Natural Regeneration in Relation to Environment in the Mixed Conifer Forest Type of California

H. A. Fowells and N. B. Stark

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Contents

The Authors

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The study they report here was begun by Duncan Dunning, then Silviculturist at the Station. H. A. Fowells carried out the study under Dunning's supervision from 1934 to 1941 and later summarized most of the data. N. Stark deserves much credit for assembling the data for publication.

To provide information on factors affecting natural regeneration in the mixed conifer type in California, the Forest Service started in 1931 an intensive study on the Stanislaus-Tuolumne Experimental Forest in the Sierra Nevada of California. The specific objective of the study was to determine the environmental factors favoring or inhibiting the establishment of reproduction of the major species of the mixed conifer type. These species are ponderosa pine (*Pinus ponderosa* Laws.), sugar pine (*P. lambertiana* Dougl.), white fir (*Abies concolor* [Gord. and Glend.] Lindl.), and incense-cedar (*Libocedrus decurrens* Torr.).

Some phases of the study have been reported, and observations of research workers and others at the experimental forest have helped formulate silvicultural practices for the type. But this paper is the first publication of the results giving in detail some of the environmental factors which directly or indirectly affected the establishment of reproduction.

Method of Study

Five study areas were selected on the experimental forest, located within the Stanislaus National Forest at 120° 01' W. longitude, 38° 30' N. latitude, at an elevation of about 5,200 feet. The study areas were in the drainage of the South Fork of the Stanislaus River, with two on the south-facing slope in a sugar pine-ponderosa pine type and three on the north-facing slope in a sugar pine-fir type. The general area is of high site quality, with some mature trees exceeding 200 feet in height and 7 feet in diameter. The climate of the area is characterized by dry summers, an average annual precipitation of about 36 inches with heavy snowfall, long-term temperature extremes of –12°F. and 101°F., and a frost-free season of 112 days.[1] Soils are derived from granite or diorite and were classified in the Holland and Olympic series.

In each of the five study areas a site factor plot was established, with a rodent-proof fence enclosing 2,000—2,500 square feet. The fence extended 18 inches below the ground surface and was about 5 feet high, topped with 8 inches of thin sheet metal. A description of each study area follows :

Study Area 1.—Located on a north slope at 5,280 feet elevation, about 75 feet above the level of the river and 525 feet lower than the ridge. The ground slopes 17 percent to the northwest. The area was clearcut in 1927. Only a few white firs, 1 and 3 chains to the east of the area, remained. The logging left considerable debris, and the slash was not burned. The debris was removed from the enclosure before the study began, and no weeds were allowed to grow on the bare mineral soil (fig. 1). The area received full sunlight except between the dates of July 27 to September 4, when a slight amount of shade was cast in the early morning by a large white fir.

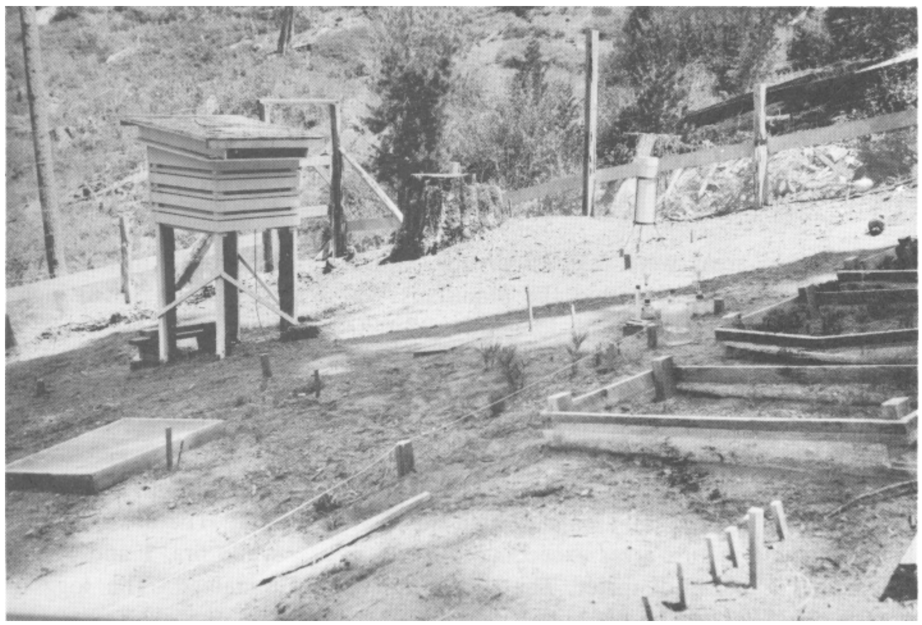
Study Area 2. —Located on a partially logged area at 5,525 feet elevation. It lies 400 feet above the river on a 17 percent northwest slope. Timber on the area was selectively cut in 1928, and logging slash was burned. The remaining debris was raked off to expose mineral soil. Partial shade fell on this area from the trees left after logging (fig. 2).

Study Area 3.—Located on a clearcut south slope at 5,290 feet elevation and 100 feet above

[1] Stark, N. **Thirty-year summary of climatological measurements from the central Sierra Nevada.** Berkeley, Calif., Pacific SW. Forest & Range Expt. Sta. U.S. Forest Serv. Res. Note PSW-36, 15 pp., illus. 1963.

Figure 1.— *Study area 1 as it looked about 1933.*

Figure 2.— *Study area 2 as it looked about 1933.*



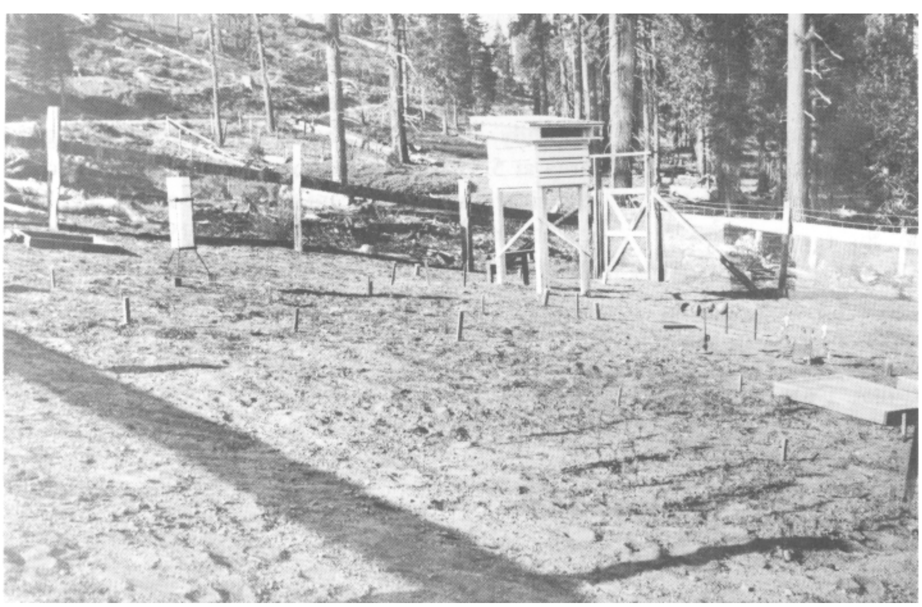


Figure 3.— *Study area 3 as it looked about 1934.*

Figure 4.— *Study area 4 as it looked about 1934.*

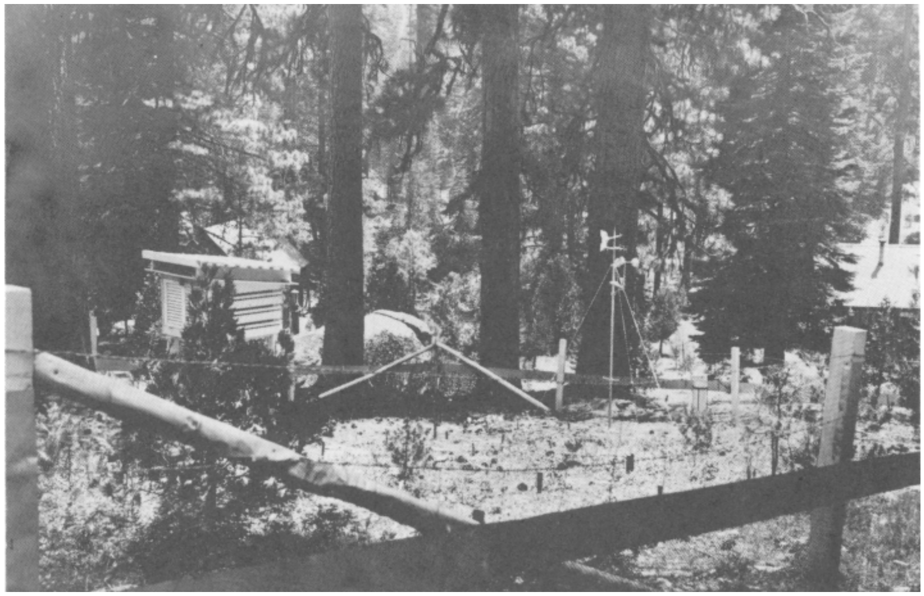


Figure 5.— *Study area 5 as it looked about 1934.*

the river. The ground slopes 24 percent to the south. The timber was cut in 1927. Although some slash was burned, the area was covered with logging debris which was raked to expose mineral soil (fig. 3). During summer days study area 3 received full sunlight except that weak shade fell on the area between 7 and 8 a.m. in early summer.

Study Area 4. — Located in an uncut stand on a south slope at 5,220 feet elevation, 30 feet above the river. The ground slopes 22 percent to the south. The litter was undisturbed (fig. 4). The area is shaded considerably in the morning, whereas full sunlight reaches the ground through part of the afternoon.

Study Area 5. — Located in a heavily shaded, uncut, north slope stand at 5,400 feet elevation, 25 feet above the river. The ground slopes 20 percent to the north. No litter was removed (fig. 5). Except for pinpoints of early morning sun, heavy shade from a dense stand of white fir poles and old sugar pines blanketed this station.

Soils in all five areas are fine sandy loams. Soil acidity varied from pH 4.8 to pH 5.5. The approximate proportions of soil fractions and wilting points as determined with sunflowers are given in table 1. From 10 to 16 wilting-point determinations were made for each sample depth at each study area.

Table 1.--Sand, *silt, and clay fractions and wilting points of soil at specified depths, Stanislaus-Tuolumne Experimental Forest*

	Study area	Soil depth	Soil fraction, mm.				Wilting point
			Fine gravel	Sand	Silt	Clay	
			1 mm	.05-.5 mm	.005-.05 mm	.005 mm	
		In.	*Percent*				
1	Clearcut north slope	0- 3	3.2	74.6	12.2	10.0	6.6
		6- 8	2.9	75.5	11.9	9.7	6.9
		11-13	2.4	70.6	12.8	14.2	6.8
		18-21	2.2	71.9	11.9	14.0	6.2
2	Partially cut north slope	0- 3	3.6	74.5	13.5	8.4	7.4
		6- 8	3.3	76.4	12.2	8.1	7.3
		11-13	3.4	75.4	12.4	8.8	7.1
		18-21	2.7	74.3	12.7	10.3	6.7
3	Clearcut south slope	0- 3	2.6	75.1	11.4	10.9	6.2
		6- 8	2.5	77.6	9.9	10.0	6.5
		11-13	3.2	77.7	8.8	10.3	5.9
		18-21	3.2	74.1	7.6	15.1	5.7
4	Uncut south scope	0- 3	3.6	76.3	11.5	8.6	6.2
		6- 8	3.2	76.6	9.5	10.7	5.3
		11-13	2.6	77.8	9.4	10.2	5.0
		18-21	3.4	75.3	9.7	11.6	4.4
5	Uncut north slope	0- 3	3.6	73.6	14.1	8.7	8.8
		6- 8	2.6	75.9	14.6	6.9	8.2
		11-13	2.1	74.0	15.0	8.9	8.2
		18-21	2.1	72.8	15.0	10.1	8.3

Climatic Measurements

At each study area the following data were recorded:

1. Air temperatures within a louvered shelter (standard U.S. Weather Bureau type) at 4.5 feet above ground, recorded by a hygrothermograph and checked daily by maximum and minimum thermometers.
2. Relative humidity in the shelter by a hygrothermograph, checked daily by a psychrometer; and evaporation from black and white Livingston porous cup atmometers set at 8 inches above the ground, during the frost-free period.
3. Wind movement (miles per day) at 15 inches above ground by 4-cup anemometer. Wind was also measured at 8.5 feet above ground at study area 4 with a 3-cup anemometer.
4. Light intensity in foot-candles—in full sunlight, partial shade, and full shade—taken with a photronic cell.
6. Soil temperatures were measured with soil thermographs and checked by "Sixes" type thermometers. Temperatures were recorded at depths of ¼, 3, and 7 inches below the surface of the bare mineral soil in the study areas. The surface of the soil was bare in areas 1, 2, and 3 but covered with litter in areas 4 and 5. Consequently soil temperatures in study areas 1, 2, and 3 are not strictly comparable with those in areas 4 and 5.
7. Soil moisture was determined by the gravimetric method weekly or at 10-day intervals from May through October for most of 8 years. Samples were taken from 0 to 3, 6 to 8, 11 to 13, and 18 to 21 inches depth in the five stations.
8. Precipitation was estimated during the growing season with standard 8-inch rain gages.

Daily observations were made between 8 and 10 a.m. and charts of recording instruments were changed on Monday morning.

Seedling Observations

Replicate groups of seed spots of the four species (sugar pine, ponderosa pine, white fir, and. incense-cedar) were set out each fall to provide seedlings for study. For several years equal numbers of seeds were planted in each spot to provide germination comparisons. Later, more seeds of the poorly germinating incense-cedar and white fir were planted to provide comparable numbers of seedlings for observation.

Seedlings were counted every 2 or 3 days during the period of germination and severe losses. Later, checks were made at weekly intervals. The losses were recorded by cause whenever it was possible to determine the cause with reasonable certainty. Principal causes of loss were:

1. Frost.—Seedlings collapse, with brown discoloration spreading from tip of cotyledons into the stem. Ultimately the seedlings wither.
2. Rodents.—Mice and pine squirrels clip off the cotyledons of pine when the seed coat is still attached, or they scratch out seedlings in search of seed; gophers burrow beneath seedlings, severing the roots (tops of a group of seedlings turn brown).
3. Insects.—Cutworms (*Euxoa excellans infelix* [Sm.]) kill seedlings by cutting their stems near the ground surface. The severed tops generally are pulled into the ground as the insect larvae feed on them. Partially eaten plants often are found protruding from the soil. Most cutworm damage occurs at night during the first month after seed germination.
5. Heat.—High soil surface temperatures cause heat lesions and killing of the cambial layer; the stems become constricted and may topple. Damage decreases as the seedlings develop woody stems.
6. Drought.—Seedlings turn brown and wither as soil moisture is depleted to the wilting point.
7. Fungi.—Damping-off organisms produce lesions on young stems at ground level, or lower.
8. Miscellaneous causes.—When none of the above causes could be identified, this category was used.

Total height of seedlings was measured at the end of each growing season for several years.

Root penetration was measured periodically by lifting seedlings to determine whether the roots were reaching depths where the soil moisture was above the wilting point.

Internal stem and surface soil temperatures were measured with thermocouples during the early part of the season when succulent stems would be most susceptible to heat damage.

Seedling survival was recorded annually for 5 years.

Environmental Differences Among Study Areas

The areas differed with respect to air temperature, precipitation, evaporation, wind movement, light intensity, soil temperature, and soil moisture, but many of the differences between areas appear minor in the averages presented here (tables 2-11).[2] Nevertheless, the differences were sufficient to produce environments favorable to different species.

It is rarely possible, however, to isolate from the data summaries one factor of the climatic environment to show its effect on the seedling. Excessively high or low temperatures which occurred when seedlings were young could be related to responses, but such occurrences are masked in the presentation of average figures in the summaries.

Air temperature.—Air temperatures have relatively little direct effect on the germination, growth, or survival of seedlings. The effect more commonly is observed indirectly in the relationship to soil temperatures and moisture.

Precipitation.—Dryness of the summer season is indicated by May-to-October precipitation (table 3). In terms of moisture which might become available to seedlings, however, the average monthly amounts of precipitation are misleading. For example, June precipitation was so dispersed that in only 2 of 8 years did it wet the soil more than a few inches below the surface. Penetration of moisture into the bare mineral soil occurred at the rate of about 1 inch per tenth-inch precipita-

[2] For a complete summary of the climatological data, see N. Stark, op. cit.

tion. Rainfall during July and August was ineffective in wetting the soil. Precipitation in September was effective only twice in 8 years. One of these months occurred in a year when precipitation was effective in June. Thus, in 5 of 8 years drought existed for a 4-month period—June, July, August, and September.

Wind movement.—Anemometers of the type used do not record low wind velocities accurately. Data on daily wind movement (table 4) should be considered on a comparative rather than an actual basis.

Evaporation.—The integration of several climatological factors is reflected in the amount of water evaporated from the white spherical Livingston atmometers (table 5). These instruments were in operation only from the middle of June to the middle of September because of the dangers of freezing before and after those dates.

Radiation and light intensity.—Black spherical Livingston atmometers were operated concurrently with the white atmometers from 1938 to 1941. The radiant solar energy occurring in the five study areas is related inversely to the ratio of the evaporation from the white spheres to that from the black spheres for the same periods of exposure. These ratios are given in table 6.

Irradiation.—Light intensity was measured photoelectrically in full sunlight, in part shade caused by the crowns of trees, and in full shade caused by the boles of trees. The measurements were taken on consecutive clear days during the latter part of August. A few measurements taken in full sunlight in mid-June gave intensities of about 10,000 foot candles.

Soil temperatures.—Soil temperatures at study areas 1, 2, and 3 differed noticeably from those at areas 4 and 5 (tables 8-10), but it must be remembered that measurements at 4 and 5 are not strictly comparable.

Soil moisture content.—Moisture apparently was available to the seedlings at depths of 6 inches or deeper during the summer at all study areas except number 4. Here the moisture content of the soil was reduced to near or below the wilting point, determined with sunflowers, for a period of a month or more each summer. In fact, near the end of the dry season in 1937, the moisture content of the soil in this area was close to or below the wilting point for the complete soil layer of 30 to 40 inches. Surprisingly, moisture was available below 6 inches in study area 5 during the growing season.

As an example of the seasonal trends, soil moisture contents in the 5 areas are given in table 11 for the year 1937.

Germination, Survival, and Growth in Relation to Environment

Germination.—Ponderosa pine germinated best of the four species. Sugar pine ranked second, incense-cedar third, and white fir last. Highest germination of ponderosa pine occurred in the south-facing open plot (area 3), but highest germination of the other species occurred on the partially cut, north-facing plot (area 2). Germination of all species on the uncut plots on both slopes (areas 4 and 5) was appreciably lower than at the other three areas.

First-year survival.—In the 8-year period, sugar pine seedlings had the highest first-year survival—42.8 percent. Survival rates of ponderosa pine, incense-cedar, and white fir were 27.3, 11.6, and 11.1 per cent, respectively.

For all species combined, the highest first-year survival was on the open north-facing plot (area 1). Survival at the end of the first year was:

Study area	*Survival percent*
1	35.1
2	31.5
3	28.4
4	6.0
5	16.9

However, the environments of the five areas affected the survival of some species more than others. Although 30 to 40 percent of the pines survived on the open south-facing slope, no white firs and only 18 percent of the incense-cedars survived on this plot. Ponderosa pine had the poorest survival under the dense white fir-sugar pine stand on the north-facing slope (table 12).

Table 2.--*Average maximum and minimum air temperatures, Stanislaus-Tuolumne Experimental Forest, May-October, 1934-41*

Month	Study area									
	1 Clearcut north slope		2 Partially cut north slope		3 Clearcut south slope		4 Uncut south slope		5 Uncut north slope	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
	°F.									
May	67.8	34.3	66.1	40.7	66.8	34.8	66.1	34.7	63.6	38.9
June	74.1	38.7	72.7	46.3	73.3	38.9	72.4	39.0	70.8	44.7
July	82.0	42.7	80.8	52.7	81.7	43.2	81.2	42.7	77.6	50.6
August	83.2	42.8	80.7	53.5	83.1	43.3	82.7	42.2	78.3	51.5
September	75.4	37.9	72.5	47.8	75.9	38.4	75.3	36.8	71.5	45.8
October	63.8	31.5	61.5	39.6	64.9	31.8	63.8	31.1	59.8	38.0

Table 3.--*Average monthly precipitation, Stanislaus-Tuolumne Experimental Forest, May-October, 1934-41*

Month	Study area				
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
	Inches				
May	1.17	0.95	1.10	1.06	0.67
June	.84	.82	.82	.67	.56
July	.13	.12	.09	.10	.08
August	.04	.03	.03	.02	.02
September	1.11	1.05	1.06	.71	.72
October	2.52	2.46	2.65	2.24	2.14

Table 4.--*Average daily wind* movement, *Stanislaus-Tuolumne Experimental Forest, May-October, 1934-41*

Month	Study area				
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
	Miles				
May	28.5	20.5	23.9	14.9	7.7
June	25.4	18.2	21.1	11.6	6.8
July	22.6	16.9	21.8	11.2	4.8
August	22.6	15.9	22.0	12.3	5.0
September	20.7	15.8	20.0	11.7	3.4
October	15.1	11.2	15.0	9.8	1.8

Table 5.--*Average daily evaporation from white atmometers, Stanislaus-Tuolumne Experimental Forest, June-September, 1934-41*

Month	Study area				
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
	Cubic centimeters				
June	36.1	39.0	38.4	27.5	24.9
July	40.2	42.8	42.7	30.4	27.2
August	41.3	41.6	45.6	32.6	29.3
September	35.0	35.1	38.6	28.2	25.0

Table 6. --*Ratio of evaporation from white atmometers to evaporation from black atmometers, Stanislaus-Tuolumne Experimental Forest, June-September, 1938-41*

Month	Study area				
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
June	0.68	0.78	0.73	0.74	0.94
July	.72	.81	.75	.76	.94
August	.73	.86	.74	.80	.96
September	.75	.84	.76	.83	.95

Table 7.--*Light intensity at midday, by degree of shade, Stanislaus-Tuolumne Experimental Forest, late August, 1934-41*

Degree of shade	Study area				
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
	Foot-candles				
Full sun	6,200	6,100	6,800	6,800	5,900
Part shade	--	470	--	810	450
Full shade	--	320	--	330	160

Table 8.--*Average monthly maximum and minimum soil temperatures, 1/4-inch depth, Stanislaus-Tuolumne Experimental Forest, May-October, 1934-41*

Month	Study area									
	1 Clearcut north slope		2 Partially cut north slope		3 Clearcut south slope		4 Uncut south slope		5 Uncut north slope	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
	°F									
May	99	35	94	39	106	38	66	47	53	43
June	117	39	115	46	123	42	76	50	59	47
July	132	43	129	52	138	45	92	54	71	53
August	130	41	125	50	142	44	92	54	72	54
September	109	34	105	44	110	38	81	48	64	49
October	79	30	70	36	92	34	59	41	49	41

Table 9.--*Average monthly maximum and minimum soil temperatures, 3-inch depth, Stanislaus-Tuolumne Experimental Forest, May-October, 1934-41*

Month	Study area									
	1 Clearcut north slope		2 Partially cut north slope		3 Clearcut south slope		4 Uncut south slope		5 Uncut north slope	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
	°F.									
May	72	46	64	46	74	48	54	47	49	44
June	82	53	75	55	82	54	60	52	54	49
July	90	60	82	63	90	62	67	57	60	55
August	87	58	78	61	91	61	67	58	61	56
September	74	48	70	52	78	52	60	51	57	52
October	57	38	49	40	63	42	48	42	47	44

Table 10.--Average *monthly maximum and minimum soil temperatures, 7-inch depth, Stanislaus-Tuolumne Experimental Forest, May-October, 1934-41*

Month	Study area									
	1 Clearcut north slope		2 Partially cut north slope		3 Clearcut south slope		4 Uncut south slope		5 Uncut north slope	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
	°F.									
May	61	51	54	49	64	54	52	50	45	44
June	70	59	64	57	71	61	56	54	50	49
July	77	66	72	66	78	69	62	60	57	55
August	74	65	68	64	78	70	62	61	58	56
September	63	56	59	56	70	63	57	56	54	52
October	50	44	46	43	67	50	48	47	46	45

Table 11. --Soil moisture content, oven dry weight basis, at four depths, Stanislaus-Tuolumne Experimental Forest, May 21-November 26, 1937

Date	Study area 1 Clearcut north slope				Study area 2 Partially cut north slope				Study area 3 Clearcut south slope				Study area 4 Uncut south slope				Study area 5 Uncut north slope			
	Depth in inches				Depth in inches				Depth in inches				Depth in inches				Depth in inches			
	0-3	16-8	11-13	18-21	0-3	6-8	11-13	18-21	0-3	6-8	11-13	18-21	0-3	16-8	11-13	18-21	0-3	6-8	11-13	18-21
	-Percent-																			
5/21	10.4	14.5	15.2	16.9	27.8	18.0	18.1	18.7	9.8	13.6	14.1	16.4	13.2	15.7	14.8	9.5	28.0	19.6	21.3	20.4
5/28	7.9	14.6	14.9	15.1	15.4	17.0	17.5	17.8	6.0	13.1	12.1	13.2	14.3	15.4	14.2	9.3	16.0	19.2	20.9	20.2
6/4	10.0	13.6	14.1	15.4	15.8	15.2	15.7	16.2	6.3	11.7	12.0	11.1	15.0	13.3	13.5	10.4	15.8	18.2	20.1	20.2
6/11	10.7	15.0	14.4	15.4	20.3	16.3	16.0	16.0	7.4	10.6	10.4	10.8	16.9	12.8	11.6	10.5	15.4	18.0	19.2	20.1
6/18	11.5	14.8	14.6	14.4	27.2	20.3	19.2	17.1	11.6	10.9	11.4	11.1	11.3	10.7	12.1	11.4	24.5	18.6	18.7	19.6
6/25	6.1	14.0	14.1	14.5	14.0	16.4	15.8	16.1	7.4	10.9	10.7	11.0	9.0	9.6	11.4	9.6	16.3	17.4	19.3	19.4
7/2	4.1	13.2	14.0	13.3	8.5	'14.7	15.1	15.2	3.9	10.9	11.2	10.9	9.5	9.3	8.3	7.4	10.9	16.6	17.3	17.8
7/9	3.5	12.5	13.4	14.3	4.3	13.2	13.7	13.5	2.4	10.4	10.8	10.4	4.5	7.4	6.8	5.6	4.8	16.2	16.7	17.9
7/16	7.2	13.0	13.9	14.6	6.2	14.5	13.6	14.0	3.3	10.3	11.1	10.8	2.8	7.7	7.2	7.6	10.0	15.0	16.3	17.0
7/22	7.5	13.8	14.0	13.0	6.3	12.6	12.4	13.0	2.8	11.2	11.1	11.4	4.5	6.9	6.3	6.0	7.5	13.5	14.3	16.1
7/30	3.1	11.9	13.1	12.2	5.6	10.7	11.6	12.2	3.2	10.8	11.0	10.5	5.5	6.6	6.0	5.5	8.3	12.8	13.0	14.2
816	4.6	12.0	12.6	12.6	6.3	10.1	11.7	10.9	3.0	9.1	10.7	10.5	4.8	6.1	5.8	5.4	7.5	12.6	12.5	13.2
8/13	1.8	9.2	11.9	11.9	4.3	8.5	10.0	9.8	2.1	8.8	10.2	10.0	3.2	5.9	5.5	5.1	6.8	11.4	10.6	10.6
8/20	2.2	9.2	11.4	15.3	4.0	8.2	9.5	10.0	2.3	9.3	10.8	10.5	3.5	5.1	5.1	4.8	5.5	10.3	10.2	9.7
8/27	2.0	10.4	12.0	14.5	2.7	7.4	9.5	9.7	2.0	9.9	10.5	10.5	2.4	6.2	5.6	5.1	4.1	10.2	9.9	10.1
9/3	1.9	11.3	13.5	15.1	5.2	9.2	9.7	9.2	2.3	10.1	9.8	10.0	1.7	5.5	5.8	5.4	3.2	10.0	10.5	10.6
9/10	2.2	10.8.	11.3	12.3	3.8	7.6	9.2	9.4	2.2	8.4	10.5	10.6	5.8	5.2	5.1	5.1	4.1	10.0	10.4	10.1
9/17	1.8	11.4	15.8	12.6	3.2	7.4	9.0	9.3	2.0	7.2	9.9	10.0	2.1	4.7	5.0	5.0	3.2	10.7	10.4	10.2
9/24	3.2	10.7	11.4	11.0	3.4	8.1	8.2	8.2	2.0	8.5	9.9	9.7	1.9	5.3	4.9	4.7	3.9	9.4	10.2	10.1
10/1	3.9	11.2	12.3	12.3	5.3	8.7	8.5	7.7	2.8	8.2	9.1	9.8	3.9	5.1	4.8	4.8	6.6	9.9	11.3	11.3
10/3	21.2	15.4	--	--	30.2	20.0	--	--	20.6	7.7	--	--	13.9	14.0	--	--	12.7	10.3	--	--
10/8	11.3	13.4	13.8	13.2	23.4	17.9	16.9	12.9	9.8	10.2	9.5	9.2	13.2	11.1	5.0	5.4	22.2	9.6	9.4	9.4
10/15	20.0	19.7	13.0	10.9	25.6	20.2	18.9	10.1	16.8	13.5	9.7	9.8	12.9	6.3	5.5	3.6	12.7	9.8	10.0	10.4
10/22	8.8	13.6	15.5	10.8	12.1	17.4	16.4	16.5	7.1	10.4	10.6	11.3	10.4	10.5	5.8	5.7	11.3	10.0	10.1	10.8
10/29	8.2	15.1	14.0	13.9	20.1	15.4	14.4	14.1	4.6	12.2	12.0	11.1	9.1	7.7	6.4	5.9	19.3	11.2	11.2	10.9
11/5	5.3	13.8	15.2	12.8	9.4	12.7	12.0	13.1	2.8	10.4	10.2	9.9	7.3	6.2	5.5	5.0	7.9	10.8	10.2	10.1
11/8	42.4	21.9	19.8	17.6	38.2	23.6	19.7	19.0	38.7	20.8	18.7	19.4	28.5	18.4	19.5	18.6	56.5	11.6	11.7	10.6
11/26	20.5	19.8	16.7	19.9	27.6	20.2	20.3	20.2	30.7	23.2	19.8	19.7	27.9	20.0	16.7	19.9	44.2	27.1	23.2	23.3

Causes of first-year mortality.—Cutworms and drought were the two greatest causes of loss. [3] During the 8-year period cutworms killed 30 percent and drought killed 25.5 percent of all the seedlings which started in the five study areas. Cutworms showed a preference for incense-cedar, taking 52 percent of the seedlings. Other losses to cutworms were white fir, 31 percent; ponderosa pine, 29 percent; and sugar pine, 10 percent. Insect-caused losses were greater on the north-facing slope than on the south-facing slope.

Losses from drought differed but little by species, ranging from 20 to 29 percent. Incense-cedar was apparently the most resistant, but the differences among the species may not have been significant.

Losses from drought did vary appreciably among the five study areas. The losses were: area 1, 8 percent; area 2, 19 percent; area 3, 24 percent; area 4, 50 percent; and area 5, 44 percent. The very low loss in area 1 and relatively low losses in areas 2 and 3 can be explained partly by the amount of available moisture and by the root development of the seedlings. Moisture was always available there below a depth of 6 inches. Clearing of vegetation in areas 1 and 3 decreased the use of moisture, and evaporation did not reduce the soil moisture content must below the surface. Soil moisture contents were lower in area 2, with partial timber cover, but still did not reach the wilting point below 6 inches. There is evidence that reduction to the wilting point as determined by sunflower does not necessarily indicate inavailability of moisture to pine seedlings. [4] Although moisture appeared to be available at study area 5, roots may not have penetrated deeply enough to reach the moisture (table 13).

[3] Fowells, H. A. **Cutworm damage to seedlings in California pine stands.** Jour. Forestry 38:590-591. 1940.

[4] Fowells, H. A., and Kirk, B. M. **Availability of soil moisture to ponderosa pine.** Jour. Forestry 43:601-604. 1945.

Table 12.--*First-year survival, by species and study area, Stanislaus-Tuolumne Experimental Forest, 1934-41*

Species	Study area: 1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
	Percent				
Ponderosa pine	48.6	26.7	30.9	2.4	4.0
Sugar pine	51.5	60.7	37.5	13.2	36.0
Incense-cedar	8.8	13.6	17.8	0.0	11.1
White fir	1.3	19.9	0.0	1.0	18.5

Table 13.-- *Root penetration of current year seedlings, Stanislaus-Tuolumne Experimental Forest, mid-July, 1940*

Species	Study area: 1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut north slope
	Inches				
Ponderosa pine	14.4	8.6	9.2	7.0	5.1
Sugar pine	17.2	17.0	--	9.0	6.9

Rodents, frost, and heat were only minor causes of loss under the conditions of study, in which screen covers protected the seedlings in the early part of the season. But even with the protection of screens, rodents took 6 percent of the seedlings; without screens, they probably would have taken all the seed planted.

Measurements of temperatures showed that minimums were higher and maximums were lower under the screens.[5] Nearly all the losses from frost occurred in the cleared areas. White fir and sugar pine were the most susceptible to frost injury. In the cleared area on the south-facing slope, 18 percent of the sugar pine and 26 percent of the white fir were killed by frost, but only 3.5 percent of the ponderosa pine and 6 percent of the incense-cedar. Average losses from frost at all study areas were: ponderosa pine, 1.3 percent; sugar pine, 8.0 percent; white fir, 9.9 percent; and incense-cedar, 2.4 percent.

Although protective screens covered the seedlings during the early part of the season, they were removed after the seedlings shed their seed coats. Surface-soil temperatures—or actually temperatures at ¼-inch depth—sometimes reached 160°F. at area 3, but very few seedlings were killed by heat lesions. Only about 1 percent of the seedlings in area 3, a small fraction of a percent in areas 1 and 2, and none in areas 4 and 5 were killed by high surface-soil temperatures. Of areas 1, 2, and 3, number 2 had the fewest hours per year during which the surface-soil temperature exceeded 130°F. (table 14). No temperatures over 130° were recorded in areas 4 and 5, partly because of the overhead shade and partly because of the placement of the elements beneath litter and in the soil.

A stem temperature of about 130°F. is considered to be lethal to very young seedlings.[6] Temperatures were measured in the stems of ponderosa and sugar pine seedlings several months old with a copper-constantan thermocouple drawn into a glass capillary. Internal temperatures of sugar pine seedlings averaged 125° when the soil-surface temperature averaged 135°, and the temperatures of ponderosa pine seedlings averaged 134° with a soil-surface temperature of 136°.

Fungi also were a negligible cause of first-year loss (tables 15 and 16).

Subsequent survival.—After 5 years, survival of sugar pine was best; ponderosa pine, second; incense-cedar, third; and white fir poorest (fig. 6). Considering all species together, highest survival after 5 years was in areas 3 and 2; lowest in areas 4 and 5, the heavily timbered sites (fig. 7). The rapid drop in survival in area 1 resulted from loss of sugar pine seedlings which had been attacked by an unidentified tip insect.

It is of interest that the best survival of sugar pine occurred in area 2, the partially cut plot where minimum air temperatures were higher than in the other study plots. Also, only in this plot did any white fir survive as long as 5 years. Sugar pine. and white fir were the most sensitive

[5] Fowells, H. A., and Arnold, R. K. **Hardware cloth seed-spot screens reduce high surface soil temperatures.** Jour. Forestry 37:821-822. 1939.

[6] Baker, Frederick S. **Effect of excessively high temperatures on coniferous reproduction.** Jour. Forestry 27: 949-975. 1929.

Table 14.--*Hours per year during which soil temperatures at 1/4 inch exceeded 130°F., Stanislaus-Tuolumne Experimental Forest, 1934-41*

Years	Study area		
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope
1934	17	12	150
1935	88	0	152
1936	56	0	189
1937	33	0	380
1938	48	8	246
1939	136	63	198
1940	161	43	380
1941	52	23	194

to frost. Best survival of ponderosa pine and incense-cedar occurred in area 3, the cleared, south-facing plot. But survivals of ponderosa pine in areas 1 and 2 were 19 and 15 percent, respectively. No ponderosa pine seedlings survived for 5 years in areas 4 and 5, the heavily timbered areas.

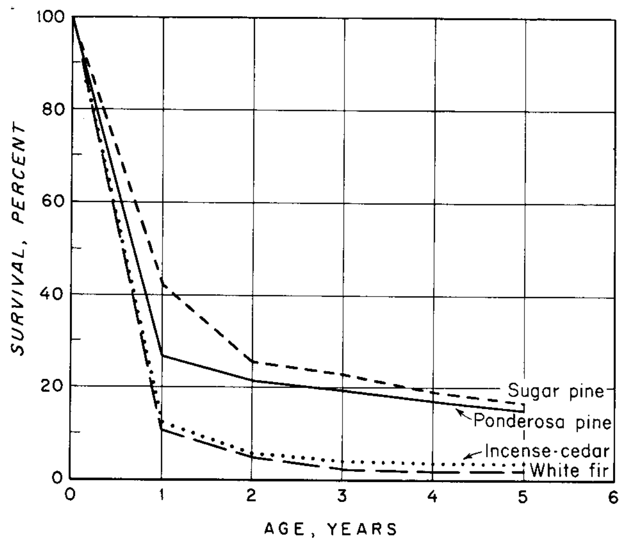
Seedling growth. —The heights attained by seedlings in 5 years is not meaningful in terms of site potential. All the plots are in an area classed as site 1. But the heights do reflect the competition imposed by the overstory and additionally by the neighboring seedlings in spots or rows. After 8 years ponderosa pine seedlings averaged 50 inches tall in area 3, 35 inches in area 1, but only 5 inches in area 2, the partially cut plot. Also after 8 years sugar pine seedlings averaged 30 inches tall in area 3, 16 inches in area 1, but only 7 inches in area 2. Growth of these species in areas 4 and 5 was negligible. Too few seedlings of incense-cedar and white fir survived for a period of 5 years or more to provide an estimate of height.

Table 15.-- *Percent of first-year seedlings killed, by species and by cause of mortality, Stanislaus-Tuolumne Experimental Forest, 1935-42*

Species	Frost	Rodent	Insect	Fungi	Heat	Drought	Misc.
Ponderosa pine	1.3	7.3	29.4	1.6	0.5	27.8	4.8
Sugar pine	8.0	5.1	9.9	.2	0.0	28.8	5.1
White fir	9.9	8.3	30.7	4.0	0.0	25.1	10.8
Incense-cedar	2.4	4.8	52.0	3.1	0.0	19.8	6.2

Table 16.-- *Percent of first-year seedlings killed, by study area and by cause of mortality, Stanislaus-Tuolumne Experimental Forest, 1935-42*

Cause of loss	Study area				
	1 Clearcut north slope	2 Partially cut north slope	3 Clearcut south slope	4 Uncut south slope	5 Uncut south slope
Frost	5.8	1.9	8.6	2.7	0.5
Rodent	3.6	4.2	14.3	2.9	4.1
Insect	42.4	36.5	18.4	22.6	24.6
Fungi	1.9	1.9	1.0	7.8	.9
Heat	.1	.2	1.0	0.0	0.0
Drought	8.0	18.9	23.3	49.7	44.0
Misc.	3.3	4.9	5.2	8.2	8.8



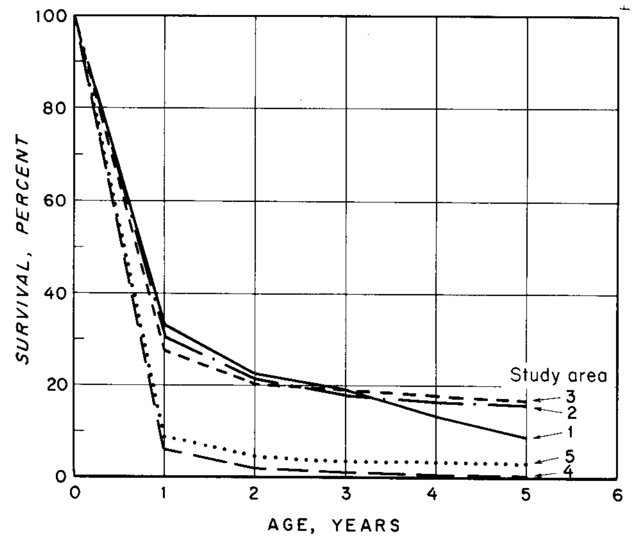


Figure 6.—*Survival rates for ponderosa pine, sugar pine, white fir, and incense-cedar combined for five study areas for a period of 5 years. (Based on survival records of more than 10,000 seedlings.)*

Figure 7.—*Combined survival rates of four species in five study areas for a period of 5 years. (Based on survival records of more than 10,000 seedlings.)*

Implications for Silviculture

The results of the study have had important implications in the development of silvicultural practices in the mixed conifer type in California. First and most important is that the study demonstrated that climatic factors in this region are not so severe as to preclude natural regeneration. Despite the 4-month drought, soil moisture was nearly always available to seedlings—provided competition from other plants was minimized.

Locally, low temperatures influenced the species composition of the reproduction. Sugar pine and white fir were favored by a light overstory which prevented frosts. However, the overstory held back growth of the seedlings severely. Careful removal of the overstory, as in a shelterwood system, would be necessary to capitalize on this type of advance reproduction. Insects apparently play an important part in determining species composition. Incense-cedar might have been a much greater component of the stand if cutworms had not selectively taken this species.

The study showed that sugar pine is not as difficult to regenerate as many had believed on the basis of the scarcity of sugar pine seedlings. With rodent protection, the first-year and five-year survival of sugar pine was higher than survival of any other species. The good survival of sugar pine—and of ponderosa pine—with rodent protection suggested the need for some form of rodent control as a prerequisite, to obtaining satisfactory regeneration of the pines.

Although complete clearing created conditions leading to high surface-soil temperatures, particularly on south-facing slopes, stem insolation does not appear to be a critical factor in survival.

The many years of observation of environmental factors and seedling responses can lead only to the conclusion that regeneration of the pines is favored by removal of the overstory, understory, and ground competition, by soil disturbance, and by protection of the seed from rodents.

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