus minimizing the chance of death by fire in the first few years of a seedling's life.

Therefore, management strategies attempting to mimic presettlement conditions need to develop harvesting options at the scale of the individual tree.

Generally after a tree is > 6" dbh it is relatively immune to the death by surface fire. If a tree survives beyond the seedling stage (most do not) it slowly increases in diameter and height, progressing through various age/size classes termed sapling, pole, blackjack, intermediate and yellow pine. Sapling refers to a tree taller than breast height (approximately 4.5 ft) but < 4" dbh, poles refer to any tree 4–12" dbh, blackjack refers to trees > 12" dbh and generally less than 150 years, intermediates (between a blackjack and a yellow pine) are between 150–200 years and yellow pines are 200 years and older (Pearson 1950:37; Moir and Dieterich 1988). Finally, the tree is killed, a snag is created, and the process begins again.

Such a process suggests that there may be small clusters of trees within a larger group that are the same age, having simultaneously established in the ashes of the same fallen snag. We would also expect that given the right microsite conditions, large cohorts of trees would become established when the climate was favorable, so that a stand of trees might contain a number of trees of the same age. In general however, establishment and death were individual events that occurred at irregular intervals in both time and space. Our proposed successional model explains the uneven-aged character of ponderosa pine groups as well as explaining the tendency for these trees to occur in clusters. It also explains why colonization of open grasslands was rare in presettlement times.

CONCLUSIONS

Our analysis of existing data on the characteristics of presettlement ponderosa pine forests in the Southwest suggests that they were open forests mixed with treeless grasslands. There was considerable variation in the tree density of these forests in all sizes of trees. Trees > 18" dbh typically ranged from 5–15 trees/acre, trees > 12" dbh typically ranged from 15–45 trees/acre, and total tree densities were often in the range of 100–200 trees/acre. Tree densities varied as a function of site condition.

Trees were grouped in clusters of 2–40 trees occupying spaces of 0.05–0.7 acres and averaging about 0.25 acres. These groups were mixed among open, grass-covered patches of about 0.25–0.5 acres. Some trees occurred individually. Tree canopy usually covered less than a third of the stand. Grasses and forbs extended underneath the canopy of tree groups except where trees were exceptionally dense. Together these small patches of forest and grassland constituted a stand. At a larger scale, these stands mixed with large areas of grassland parks which were devoid of trees. These treeless areas occupied anywhere from 15–32% of the landscape in the ponderosa pine forest belt.

Mortality of ponderosa pines was generally an individual event. Mature trees died primarily from lightning, wind, bark beetles, and mistletoe. There is little evidence to suggest that entire stands or tree groups were simultaneously killed. Regeneration was dependent on the coincidence of microsite availability and tolerable climatic conditions, and thus occurred sporadically. We hypothesize that favorable microsites for seedling establishment were created when a fallen snag was consumed by fire, thus killing the competing understory vegetation. Occasionally, a succession of years particularly favorable to seedling establishment resulted in the development of even-aged cohorts, but in general, the irregular patterns of mortality and regeneration meant that stands consisted of groups of uneven-aged trees. This implies that successional processes in ponderosa pine forests occurred at the scale of the individual tree.

MANAGEMENT RECOMENDATIONS

The management implications from such a successional model are quite clear. The model indicates that succession occurs at the scale of the individual tree. Therefore, management strategies attempting to mimic presettlement conditions need to develop harvesting options at the scale of the individual tree. Current management strategies for mimicking presettlement conditions assume that succession occurs in even-aged patches, and call for harvesting techniques to create even-aged patches of various successional stages up to two acres in size (Reynolds et al. 1992). Such a strategy may be economically attractive, but it is a scientifically indefensible method for recreating presettlement conditions. Management techniques for returning to presettlement conditions should include thinning to remove small trees (keeping densities at the level of 100–200 trees/acre) in historically forested areas, removing all trees in areas that were non-forested prior to European settlement, restoring the landscape to be dominated by old growth, limiting management to small trees, and removing domestic cattle. The trees that are retained should be left in groups, with open patches of 0.25–0.5 acres between groups. This mosaic of tree groups and open (grassy) areas should be viewed as a relatively stable pattern. Where the pattern is maintained by the presence of an abundant herbaceous (primarily grass) understory which prevents most seedlings from becoming established, and understory fires, which eliminate most of the few seedlings that do become established. Boundaries between the tree groups and grass patches will slowly change in time, but it is not appropriate to consider a grass patch an early successional stage of a forest patch.

In summary, if harvesting...managing for presettlement conditions requires harvesting at the level of the individual tree rather than groups of trees, thinning high density stands, recreating a healthy understory of grasses in order to minimize forest encroachment into open areas, and finally, once grass covers have been established and trees have been thinned, reinitiating ground fires in order to further aid in the maintenance of a relatively stable forest-grassland mosaic.

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