THE STAND DYNAMICS OF SHASTA RED FIR
IN NORTHWESTERN CALIFORNIA

by

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IN NORTHWESTERN CALIFORNIA

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ABSTRACT

Structural analysis of the Shasta red fir (Abies magnifica A. Murr. var. shastensis Lemm.) forests of northwestern California shows that they are largely all-aged. These forests are mostly composed of uneven-aged groups, with a distinct lack of trees of intermediate heights. Reproduction is continuous in such stands, but subsequent growth is slow. Few fir reach a height over 0.5 meters until an opening in the canopy occurs. Saplings under this opening are then released and grow up into the canopy relatively rapidly. Fir in the understory do not have an exceptionally high mortality rate, but rather, are able to survive in a highly suppressed state. The mosaic of even-aged groups commonly reported in other areas does not appear to exist in this region, though individual even-aged groups do occasionally develop. In this manner Shasta red fir, which is of intermediate shade tolerance, is able to maintain its highly dominant status in the forest.
ACKNOWLEDGEMENTS

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INTRODUCTION

Forests of California red fir (*Abies magnifica* A. Murr. var. *magnifica*) and Shasta red fir (*A. magnifica* A. Murr. var. *shastensis* Lemm.) dominate much of the high montane and subalpine zones of California. These forests are generally considered to be the climax stage there. Red fir is the dominant tree, often forming almost pure stands.

There has been some disagreement over the nature of the stand dynamics of this little understood species. Gordon (1970, and Gordon et al. 1977), who has done extensive work with it in the northern Sierra Nevada, reports that the species is dependent on episodic or gap-phase regeneration. He points out that these forests consist of a mosaic of even-aged groups of varying size. Such groups probably result from the rapid disintegration of the canopy trees. The openings that are formed are soon occupied by seedlings, which develop into a dense sapling thicket and eventually form a new even-aged canopy. Talley (1976) working in the central Sierra Nevada and Hallin (1957) who has reported on the silvics of the species in general, have both come to the same conclusion. Oosting and Billings (1943), however, concluded from their research in the central Sierra Nevada that while such episodic openings occur, California red fir is also capable of reproducing and maturing under a closed canopy.

These conclusions about red fir's reproductive patterns have never been thoroughly tested. Nor have the stand dynamics of old
growth red fir forests in northwestern California been investigated.

The objectives of this study were to investigate the forests' stand
dynamics and determine whether Shasta red fir is capable of reproducing
and maturing under a closed canopy.
STUDY SITES

Two areas of greatly different conditions in the Klamath Mountain Region of northwestern California were sampled during the summer of 1977 (Fig. 1). The Haypress Meadows area is a plateau on the western edge of the Marble Mountains. The terrain consists of a series of low, forested ridges running in various directions. Between these are wet meadows. Average elevation of the forest is about 1525 m. Parent material is granitic.

Forests within the site vary from mixed white fir (Abies concolor (Gord. & Glend.) Lindl.) and Douglas-fir (Pseudotsuga mensiesii (Mirb.) Franco) stands to Shasta red fir stands, with white fir as an important subdominant. This mix is part of the transition zone between the white fir and red fir zones described by Sawyer and Thornburgh (1977) for the Klamath Region. Mountain hemlock (Tsuga mertensiana (Bong.) Carr.) and lodgepole pine (Pinus contorta Dougl. ssp. murrayana (Grev. & Balf.) Critchfield) are common on the edges of meadows. Other conifers found are western white pine (Pinus monticola Dougl.), sugar pine (P. lambertiana Dougl.) and incense-cedar (Calocedrus decurrens (Torr.) Florin). Individuals of Jeffrey pine (Pinus jeffreyi Grev. & Balf.) and Brewer spruce (Picea breweriana S. Wats.) were also found in this area.

The second area, North Trinity Mountain, is on the western edge of the Trinity Alps. The red fir forest is densest and most continuous on the southwestern slope of the mountain, between 1670 m and 1900 m.
FIG. 1. Location of study areas in the Klamath Region of northwestern California.
Outside of these stands the trees are scattered among rocks and dry meadows, occasionally forming small, closed stands. Sampling was limited to the southwest slope forest.

The forest has an appearance similar to those in Haypress Meadows, but with much less complexity. It is nearly pure Shasta red fir, with an occasional white fir, sugar pine, western white pine, and incense-cedar. Soils are developed from granitic parent material.

In both areas individual trees, rather than groups, appear to have been the main victims of natural disturbances. The overall effect on the forest has been a somewhat uniform thinning of the canopy. There is little evidence of the rapid, localized disintegration of the canopy reported in other red fir forests (Gordon 1974; Talley 1976; Hallin 1957).

The importance of fire in these forests is mostly conjecture. Whittaker (1960) stated that the high elevation forests in this region have probably been burned at sometime. Though occasional fire scars and old charcoal can be found in both areas it does not appear that fire has had a serious impact on the forest during the last 50 to 100 years. Whether this is the result of man's suppression of fire or part of the natural pattern is unknown.

Shasta red fir and the very similar noble fir (Abies procera Rehd.) are both found in this region. Their taxonomic status is still unclear where they intermix (Franklin and Dyrness 1973; Griffin and Critchfield 1972). The only reliable field characteristic for separating them is the degree by which the cone bracts cover the cone scales. In both species the bracts extend beyond the scales and are reflexed. On noble fir cones the bracts hide the scales, whereas on
Shasta red fir they only partially cover the scales. Fortunately, cones were common in both areas during the study. On North Trinity Mountain all cones were clearly Shasta red fir. In Haypress Meadows cones that we found in the stands that were sampled were also of the Shasta red fir type. However, cones found on an adjacent ridge were more of the noble fir type. This is a drier, more open site, which may explain the separation. To avoid taxonomic confusion in this study all red fir referred to is presumed to be of the Shasta variety. California red fir is not found in this region.
METHODS

Thirty-five plots were located in each area. On North Trinity Mountain plot center points were located on pace lines which followed the contour of the slope. Distances between center points were used. In Haypress Meadows the more variable terrain was more suitable to use of compass lines, with a random number used to determine the distance between plot centers. The direction of these lines was based upon the expectation of passing through red fir forest and avoiding meadows. Unlike North Trinity Mountain, a large amount of the forest was deemed unsuitable for sampling, because it was more typical of lower elevation forest. These slopes, which were dominated by white fir and Douglas-fir, were avoided.

Plots were 0.04 ha circles. Since one objective of this sampling was to determine the relative proportions of even-aged and uneven-aged groups, plots were always located wholly within such a group, where they were apparent and larger than 0.04 ha. When necessary the center point was adjusted so that the plot would meet this criterion. When this was done the center was always moved such that it remained within the stand type it originally fell. Where the group was smaller than the plot, it was simply centered within it.

Heights of all conifers less than 5.1 cm in diameter at 0.3 m above ground level were measured within each plot. Diameters of trees larger than this were measured at 0.3 m above ground level.

A subsample of red fir was aged in each plot. In those plots
with more than 40 stems 20 were aged. In those few plots with a lower density half of the red fir were aged. Trees chosen for aging were those that were closest to the center of the plot.

Seedlings and saplings under 5.1 cm in diameter were cut down at ground level and discs prepared at the base of the stem and at 0.3 m intervals. Those over 1.5 m in height were aged at ground level, at 0.3 m, and at 0.6 m intervals above this.

Larger trees were cored at 0.3 m above ground level. Coring a larger red fir to its center was not practical, because they reach great diameters and very often suffer from heart rot. To avoid these problems, no trees were cored deeper than 38 cm. Trees larger than this were automatically placed in the largest age class (>150 years). The number of years it took the saplings to reach 0.3 m in height was averaged for each site and added to the ages obtained by coring. While this method is not precise, it was the best possible, since it was not feasible to determine early growth rates for these trees.
RESULTS

Forest Stand Structure

The average density of conifers in the Haypress Meadows forests is 1883 per hectare, of which 78.3% are red fir and 21% white fir. On North Trinity Mountain the average density is 643 conifers per hectare, of which 99.7% are red fir. The higher density in the first area is mostly due to the greater proportion of open sites found in the forest and meadow mosaic. These openings often contain a very high density of young fir. Table 1 shows the relative abundance of trees in the sampled sites.

Stand structure by age and size is summarized in Figs. 2 and 3. Our choice of size classes closely follow those used by Jackson and Faller (1973) for Shasta red fir, and is similar to that used by Talley (1976) and Oosting and Billings (1943). This system partially compensates for the increase in variability in growth rates with age and bridges the gap between saplings and trees.

Red fir in both sites is nearly all-aged. The mortality rate is higher during the first 20 years, but becomes relatively constant after this for both sites. The survivorship curves in Fig. 3 fluctuate about a straight line after the first 20 years. This distribution is generally expected for an all-aged forest. Most of the fluctuations in the curve for the larger age classes are probably due to small sample sizes in these classes. However, some of them are certainly
<table>
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<tr>
<td>Total</td>
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Table 1. Total number of trees sampled by species. Includes full 1.4 hectares sampled in each area.
FIG. 2. Size survivorship curves for the two sites. Size classes below 5 cm in dia. are seedling heights in centimeters.
FIG. 3 Age survivorship curves for the two sites.
due to periods of unusually high or low mortality and/or reproduction.

While the linearity of the size survivorship curves indicates an all-sized forest (Fig. 2), the stands are conspicuously two-storied. Typically the canopy is of fairly uniform height, but composed of trees of several diameters. The understory often consists of a moderately dense cover of fir that are less than 0.5 m in height. Seldom is the forest floor completely devoid of young fir. Red fir of intermediate heights are not common.

The distribution of white fir more closely approaches the straight line which is indicative of an all-sized forest. Further, the intermediate size trees are more widely dispersed in the forest. This would be expected, since it is a more shade tolerant tree (Maul 1958).

Regression of Size Against Age

The correlation between age and size is very low. Four linear regression tests were done using the method of least squares (5%-level). These compared age and height, and age and diameter for the appropriate size classes in each area. In Haypress Meadows the values of $r^2$ were determined to be 0.62 and 0.58 for small and large red fir, respectively. The corresponding figures for North Trinity Mountain are 0.64 and 0.45. These figures clearly show that one cannot judge the age structure of a stand by the size of the trees.

Patterns Within the Forest

Red fir distribution in most of the forest is uneven-aged. Although distribution of the species by size and age is not uniform
within the forest, it is not composed of even-aged clumps like those forests described by Gordon, Hallin, and Talley in other regions. Such patches do exist, but make up only a small part of the forest.

In order to ascertain this pattern, each plot was classified as even-aged or uneven-aged. Although these terms are often used in a general sense, they are poorly defined in a quantitative one. One definition of even-aged given by the Society of American Foresters (1971) is as follows:

A forest stand that contains trees having no or relatively small differences in age. By convention the maximum difference admissible is generally 10 to 20 years, though with rotations of less than or equal to 100 years differences up to 30 percent of the rotation age may be admissible.

Gordon et al. (1977), who has studied regeneration by red fir in clear cuts, used a figure of 20 years. For this study a more flexible definition was developed; one which we feel better accounts for natural conditions and the limited age data available. A plot was classified as even-aged if the trees follow a normal distribution in which 90% of them are within 10 years of the mean age of the plot.

For each plot the age data was averaged and a normal curve generated, using the mean as its midpoint. These were then compared to the actual distribution of ages, using a Kolmogorov-Smirnov one-sample goodness of fit test (5%-level). On North Trinity Mountain 77% of the plots failed to be accepted as even aged. For Haypress Meadows the figure was 71% (precision levels were 13% and 14%, respectively). In all cases of non-acceptance our inspection of the data showed that it was due to too great a variability of ages; showing these plots to be uneven-aged.
Since in most cases the age data was collected over a very small part of the plot, a better test would be to classify the entire plot, using size data. A goodness of fit test was not appropriate since the correlation between size and age is so poor. Baker (1950) suggests that a stand can be classified as even-aged if the standard deviation of the diameters is within $1/4$ to $1/3$ of their mean. This is a rather simple definition but does attempt to compensate for the increasing variability in size as the stand ages. To be on the safe side for this study plots with a standard deviation equal to or less than the mean were classified as even-aged. Trees under 5.1 cm in diameter were all considered to be 2.5 cm. Even with this conservative definition, 94% of the plots on North Trinity Mountain and 91% of those in Haypress Meadows were determined to be uneven-aged (8% and 9% precision levels, respectively). These figures are similar to those obtained by visual inspection of the survivorship curves of the individual plots.

Individual Tree Growth

Fig. 4 shows the average sapling height growth rates for the two areas. Growth rates, particularly for the first meter, are very slow: 1.9 to 4.2 cm per year. In closed stands the rates are even lower, since a high proportion of the saplings over 0.3 m tall were collected from a few open or immature stands. When such suppressed saplings are released their height growth will increase greatly (Gordon 1973).
FIG. 4. Average growth rates for red fir seedlings and saplings for the two sites.
DISCUSSION

Stand Dynamics of Red Fir

Despite the great differences in physical conditions, the stand dynamics of the two areas are similar. In general the forests are nearly all-aged, with a disproportionately large number of fir under 20 years old. The distribution by size is not quite as even; there is a significant lack of intermediate height trees.

If this lack of intermediate height trees was due to failure of red fir to survive in a closed forest, there would be a correspondingly low density of fir under 100 years old. The age-survivorship curves in Fig. 3 do not exhibit such a dip. This is in agreement with the very low correlation between size and age.

The very low proportion of the forest that can be considered even-aged indicates that canopy openings are not important in maintaining these forests. There is not enough reproduction occurring in open sites to match the mortality rate of mature trees in the forest as a whole. Less than 10% of the forest consists of immature thickets. Since red fir normally takes far more than 10% of its lifespan to reach canopy heights, these forests do not rely on episodic disturbances for regeneration.

However, neither does the structure of these red fir forests fit the all-aged, all-height pattern expected of highly shade tolerant trees. Instead, the pattern that appears to have developed in the
past, and has continued, is one that could be expected of a tree of intermediate to moderately high shade tolerance. Every few years an abundant seed crop results in a wave of seedlings. Those which survive the first few years probably continue to grow in a highly suppressed state: around 2 cm or less of height growth per year. When an opening of any size occurs in the canopy those suppressed saplings can increase their growth rate considerably; growing up into the canopy in a relatively short time. Most of these openings appear to result from one or two trees falling.

The occasional larger openings that occur allow considerable new reproduction. These new seedlings can grow rapidly, and not become suppressed by the overstory trees. This is the cause of those sapling thickets and even-aged stands which have developed. Once these stands mature though, reproduction can be expected, and the two-storied pattern is reestablished.

Sapling thickets, however, stand out on the otherwise open forest floor and may have led observers to overemphasize their importance. This conspicuousness may partially account for the emphasis previous researchers have tended to place on them. The lack of intermediate height trees in the forest also suggest a mosaic of even-aged or two-aged stands. But this too can be deceptive. The very poor correlation between age and size indicates that such stands probably contain a considerable range of ages.

Most work on red fir has been in other regions, where conditions are considerably different. In regions where episodic openings are much more common, they would be an important part of the regeneration pattern. Oosting and Billings (1943), however, noted both patterns in
the Sierra Nevada and concluded that red fir is capable of reproducing and maturing in both situations. It seems likely that red fir throughout its range is not dependent on episodic disturbances, but is capable of exploiting such openings when available.

Whether or not there are relevant differences between the two varieties of red fir is not known. There have been no comparative studies of the ecology of the two types.

Succession

Red and white fir appear to be in equilibrium in Haypress Meadows. Red fir is the more important dominant in nearly all size classes. But, while red fir has by far the most reproduction, its early mortality rate and suppression is so great that the number of trees in the larger size classes approach the number of white fir in these classes, Fig. 2. Since white fir is a more shade tolerant tree, this would be expected. Red fir is favored by being better adapted to the physical conditions at these higher elevations, occasional openings in the canopy, and its ability to reproduce so copiously. Conceivably, if all disturbances were eliminated white fir would increase its abundance to the disadvantage of red fir. On North Trinity Mountain red fir so thoroughly dominates that white fir has been almost totally excluded, and no significant succession is taking place.
LITERATURE CITED


