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THE COMPOSITION AND DYNAMICS OF THE TREE STRATA WITHIN AN OLD GROWTH DOUGLAS-FIR FOREST IN WESTERN MONTANA

By

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A virgin, predominantly inland Douglas-fir (*Pseudotsuga menziesii* var. glauca (Beisnn.) Franco) forest was studied to record its composition and structure, and to gain some insight into the developmental processes involved in reaching the observed stage of forest maturity. The study area, located on the Lubrecht Experimental Forest near Missoula, Montana, lies between 5200 and 5600 feet above sea level.

The drainage pattern within the section makes possible the observation of forest communities on four different aspects within this natural area.

The species composition, stand structure, and age structure of the trees within these communities vary with differences in aspect. The differences in community appearance are due partly to the abiotic influence associated with aspect and partly to the biotic influence associated with the developmental maturity of each stand.

Douglas-fir is ubiquitous throughout the study area, dominating both small and large size classes. Ponderosa pine and Rocky Mountain juniper are minor components of stands on the warmer, drier aspects. Subalpine fir and Engelmann spruce are occasionally found on the cooler, moister aspects. Lodgepole pine is important in larger size classes on the north-facing slope.

The four study stands appear to be between 200-240 years old. Stand development, in terms of canopy closure, has apparently occurred most quickly on the cooler, moister site; taking progressively longer on the warmer and drier sites. A closed canopy may never occur on the harsh south-facing slope.

Two types of gap-phase stand replacement are possible in non-catastrophically disturbed stands. Stands which become established quickly, forming a more even-aged canopy, probably develop small openings which allow advanced reproduction to become established. As canopy breakup increases, the advanced regeneration is released to replace deceased overstory individuals. The uneven-aged character of more slowly established stands inhibits large scale canopy breakup. Small canopy openings may be constantly available for seedling establishment due to single tree deaths. Once stems become established on these generally harsher sites, environmental conditions no longer appear to inhibit the continued development of the individual.

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Chapter 1

INTRODUCTION

Interest in naturally developed forests, i.e. forests apparently little affected by man, has surged in the past two decades. Although the majority of the interest in naturally developed forests has stemmed from an orientation toward preservation and recreation, the additional values of natural areas have also received increasing recognition (Bruce, 1955; Shaklin, 1951; Ohmann, 1973). Natural areas serve many purposes, among them aesthetic and preservational, but perhaps their greatest value is as control sites for research in ecology, silviculture, genetics, pathology, and hydrology. The study of natural areas can provide the necessary baseline data for use in analyzing the effects of management practices on wildlife population stability, changes in forest disease risks, soil degradation and erosional processes, and water quality and yield from forested systems. These areas may also provide unique opportunities to study successional processes, reproductive strategies, and tree growth characteristics. Ultimately, these baseline data will be valuable in enhancing the quality of management on our forested lands (Franklin and Trappe, 1968).

Early foresters and ecologists recognized the need for the study of natural forests, particularly the successionally mature forests, in determining correct management programs for an area. This recognition was shared by Lutz (1930), who believed virgin forests to represent "an integrated picture of the cumulative effects of the factors of site on vegetational development. The most intimate influences of the edaphic and climatic factors upon the organic community, and the coinciding equally important influences of the organic community upon the environmental factors, are faithfully recorded in the climatic climax forest." Lutz further commented that the best places to study tree growth are in virgin stands, where disturbing influences have been minimized. He realized that foresters are chiefly interested in the regrowth of forests following logging, but felt they should use the virgin forest to develop ecological information upon which to base silvicultural programs. He contended foresters must be aware of natural processes and strive to build their silvicultural programs around them (Lutz, 1959). To work against natural tendencies is often to practice inefficient silviculture as well as poor business.

Many ecologists have conducted ecological studies on tracts of virgin or natural forests in hopes of characterizing, for posterity, the composition and structure of stands of representative forest types (e.g. Cooper, 1913; Daubenmire, 1943; Gleason, 1924; Cain, 1932; Williams, 1936). Oosting and Billings (1943) sought to develop a detailed phytosociological record of the original virgin condition of an undisturbed stand of mature red fir (Abies magnifica) in the Sierra Nevadas. In attempting to provide a quantitative ecological analysis of the community, their main viewpoint was "essentially geobotanical with emphasis on the plant population pattern and its general relation to climate and geological history." Another study, conducted in the Appalachian Mountains (Oosting and Billings, 1951), dealt with recording the composition and structure of representative virgin stands of the spruce-fir type. This study's objective beyond recording stand composition and structure, was to compare vegetation data from stands in the northern and southern Appalachians.

More recently, modern techniques of vegetational analysis have been utilized to analyze the vegetation of undisturbed forest stands. These techniques were used to analyze the successional development of an old-age stand of hemlock-northern hardwood forest in Vermont as the investigators sought to determine whether the stand was in a state of dynamic stability or undergoing directional change (Bormann and Buell, 1964). The analysis also sought to determine to what extent the shrub and herb layers reflect the influence of the microhabitats resulting from the forest itself or from the microtopography within the forest. At Hubbard Brook, the tree stratum of an undisturbed control watershed was analyzed (Bormann, et al., 1970) to characterize the synecological parameters of the ecosystem, ultimately providing information on tree species to be used in estimating the production and nutrient parameters of the ecosystem. The information was also used to determine the relationship of the distribution and reproduction of tree species to such site factors as elevation, slope inclination, aspect, and soil moisture. In northern Minnesota, the wilderness vegetation of the Boundary Waters Canoe Area has been characterized (Ohmann and Ream, 1971a and 1971b) in an attempt to provide a basis for specific goal management. One particular goal may include the maintenance and restoration of vegetational complexes in light of heavy recreational use. Old growth stands of spruce in southern Alberta were studied

(Day, 1972) to assess their successional origin, development and structure in view of the rapid reduction in numbers and in size of such stands due to fire and logging. The study was cited as providing a unique ecological record for the future management and silviculture of the Rocky Mountain Forest Reserve and the adjacent Waterton-Glacier and Banff National Parks.

Although most of these past studies of natural old growth stands list as primary goals the recording of stand composition and structure, more recent studies appear to go further in relating this composition and structure to a greater understanding of forest ecology as a whole. The statement that "a major goal of federal land management agencies in setting aside research natural areas is to have them serve as comparisons with managed, utilized, and artificial ecosystems" (Ohman, 1973) is encouraging. Current trends and goals show progress towards a greater use of the remaining natural forest environments to obtain information on which to partially base quality management programs. However, despite advocacy by scientists and the actual reservation of areas by government agencies and private sources, there remains a paucity of research results. That is, few people have yet to appreciate the unique research opportunities afforded by existing or potential natural areas (Cowan, 1968).

Within the northern Rocky Mountains little work has been completed which describes the biology of major commercial species in undisturbed areas. Ecological information regarding interior Douglas-fir (_Pseudotsuga_ _menziesii_ var. glauca (Beissn.) Franco)[1] in natural

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[1] Vegetation nomenclature follows Hitchcock and Cronquist (1973).

situations is incomplete. Apparently most of the research effort on Douglas-fir has been concentrated on its coastal form (Pseudotsuga menziesii (Mirb.) Franco var. menziesii). Even though the coastal form has always been considered of higher commercial value, and ponderosa pine (Pinus ponderosa Dougl.) has been considered a more desirable timber species in western Montana, interior Douglas-fir is a major commercial timber species and a major ecological component of western Montana ecosystems (Navratil, 1952; Harlow and Harrar, 1969; and Record, 1973). About 27% of the nation's softwood timber inventory in 1970 was Douglas-fir; two-fifths of this total was located in the Rocky Mountains (Forest Resource Report No. 20, 1973). In the northern Rocky Mountains, Douglas-fir is the leading species in terms of volume (Barrett, 1962).

Of the two distinct varieties of Douglas-fir which have been reported,coastal Douglas-fir has been described as having the best development, while interior or Rocky Mountain Douglas-fir has been described as having the greatest resistance to environmental pertubations (Frothingham, 1909). Frothingham contrasts the two varieties in detail, however, he and Fowells both recognize areas in which the ranges overlap in northeastern Washington, northern Idaho, and northwestern Montana. Rocky Mountain Douglas-fir is found in the mountains of southwestern Alberta, central British Columbia, Montana, Idaho, eastern Washington, and Oregon, and south in the mountains of Utah, Nevada, Arizona, New Mexico, Texas and northern Mexico. Throughout this range the Douglas-fir zone occurs elevationally above the ponderosa pine zone and below the spruce-fir zone. At the lower, less mesic extremes of the Douglas-fir zone, the species is confined to north slopes or shaded areas. At higher elevations, it is found mostly on the warmer, drier south-facing exposures (Fowells, 1965). In the northern Rockies common associates of Douglas-fir include western larch (Larix occidentalis nutt.), lodgepole pine (Pinus contorta var. latifolia Engelm.), ponderosa pine, western hemlock (Tsuga heterophylla (Raf.) Sarg.), Engelmann spruce (Picea engelmannii Parry), subalpine fir (Abies lasiocarpa (Hook.) Nutt.), and western white pine (Pinus monticola Dougl.) (Harlow and Harrar, 1969; Barrett, 1962).

One of the few studies investigating undisturbed Rocky Mountain Douglas-fir was completed in the Big Belt Mountains in central Montana (Jansson, 1949). This project was designed to gather information on the life history of Douglas-fir forests and to gain additional insight into the silviculture and growth habits of the species. The study emphasized improved timber management techniques. The stands described were mostly Site IV or Site V and were originated between 220 and 260 years ago following fire. Jansson stated that healthy reproduction in these stands was lacking, apparently due to low light conditions on the forest floor.

Habeck (1968) studied the forest community structure within a Douglas-fir-subalpine fir ecotone on the Lubrecht Experimental Forest in western Montana. Results indicated varying degrees of dominance for the respective species along the ecotone, with the variation generally attributed to habitat heterogeniety. The two species were found to co-dominate in some cases.

We must increase our knowledge of the ecological characteristics and dynamics of interior Douglas-fir under natural conditions if we are to most successfully manage this species in the future. A unique opportunity to study the behavior of interior Douglas-fir in a relatively undisturbed situation exists on Lubrecht Experimental Forest. This research opportunity takes on greater significance as a contribution to the present Lubrecht Ecosystem Project activities on second growth stands (Forcier and Wambach, 1971). Comparable data from undisturbed and disturbed sites within several miles of each other will ultimately provide an opportunity for exciting and worthwhile inputs into the management of middle elevation forest ecosystems in western Montana. This particular old growth stand of primarily Douglas-fir timber type and hypothetically Douglas-fir climax (Cauvin, 1961; Habeck, 1968) has solicited additional interest from groups interested in cataloging potential natural areas in Montana, and the Coniferous Forest Biome of the IBP. Although, the study area is not presently classified as a natural area, this ecological analysis may lend support to such a classification.

Objectives

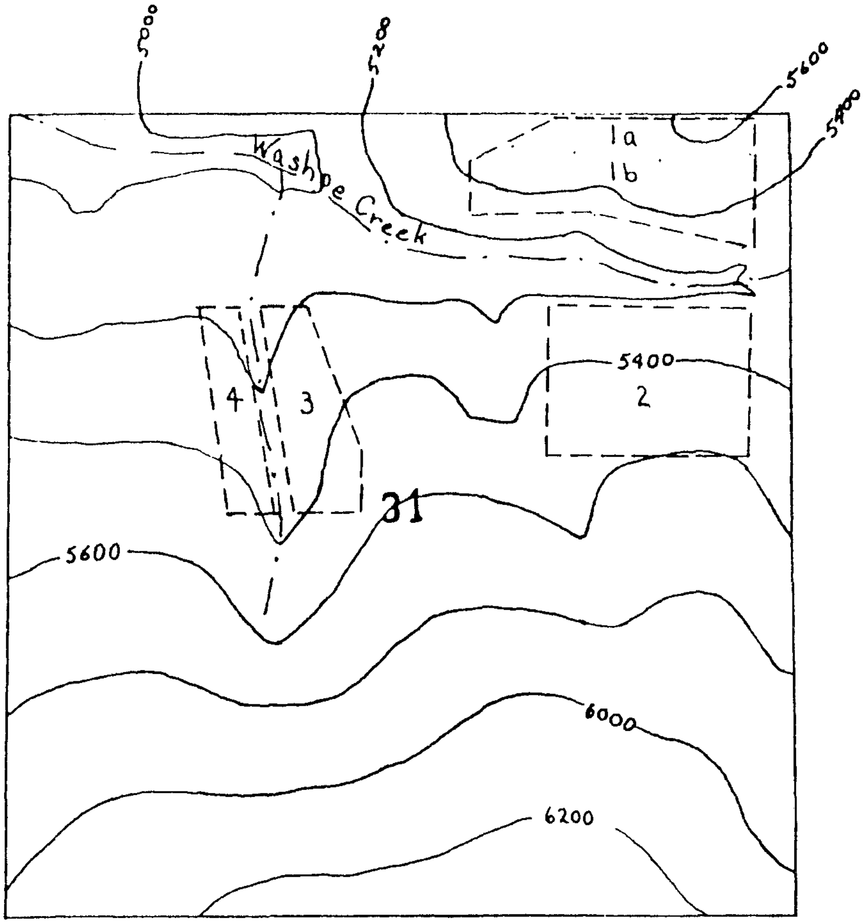
The objectives of this study were 1) to record the composition and structure of an old-growth Douglas-fir forest in western Montana and 2) to gain some insight into the developmental processes involved in reaching the present stage of forest maturity. Following detailed description of the present forest composition and structure, and analysis of available information regarding past developmental processes, some projections of future forest composition, development and structure have been attempted. Due to time limitations, these objectives relate only to tree species on well-drained slopes.

The objectives were developed to provide information on the old growth forests as a characterization of certain stands in the Northern Rocky Mountain Region prior to logging. In particular, this study was designed to contribute directly to research and demonstration programs at the Lubrecht Experimental Forest and provides data for several other studies underway or planned at that facility. Finally, this analysis of forest structure and possible developmental trends hopefully will contribute to efforts to elucidate the processes of forest dynamics in the northern Rocky Mountains.

Chapter 2

STUDY AREA

The study area lies on a portion of Lubrecht Experimental Forest situated 30 miles northeast of Missoula in the Garnet Mountains. The study was undertaken within Section 31 (T 13N, R 14W), a section with an elevational range of 1490-2100 m (4900-6300 feet) above sea level (Figure 1). A major stream, Washoe Creek, divides the section into north- and south-facing components, with the north-facing portion covering about two-thirds of the section. The topography is further characterized by smaller drainages which contribute distinct east- and west-facing components. Due to the section's remoteness and lack of previous large scale studies, annual climatologic data has not been gathered. However, annual precipitation, based upon measurements in the nearby North Fork of Elk Creek at nearly equivalent elevations (L. Forcier, personal communication) and also at a lower elevation station (Steele, 1973), should average near 56 cm. The vegetation of the section appears to vary from the drier extremes of the *Pinus-Pseudotsuga* forest to the more mesic *Abies-Picea* forest on the higher reaches of the north-facing slope (Cauvin, 1961; Habeck, 1968). Soils in this area have been derived from several parent materials, the majority being agrillites and quartzites. Some igneous parent materials may be present in the form of quartz monzonite (Brenner, 1964). In any case, the soils developed from these parent materials are generally



1a	South-facing slope study area, bench subunit
1b	South-facing slope study area, slope subunit
2	North-facing slope study area
3	West-facing slope study area
4	East-facing slope study area

Figure 1. Study Area--Section 31, T13N, R14W, Lubrecht Experimental Forest.

podzols with greater soil development evident on the north-facing slope than on the south-facing slope.

This particular section is unique to Lubrecht Forest in that it has never been commercially logged. As the section also appears to have escaped major allogenic catastrophies in recent history, the area probably represents the most advanced stages of vegetational development on a continuous portion of the forest.

Delineation of the Exposure Units

Four study units were delineated based on the area's drainage patterns (Figure 1). Using aerial photographs, north-, south-, east-, and west-facing exposure units were selected. Care was taken to keep all four units within a comparable elevational range and to maintain minimum variation in microtopographic relief, insofar as possible.

The south-facing unit encompasses 12 hectares, but should be divided into two subunits, one with a mean slope of 25% and another with a mean slope of 60%. The entire south-facing area has an elevational range of about 200m (650 feet). The north-facing unit encompasses about 11 hectares and has a mean slope of 33% and an elevational range similar to that of the south-facing unit.

The east- and west-facing units are opposing exposures within a medium sized drainage which empties into Washoe Creek from the south. These units encompass 6 and 7.5 hectares respectively and are characterized by mean slopes of 51%. The elevational difference from stream bed to ridge top along each unit is about 150m (492 feet).

Chapter 3

METHODS

A sampling system combining the point-centered quarters method (Cottam and Curtis, 1956) and the fixed area plot method was used to collect information on stand structure. Trees $>$ 1.0 cm dbh were sampled by the point quarters method and plots were used to sample seedlings and saplings. In all, four size classes were separately sampled. Trees were defined as stems $\geq$ 10.0 cm dbh; small trees, as stems $<$ 10.0 cm dbh, but $\geq$ 1.0 cm dbh; saplings, as individuals $>$ 1.0 m tall, but $<$ 1.0 cm dbh; and seedlings, stems $<$ 1.0 m tall. Dbh is defined as diameter at breast height, i.e. 1.37 m. Coniferous tree species were the only individuals sampled.

At each sample point a 1 m radius plot was initially established and all seedlings were recorded by species. A 2 m radius plot was then established around the point and all saplings were recorded by species. The area around the point was then divided into four quadrants using the direction of travel as a base line. Within each quadrant the distances to the nearest tree and small tree were measured and recorded along with their dbh and respective species. All distances were measured, on the level, from the center point to the estimated center of the trees.

In analyzing the data from each site, absolute and relative density and frequency were calculated for seedlings and saplings by species. For the trees and small trees, density, frequency, and basal area were calculated by species (Cottam and Curtis, 1956). Stand tables were constructed to illustrate the density of each species within the seedling, sapling, and successive 10 cm dbh size classes.

The relative values were used to calculate importance values. An importance value (IV) is the sum of the relative values for a species and represents the overall relative significance of the species within a size class. For seedlings and saplings, which have not yet reached 1.0 cm dbh and hence have no basal area by definition, the total possible number of points for an IV is 200. For stems larger than 1.0 cm dbh, the possible number of points increases to 300, since relative basal area can be calculated. Because of difficulty in comparing the IV of seedlings with the IV of trees of the same species, relative importance values are occasionally referred to. These values were obtained by simply expressing the traditional IV as a percentage of the total possible points.

Sampling points were randomly established throughout each study area. A base line was subjectively established as the upper boundary of each unit and 8 to 10 points were chosen at random along the line to serve as end points for grid lines. Along each grid line, 8 to 10 points were selected at random as point centers. Thus, 80 sample points were established in either 8 x 10 or 10 x 8 matrices, depending upon the configuration of the individual study units.

Sampling intensity was determined from pre-sampling information. Twenty random points were sampled within the south-facing unit. These results were used to determine the number of points required to reduce the standard error of the distances to less than 4.65% of the mean distance to each tree (Cottam and Curtis, 1956). Generally, a sample size sufficient to produce an adequate sample of distances will also produce an adequate sample of basal areas. The procedure used to determine sample size is based upon the number of distances necessary to ensure that the sample mean will fall within a chosen confidence interval at a given level of probability (Freese, 1967). Eighty sample points proved adequate on all four study units as the standard error of the distances did not exceed 4.65% of the mean distances on any of them.

Because the size of each study area varied, the proportion of the area sampled by the seedling and sapling plots also varied. No adjustment in the number of plots was made to insure sampling of equal portions of each study area. The estimated proportion of each study area sampled by seedling and sapling plots averaged .3% and 1.2% respectively (Table 1).

Table 1. The proportion of each study area sampled by seedling and sapling plots.

Study Area	Seedling	Sapling	Size of Area
North	.2%	0.9%	10.7 ha
East	.4%	1.7%	6.0 ha
West	.3%	1.3%	7.4 ha
South	.2%	0.8%	12.4 ha

Use of the point quarters method for the determination of stand structural characteristics assumes that the stems within the study area are randomly distributed (Cottam and Curtis, 1956; Pielou, 1969). No tests have been made to document the assumed randomness of the tree population in this area; however, studies in another old-growth stand relatively nearby indicate a low degree of aggregation in stems > 2" dbh (A. White, personal communication). Additionally, the point quarters method has been used successfully in the analysis of Douglas-fir--subalpine fir ecotones in western Montana by Habeck (1968). Pielou (1969), however, urged caution in the assumption of randomness and states the desirability of some independent estimates of density.

The horizontal pattern of seedlings and saplings was investigated to determine the degree of aggregation exhibited by the respective populations. Various tests for aggregation have been designed for ecological studies. Most of the indices were originally developed for discrete sampling units, but are frequently used in describing population dispersion in a continuum (Pielou, 1969; Collier, *et al*., 1973).

In determining which indices would be most applicable, general observations were made regarding seedling and sapling distribution on the various study areas. Field observations indicated that clumps are generally compact and widely spaced on the south- and west-facing study areas. Larger patch sizes appear to be evident on the east- and north-facing study areas. David and Moore's (I) and Llyod's Index of Clumping ($\overset{*}{m}$) were selected as most useful on the west- and south-facing slopes. Lloyd's Index of Patchiness ($\overset{*}{m}/m$) seemed to be most applicable to the east- and north-facing study areas.

David and Moore's (I) is an index similar to the variance to mean ratio (Pielou, 1969; Collier, *et al.*, 1973). Lloyd's Index of Clumping is defined as the mean numbers of co-occupants of those plots containing at least one subject individual. For both indices, numbers greater than zero indicate increasing degrees of aggregation. The latter index is not affected by a large number of empty plots (Lloyd, 1967). These two indices are designed for populations that occur in the form of clumps so compact and widely spaced that they are seldom cut through by the edges of the sample plot. If this is true in the sample population, these measures of aggregation do not depend upon plot size. Since David and Moore's (I) and Lloyd's ($\overset{*}{m}$) remain linearly proportional to density as a population is depleted by random deaths, these indices may be useful in describing mortality within clumps through time (Pielou, 1969).

Lloyd's Index of Patchiness ($\overset{*}{m}/m$) is used to describe spatial pattern not affected by clump density. Random deaths within a patch do not affect the index. If a pattern consists of a mosaic of varying density patches within which individuals are randomly dispersed, Lloyd's ($\overset{*}{m}/m$) may be used as a measure of contagion. If the sample plots are smaller than the average patch size, these values are independent of plot size (Pielou, 1969).

Information necessary for the determination of various growth relationships, area age structures, and incremental growth rates was collected separately from that for stand structure. A line transect was run across each study area from the corner with the highest elevation to the lowest corner. Along this line trees were sampled using crown class and stem diameter as sampling criteria. By arbitrary choice, no more than 75 trees could be sampled within each study area and representatives of all tree diameter size classes were desired. The crown classification system used was defined by Kraft and is primarily designed for even-aged stands (Baker, 1950). Since the age structure of the stand involved was unknown, crown classes, as defined, were used to assign the sample stems to a relative portion of the canopy which could then be described by age. Crown classes include dominant, codominant, intermediate, and suppressed stems. The respective crown classes cannot be construed as indicators of vigor. The suppressed crown class refers only to trees well beneath the general level of the canopy.

The sampling scheme identified representatives of all of the crown classes within each portion of the study area along the transect. In crown classes which were encountered more frequently, attempts were made to sample the range of diameter classes present. In most cases, trees were not sampled that occurred more than 2 meters from the line; but it was occasionally necessary to move farther away to obtain representatives of infrequent crown or diameter classes. Because of the stratification procedure and the deviations from the essentially belt transects, the numbers of individuals sampled within each crown class do not represent the frequency distribution of the crown classes.

The total height and diameter of each tree were measured. An increment core or a cross-section was also taken from each tree for estimation of its age and radial growth rates. When possible a core was taken, but smaller stems were destructively sampled and a cross-section was taken from near ground level. Cores were taken parallel to the contour of the slope to decrease the effects of reaction wood in the determination of radial growth rates. For trees 10 cm dbh or greater, the diameter was measured at breast height and the core was also taken at breast height. For stems < 10 cm dbh, but having a diameter at breast height, the diameter was measured at breast height and the age estimated at 15 cm above the ground. For stems < 1.3 m in height, a basal diameter measurement was made above noticeable basal swell and age recorded at ground level. Correction factors for the time taken to reach dbh are non-existent, so approximations had to suffice. A conservative estimation for the time required for Douglas-fir stems to reach breast height is 15 years (W. Schmidt, personal communication). It is also estimated conservatively, that 5 years are needed for a Douglas-fir stem to reach 6 inches in height. Using these correction factors, ages are presented as estimated total stem age unless otherwise indicated.

The increment cores were analyzed using an Addo-X-Dendrochometer, which measures the width of each increment. Utilizing a computer, the number of these increments was summed to determine age. Ten year periodic annual radial growth rates were also determined. The radial growth rates of cross-sections were not determined, nor were the radial growth rates of very small suppressed stems.

Band dendrometers were affixed to additional sample trees within each study area to study the annual pattern of diameter growth and possibly determine the length of the growing season. Tree phenology plots were established on the upper portion of each study area and several trees were banded within about a one ha area. At least five Douglas-fir were banded on each area, including a variety of crown classes and stem diameters. If other species were reasonably close by, representative individuals were banded. On the south-facing unit, 7 Douglas-fir and 5 ponderosa pine were banded. Five Douglas-fir, 3 western larch, and 3 lodgepole pine were banded on the north-facing unit. Nine Douglas-fir were banded on both the east and west-facing study units.

The dendrometers are made of 1.3 cm x 0.013 cm stainless steel tape, spring loaded to exert a tension of approximately 0.3 kg of tension per cm of extension (Forcier, et al., 1973). The primary and vernier scales were scribed onto the tape with an Exacto knife, using a band dendrometer template (Forcier, et al., 1971). The bands were placed at breast height (1.37 m) and, if necessary, the bark was smoothed with a rasp. A silicon lubricant was used between the bark and the inner surface of the band to reduce friction. The installation of the dendrometers was complete by May 1, well in advance of growth initiation. Weekly readings were completed before 1000 hrs. MDT. Changes in circumferential growth were recorded to .01 in from which average daily radial growth rates/observation period and ultimately, cumulative radial growth were calculated.

During the source of the summer many of the bands were destroyed by animals. Apparently the shininess of the stainless steel is attractive. No positive identifications of the culprits have been made, but bears, elk, bobcats, and woodpeckers are among those suspected. In the future, a covering or paint which will make the bands less conspicuous may help to overcome the problem.

Chapter 4

RESULTS

Stand Structure--Density, Frequency, Basal Area and Importance Values

Knowledge of the phytosociological relationships among the tree species present on a site is germane to the full understanding of stand structure and stand dynamics. Stand structure measurements present an overview of the study area in a two-dimensional format, describing in essence, the horizontal forest structure of an area. To complete a three-dimensional picture of the stand, one must integrate various height relationships into the analytical scheme. To begin developing a dynamic overview of interspecific and intraspecific species interactions, one must also incorporate estimates of stand age structure into the rather static picture developed from size class information. This more dynamic, three-dimensional stand or areal description should (1) enable development of hypotheses regarding the past history of the stand and (2) permit some projection of the composition and structure of future vegetational complexes within the study area.

The following results are presented in a fashion that attempts to follow the aforementioned procedure in developing a dynamic, three-dimensional description of Section 31. Initially, stand structure information by study area will be presented to depict the horizontal structure of each unit. (On the south-facing study area, because of the change in topography, an overall picture of the area, as well as a description of the subunits will be presented.) Next the age structure and the vertical stratification will be incorporated into the picture, developing the three-dimensional portrayal of each unit. Each component of the analytical scheme will be presented as a separate entity. Little attempt will be made to develop the whole picture until all of the data have been presented.

North-facing Study Area

The north-facing study unit is located on the most gentle slope (Mean Slope = 33%) of the four study units. On this expectedly more cool and mesic site we find the greatest diversity of tree species on any of the study units. Douglas-fir (Pm), ponderosa pine (Pp), western larch (Lo), subalpine fir (Al), lodgepole pine (Pc), and Engelmann spruce (Pe) are all found within this study area (Table 2).

The large tree size class constitutes 630 stems/ha on this site. The average size of these individuals is 25 cm dbh (9.8 in) and the basal area of this size class is 32.5 m^2/ha or 93.2% of the total basal area of the unit (Table 2).

Reproduction is abundant on the north-facing study unit. Saplings are numerous (2019 saplings/ha) and widely distributed throughout the area (Frequency = 62.5%). Seedlings are plentiful (15,319 seedlings/ha) and are also generally distributed (Frequency = 66.3%) (Table 2).

Table 2. Phytosociological Summary--North-facing Slope.

	Density		Frequency		Basal Area		Importance Value	
	Absolute #/ha	Relative %	Absolute %	Relative %	Absolute m^2/ha	Relative %	Absolute	Relative %
Douglas-fir								
Seedlings	14,403	94.0	58.8	72.3	--	--	166.3	83.2
Saplings	1,900	94.0	58.8	79.7	--	--	173.8	86.9
Trees <10cmdbh	888	62.8	91.3	50.0	0.95	40.3	153.2	51.1
Trees ≥10cmdbh	248	29.8	76.3	38.4	18.47	56.7	134.5	44.9
Ponderosa Pine								
Saplings	10	0.5	1.3	1.7	--	--	2.2	1.1
Western Larch								
Seedlings	80	0.5	2.5	3.1	--	--	3.6	1.8
Trees <10cmdbh	18	1.3	5.0	2.7	0.08	3.2	7.2	2.4
Trees ≥10cmdbh	20	3.1	11.3	5.7	1.43	4.4	13.2	4.4
Subalpine Fir								
Seedlings	358	2.3	7.5	9.2	--	--	11.5	5.8
Saplings	20	1.0	2.5	3.4	--	--	4.4	2.2
Trees <10cmdbh	35	2.5	6.3	3.4	0.11	4.7	10.7	3.6
Trees ≥10cmdbh	12	1.9	5.0	2.5	0.24	0.7	5.1	1.7
Lodgepole Pine								
Seedlings	239	1.6	7.5	9.2	--	--	10.8	5.4
Saplings	90	4.4	11.3	15.3	--	--	19.7	9.8
Trees <10cmdbh	402	28.4	66.3	36.3	0.87	37.1	101.9	34.0
Trees >10cmdbh	278	44.1	76.3	38.4	10.99	33.7	116.2	38.7
Engelmann Spruce								
Seedlings	239	1.6	5.0	6.2	--	--	7.8	3.9
Trees <10cmdbh	71	5.0	13.7	7.5	0.34	14.5	27.1	9.9
Trees ≥10cmdbh	73	11.6	30.0	15.1	1.43	4.4	31.0	10.3
Total								
Seedlings	15,319	--	66.3	--	--	--	--	--
Saplings	2,019	--	62.5	--	--	--	--	--
Trees <10cmdbh	1,414	--	100.0	--	2.35	--	--	--
Trees ≥10cmdbh	630	--	100.0	--	32.56	--	--	--

Douglas-fir

Douglas-fir maintains consistently high importance values throughout the four major size class divisions, although the species is most important in the seedling and sapling size classes (Figure 2). Douglas-fir seedlings dominate this unit with a density of 14,403 seedlings/ha and were recorded on 58.8% of the sample plots. The species has an importance value of 166.3 in this size class. Douglas-fir saplings also dominate that size class with 1900 saplings/ha scattered throughout 58.5% of the study area. These saplings have an importance value of 173.8.

Aggregation indices suggest a contagious Douglas-fir seedling population, with Lloyd's ($\overset{*}{m}/m$) indicating a moderately patchy distribution (Lloyd's ($\overset{*}{m}/m$) = 4.5). Saplings also appear to be contagiously distributed on this study area. The patchiness index (Lloyd's ($\overset{*}{m}/m$)) is 3.1, only slightly less than the index for seedlings. Some density dependent deaths of seedlings are suggested as David and Moore's (I) and Lloyd's ($\overset{*}{m}$) values for saplings are only 1/3 of their former values for seedlings (Table 3).

Douglas-fir is also responsible for the largest number of stems in the small tree size class (888 small tree/ha). These individuals are widely distributed throughout the study area (Frequency = 91.3%), and comprise 40% of the basal area of this size class (Table 2). However, the average diameter of the stems is only 3.6 cm dbh (1.4 in); the high density of the stems is thus largely responsible for the species' substantial relative basal area. The relative density (62.8%) and relative frequency (50%) of the species drop significantly in this

Figure 2 . Importance Values, North-facing Slope

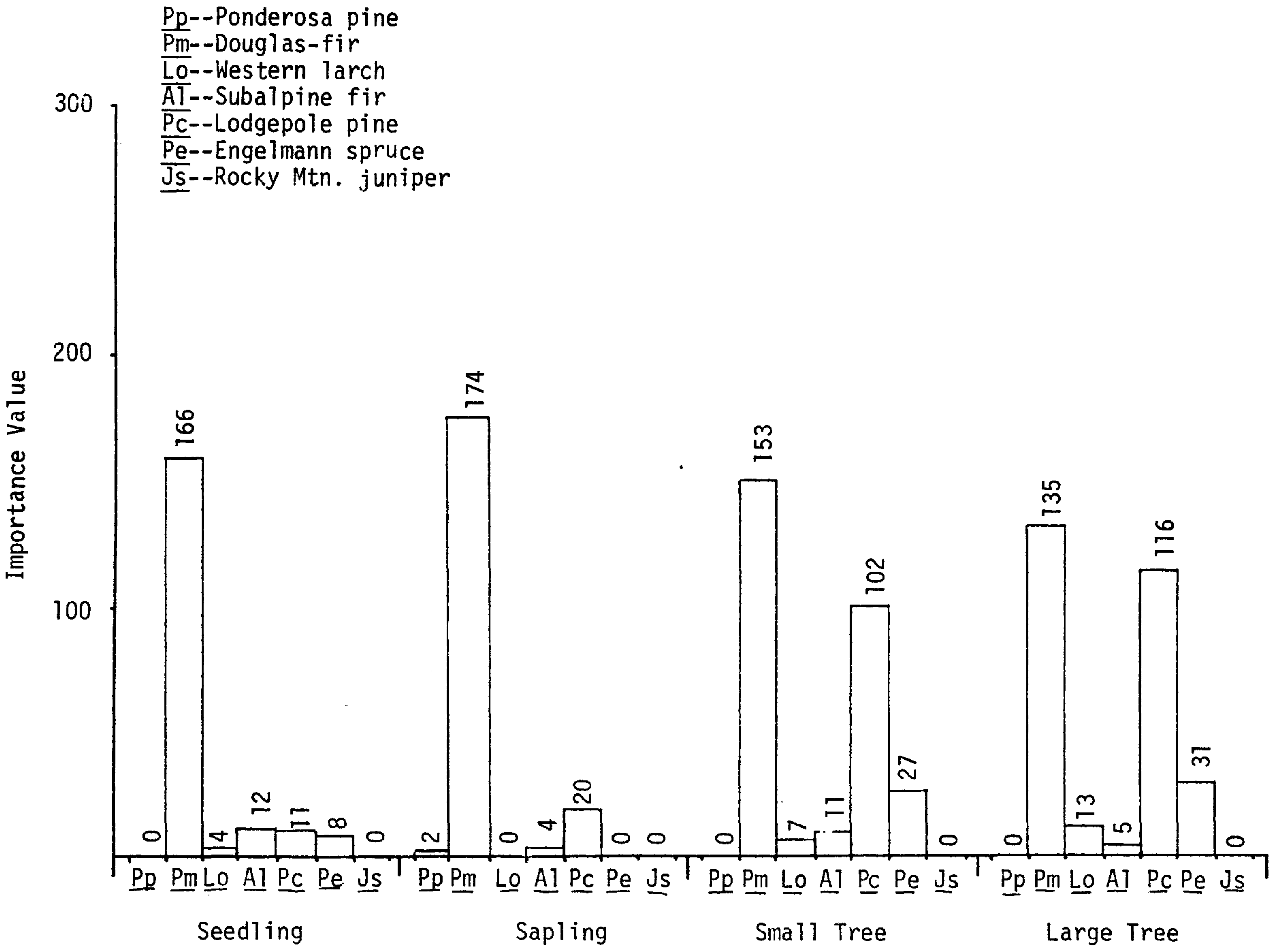


Table 3. Indices of aggregation for the seedling and sapling populations on the north-facing study area on Section 31.

	David and Moore's Index of Dispersion (I)	Lloyd's Index of Clumping ($\overset{*}{m}$)	Lloyd's Index of Patchiness ($\overset{*}{m}$)/m
Seedling	15.9	20.4	4.5
Sapling	5.1	7.4	3.1

size class compared to the smaller size classes. These declines are responsible for reducing Douglas-fir's importance value in this size class to 153.2.

In the large tree size class, Douglas-fir continues to decline in importance, but the species still remains most important (IV = 134.5) (Figure 2). The 248 large trees/ha (100 large trees/acre) are widely distributed (Frequency = 76.3%) but their relative density of only 39.4% indicates Douglas-fir does not dominate this size class based on number of individuals. A relatively large average dbh (30.8 cm, 12.0 in) allows the species to maintain its importance by contributing 56.7% of the unit's large tree basal area. However, only 3.2% of the stems in this size class are greater than 50.1 cm dbh (Table 4).

Subalpine fir

Subalpine fir seedlings are present (358 seedlings/ha), occur with low frequency (7.5%). The low frequency may suggest a clumped distribution around isolated seed sources. With an importance value of 11.5, subalpine fir seedlings are not a major component of this size class (Figure 2). Saplings of subalpine fir are even less important (IV = 4.4), contributing only 20 saplings/ha to this size class.

Although subalpine fir increases slightly in importance (IV = 10.7) in the small tree size class, primarily with an increased density to 35 small trees/ha, the frequency (6.3%) of these individuals remains low. These stems are concentrated in the 5.0--10.0 cm dbh range of the size class, averaging 6.3 cm dbh (Table 4). The species constitutes only 4.7% of the basal area of this size class, adding .11 m^2/ha of basal area to the size class total.

Table 4. Stand table of number of stems/ha on the north-facing study area in nine successive size classes.

Stand Table

Size Class	Total	Pm	Pp	Lo	Al	Pc	Pe	Js
Seedling[x]	15,319	14,403	0	80	358	239	239	0
Saplings[Δ]	2,019	1,900	10	0	20	90	0	0
1.0-10.0 cm dbh	1,414	888	0	18	35	402	71	0
10.1-20.0	274	71	0	10	12	122	59	0
20.1-30.0	187	59	0	2	0	112	14	0
30.1-40.0	118	73	0	4	0	41	0	0
40.1-50.0	41	37	0	2	0	2	0	0
50-1-60.0	10	8	0	2	0	0	0	0
60.1 +	0	0	0	0	0	0	0	0

[x] less than 1.0 meters tall

[Δ] greater than 1.0 meters tall, but not greater than 1.0 cm dbh.

In the large tree size class, subalpine fir is virtually insignificant (IV = 5.1). The species has a density of only 12 large trees/ha (4/acre) distributed with a 5.0% frequency. These individuals are not large, with an average dbh of 15.9 cm (6.2 in), and the contribution of this species to the size class basal area is minor (.24 m^2/ha; 1.04 ft^2/acre).

Lodgepole pine

Lodgepole pine seedlings are unusally abundant in view of their generally acknowledged shade intolerance and the nearly complete canopy cover. The density of lodgepole pine seedlings is 239 seedlings/ha (96/acre) and the frequency of these individuals is 7.5% (Table 2). The importance value of lodgepole pine in this size class is 10.5. The density of lodgepole pine saplings is not high (90 saplings/ha) and the individuals are only found in 11.3% of the sample plots, but the species has a higher importance value (19.7) than any other more tolerant species in this unit except Douglas-fir (Figure 2).

Lodgepole pine becomes increasingly important in the small tree size class, increasing in importance value to 101.9. The density of the species is 402 small trees/ha, with the individuals distributed widely throughout the study area (Frequency = 66.3%). While the relative density of the small trees is only 28.4%, these individuals average 5.2 cm dbh. This average diameter is a major factor in raising the relative basal area of lodgepole pine small trees to 37.1%. Douglas-fir, with a comparable relative basal area, has a much higher density (Table 2).

In the large tree size class, lodgepole pine again increases in importance, in this case achieving an importance value of 116.2.

Lodgepole pine has the highest density of all species in this size class (278 large trees/ha; 112/acre), while the species is found with equal frequency (76.3%) to that of Douglas-fir (Table 2). The average dbh of these large trees is only 22.4 cm (8.8 in.) effectively limiting the relative basal area (Basal Area = 10.99 m^2/ha; Relative Basal Area = 33.7%) of the species in relation to its high density.

Engelmann spruce

Engelmann spruce seedlings comprise a small portion of the total seedling population in this study area, contributing 239 seedlings/ha. Spruce seedlings are encountered infrequently (Frequency = 5.0%) and the relative importance of the species in this size class is small (IV = 7.8). No Engelmann spruce saplings were encountered in the study area.

Engelmann spruce is also not a major component of the small tree size class. The density of the species is 71 small trees/ha and the frequency of these individuals is only 13.7% (Table 2). The average diameter of these stems is 7.8 cm dbh with 75% of them greater than 5.0 cm dbh. The basal area of the species is .34 m^2/ha, constituting 14.5% of the basal area of the size class. The importance value of Engelmann spruce is 27.1, with a major segment of that being derived from the relatively large size of the individuals within the limits of this size class. Both the relative density and relative frequency of the species are around 5%.

Engelmann spruce increases in importance in the large tree size class (Figure 2). The density of the spruce is 73 trees/ha and the frequency is 30.0%. The average diameter of these stems is only 15.8

cm dbh (6.2 in) with over 80% of the individuals found in the 10.1-20.0 cm dbh class (Table 4). The contribution of these individuals to the study unit's basal area is small (Relative Basal Area = 4.4%), adding only 1.43 m^2/ha (6.23 ft^2/acre) to the total. Mention should be made that Engelmann spruce does not occur near the upper extremes of the study area, but is initially encountered near midslope and seems to increase in frequency downslope towards the creek bottom. In this case, one would not expect a high frequency for spruce in any of the size classes. However, a stratified analysis may show increased importance for the species in the lower one-half or one-thrid of the study area.

Western larch

Western larch, another acknowledged shade intolerant species (Baker, 1950), is perhaps surprisingly represented in the seedling size class (Table 2). Although the seedling density is 80 seedlings/ha the individuals are encountered very infrequently (Frequency = 2.5%). These seedlings are likely concentrated on particularly favorable microsites that were created by some sort of small scale disturbance. These seedlings have an importance value of only 3.6. No western larch saplings were encountered in the study area.

Western larch is present in the small tree size class, but is relatively unimportant (IV = 7.2). The species' 18 small tree/ha appear widely distributed throughout the area (Frequency = 5.0%). Individuals in this size class average 7.5 cm dbh (3.0 in) and none are less than 5.0 cm dbh. The basal area contribution of the species is only .08 m^2/ha (.35 ft^2/acre), less than 4% of the size class total (Table 2).

Large western larch occur occasionally, but infrequently, throughout the area (Density = 20 large trees/ha, 8/acre; Frequency = 11.3%). The average diameter of these large trees is 30.2 cm dbh (11.8 in) however their low density prevents any appreciable contribution to the total basal area of the size class. The basal area of the species in this size class is 1.43 m^2/ha (6.23 ft^2/acre), only 4.4% of the size class total. The importance value of western larch in this size class is 13.2.

Ponderosa pine

Ponderosa pine appears to be at the extreme of its elevational range and is easily out-competed by other individuals on this cool, moist site. Ponderosa pine is encountered in the sapling plots, but is not important (IV = 2.2).

East-facing Study Area

The east-facing study unit is located on a steeper slope (mean slope = 51%) than the north-facing unit, but still maintains essentially the same species composition. Although east-facing slopes are generally considered somewhat warmer than north-facing slopes, the only difference between the two sites in terms of species composition is the lack of any ponderosa pine on this unit. Since the presence of ponderosa pine on the north slope was somewhat unexpected, and since it certainly was not phytosociologically important on that site, its absence from the east-facing slope will not be stressed.

In this unit, the large tree size class retains a density of 426 trees/ha (172/acre) (Table 5). The average diameter of the

Table 5. Phytosociological Summary--East-facing Slope.

	Density		Frequency		Basal Area		Importance Value	
	Absolute #/ha	Relative %	Absolute %	Relative %	Absolute m^2/ha	Relative %	Absolute	Relative %
Douglas-fir								
Seedlings	16,472	95.4	71.3	80.3	--	--	175.7	87.8
Saplings	408	85.4	22.5	75.0	--	--	160.4	80.2
Trees <10cmdbh	327	84.4	96.3	70.6	0.67	81.6	236.6	78.9
Trees ≥10cmdbh	370	86.9	100	66.1	22.24	85.4	238.4	79.5
Western Larch								
Seedlings	159	0.9	5.0	5.6	--	--	6.5	3.2
Saplings	30	6.3	3.8	12.5	--	--	18.8	9.4
Trees <10cmdbh	5	1.3	3.8	2.8	.01	0.1	4.1	1.4
Trees ≥10cmdbh	15	3.4	12.5	8.3	2.53	9.7	21.4	7.1
Subalpine Fir								
Seedlings	398	2.3	6.3	7.0	--	--	9.3	4.6
Trees <10cmdbh	19	5.0	13.7	10.1	0.05	6.1	21.2	7.1
Trees ≥10cmdbh	8	1.9	7.5	5.0	0.38	1.4	8.3	2.8
Lodgepole Pine								
Seedlings	80	0.5	1.3	1.4	--	--	1.9	1.0
Saplings	30	6.3	2.5	8.3	--	--	14.6	7.3
Trees <10cmdbh	34	8.8	20.0	14.7	0.08	10.2	33.6	11.2
Trees ≥10cmdbh	29	6.9	27.5	18.2	0.83	3.2	28.2	9.4
Engelmann Spruce								
Seedlings	159	0.9	5.0	5.6	--	--	6.5	3.2
Saplings	10	2.1	1.3	4.2	--	--	6.3	3.2
Trees <10cmdbh	2	0.6	2.5	1.8	0.02	2.0	4.5	1.5
Trees ≥10cmdbh	4	0.9	3.8	2.5	0.06	0.2	3.6	1.2
Total								
Seedlings	17,268	--	72.5	--	--	--	--	--
Saplings	477	--	25.0	--	--	--	--	--
Trees <10cmdbh	387	--	100	--	0.82	--	--	--
Trees ≥10cmdbh	426	--	100	--	26.03	--	--	--

individual stems in this size class is 27.9 cm dbh (11.0 in). However, due to the moderate density of the stems, the basal area of this size class is only 26.0 m^2/ha (113.0 ft^2/acre). The basal area of this largest size class is 96.9% of total stand basal area of 26.8 m^2/ha (116.9 ft^2/acre).

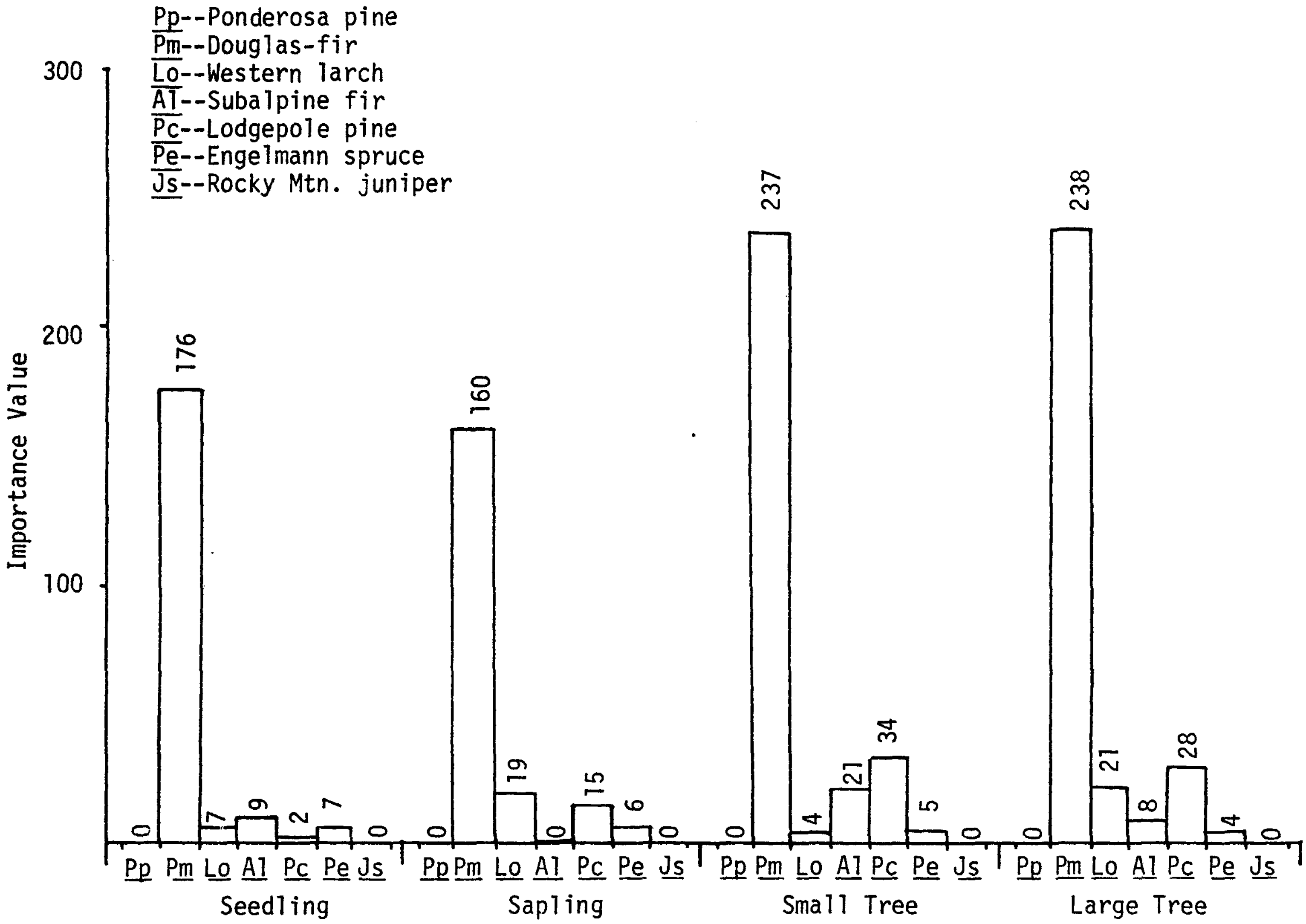
The density of the small tree size class is also modest, with only 387 small trees/ha. These small trees average 5.2 cm dbh, while adding only .82 m^2/ha of basal area to the unit total basal area.

Reproduction is abundant in both the seedling and sapling size classes. Saplings with a density of 477 saplings/ha, are distributed over only 25% of the study area, generally indicating a contagious sapling population. The density of the seedlings is very high, including some 17,268 seedlings/ha which are found throughout the study area (Frequency = 72.5%).

Douglas-fir

Douglas-fir is by far the most important species found on the east-facing study area, maintaining importance values which consistently exceed 78% of the total possible (Figure 3). Douglas-fir seedlings outnumber all other species with a density of 16,742 seedlings/ha. These individuals are widely dispersed as indicated by a frequency of 71.3%. The importance value of Douglas-fir seedlings on this slope is 175.7. Douglas-fir accounts for 85.4% of the saplings found in this study area with a density of 408 saplings/ha. However, these individuals are found in only 22.5% of the sample plots (Table 5). The importance value of the species drops slightly in this size class to 160.4.

Figure 3 . Importance Values, East-facing Slope.



A contagious Douglas-fir seedling population is probable. Lloyd's ($\overset{*}{m}/m$) has a value of 2.9, suggesting a moderately patchy population. Saplings, according to an increase in the index to 5.9, appear to be more patchy than seedlings. Death of seedlings due to density dependent factors may be indicated by sapling values for David and Moore's (I) and Lloyd's ($\overset{*}{m}$) of only 1/4 of seedling values (Table 6).

Within the small tree size class, Douglas-fir has a density of 327 small trees/ha, accounting for 84.4% of the size class density. A frequency of 96.3% shows the species to be widely dispersed throughout the study area. Although the small tree size class as a whole makes a rather insignificant contribution to the unit total basal area, Douglas-fir is responsible for 81.6% of the amount or .67 m^2/ha. About 63% of the Douglas-fir in this size class are smaller than 5.0 cm dbh. The overall dominance of Douglas-fir in this size class is summarized by an importance value of 236.6 (Figure 3).

The relative importance of Douglas-fir in the large tree size class is well illustrated through an importance value of 238.4 (Figure 3). The density of Douglas-fir is 370 large trees/ha (149/acre) comprising 86.9% of the trees recorded in this size class. With a frequency of 100%, these individuals appear to be widely distributed. Douglas-fir is responsible for 22.24 m^2/ha (96.87 ft^2/acre) of basal area, which includes 85.4% of the basal area in this size class (Table 5). The mean diameter of the large trees is 27.6 cm dbh (10.9 in). Sixty-seven percent of the large trees are between 10.0 and 30.0 cm dbh, with the number of individuals dropping off in the large size

Table 6. Indices of aggregation for the seedling and sapling populations on the east-facing study area on Section 31.

	David and Moore's Index of Disperson (I)	Lloyd's Index of Clumping ($\overset{*}{m}$)	Lloyd's Index of Patchiness ($\overset{*}{m}$)/m
Seedling	9.9	15.1	2.9
Sapling	2.5	3.0	5.9

classes. Only 2.4% of the Douglas-fir large trees are found in the 50.1-60.0 cm dbh size class and no stems are greater than 60.0 cm dbh (Table 7).

Subalpine fir

Subalpine fir is a generally unimportant species in this study area (Figure 3). Although the species may appear at mid-or upperslope, individuals are most commonly observed on the lower portion of the study area. Subalpine fir seedlings are common (398 seedlings/ha), but these individuals appear infrequently (Frequency = 6.3%). A very low relative density (2.3%) and a low relative frequency (7.0%) are responsible for an importance value of only 9.3. No subalpine fir saplings were observed in the study area. There are several potential reasons for the dearth of saplings, including (1) a lack of seeding survival, or (2) lack of seed production during a particular series of years, which left this size class unoccupied.

Subalpine fir has a density of 19 small trees/ha accounting for 5.0% of the individuals in the size class. Individuals of this species are found infrequently in this size class (Frequency = 13.7%). Sixty-three percent of the small trees are less than 5.0 cm dbh and the species comprises only 6.1% (.05 m^2/ha) of the basal area of this size class (Relative Basal Area = 6.1%). The importance value of subalpine fir in the small tree size class is 21.2.

Subalpine fir is also a minor component of the large tree size class, as illustrated by an importance value of 8.3 (Figure 3). The density of the species is 8 large trees/ha (3/acre), with the species found at only 7.5% of the sample points in this unit (Table 5). Either

Table 7. Stand table of number of stems/ha on the east-facing study area in nine successive size classes.

Stand Table

Size Class	Total	Pm	Pp	Lo	Al	Pc	Pe	Js
Seedling^{x}	17,268	16,472	0	159	398	80	159	0
Sapling$^{\Delta}$	477	408	0	30	0	30	10	0
1.0-10.0 cm dbh	387	327	0	5	19	34	2	0
10.1-20.0	174	146	0	1	5	17	0	0
20.1-30.0	119	104	0	3	0	12	0	0
30.1-40.0	83	79	0	1	3	0	0	0
40.1-50.0	36	32	0	4	0	0	0	0
50.1-60.0	13	9	0	4	0	0	0	0
60.1 +	1	0	0	1	0	0	0	0

^{x} less than 1.0 meters tall

$^{\Delta}$ greater than 1.0 meters tall, but no greater than 1.0 cm dbh these large trees are scattered throughout the study area or they might be found frequently within the lower portion of the study area. The average size of these individuals is 24.5 cm dbh (9.7 in), but the stand table shows their distribution split between the 10.1--20.0 cm dbh class and the 30.1--40.0 cm dbh class (Table 7). Consistently low relative values for density (Relative Density = 1.9%), frequency (Relative Frequency = 5.0%) and basal area (Relative Basal Area = 1.4%) account for the low importance value (Table 5).

Lodgepole pine

Lodgepole pine seedlings are found in this study area, but they are low in density (80 seedlings/ha) and low in frequency (Frequency = 1.3%). Relatively speaking, this species is insignificant in this size class, representing 0.5% of the relative density and 1.4% of the relative frequency (Table 5). Lodgepole pine saplings also are low in density (30 saplings/ha) and frequency (2.5%). The importance of the species increases somewhat in this size class, with the combined relative density (6.3%) and relative frequency (8.3%) values constituting an importance value of 14.6 (Table 5).

In the small tree size class lodgepole pine has a density of 34 small trees/ha, accounting for 8.8% of the trees in this size class. The species is found more frequently in this size class (Relative Frequency = 14.7%) than in the smaller two size classes. These small trees are distributed evenly throughout the size class, with approximately half of the trees being less than 5.0 cm dbh and half being greater than 5.0 cm dbh. Lodgepole pine small trees constitute 10.2% of the size class basal area contributing .08 m^2/ha of the size class total. The importance value of ldogepole pine increases to 33.6 in this size class.

In the large tree size class, lodgepole pine represents 6.9% of the density and again increases compared to smaller size classes in relative frequency (18.2%). Virtually all of the large trees of this species are concentrated in the 10.0--30.0 cm dbh class (Table 7). With a density of only 29 large trees/ha (11/acre) and an average stem diameter of only 19.2 cm dbh (7.5 in), the basal area of lodgepole pine is .83 m^2/ha (3.5 ft^2/acre). Thus, lodgepole pine, which does not usually attain large diameters, constitutes only 3.2% of the relative basal area of this size class. Although relative density and relative basal area dropped from the previous size class, an increase in the relative frequency of lodgepole pine allows the species to maintain an importance value of 28.2.

Engelmann spruce

Engelmann spruce is a relatively unimportant species on the east-facing slope. The species is seldom found in the study area except on the lower portion of the slope. Engelmann spruce seedlings are found on this east aspect, but account for only .9% of the total seedlings in the study area. The 159 seedlings/ha are found infrequently throughout the unit (Frequency = 5.0%). The low relative significance of the species in this size class is characterized by an importance value of 6.5 (Table 5). The density of Engelmann spruce saplings is 10 saplings/ha and these individuals are discovered even less frequently (1.3%) than the seedlings despite the larger size of the sapling sample plots. The importance value of Engelmann spruce saplings is a low 6.3 (Table 5).

In the small tree size class, Engelmann spruce is virtually insignificant as noted by an IV of 4.5. The 2 small trees/ha constitute only 0.6% of the stems in the size class. The frequency is obviously low, only 2.5%.

The species is also unimportant in the large tree size class, as illustrated by an importance value of only 3.6 (Figure 3). The four large trees/ha (1/acre) are necessarily found infrequently (Frequency = 3.8%). Most stems measured are in the 10.1--20.0 cm dbh size class (Table 7) and hence do not contribute greatly to stand basal area (Relative Basal Area = 0.2%).

Western larch

Western larch is found throughout the entire range of size classes in the east-facing study area, although it is not an important species in any of the four major size classes.

Seedlings of the species are present in the study area (Density = 159 seedlings/ha), but are not distributed widely (Frequency = 5.0%). However, western larch is not an important species in this size class, with a relative density of 0.9% and a relative frequency of 5.6% combining to form an importance value of 6.5 (Table 5). Surprisingly, western larch saplings are more important than any other species' in the study area except Douglas-fir (Figure 3). It is more important than other shade tolerant species such as subalpine fir and Engelmann spruce. This phenomenon may be some indication of the openness of the canopy as it is unlikely that western larch saplings would survive unless a fair amount of sunlight and soil moisture were available to them. The importance value for western larch saplings of 18.8 is much less than the importance value of Douglas-fir. The number of saplings is not large (Density = 30 saplings/ha) and their frequency is low (3.8%), perhaps suggesting that more open microsites occur within the study area in which the western larch reproduction is concentrated. A relative density of 6.3% and relative frequency of 12.5% combine to form an importance value of 18.8 (Table 5).

The importance of larch drops considerably in the small tree size class. With only 5 small trees/ha distributed with a frequency of 3.8%, these individuals could easily be end-products of natural competition within older once-disturbed areas or these stems may be the faster growing individuals of an even-aged patch of reproduction. Most of these individuals have barely achieved 1.0 cm dbh, as their combined basal area is less than .01m^2/ha or 0.1% of the total basal area of the size class (Table 5). This low relative basal area value combines with a low relative density value (1.3%) and a low relative frequency value (2.8%) to form an importance value of 4.1.

In the large tree size class, long-lived western larch again increases in importance (Figure 3). The species has a higher density (15 large trees/ha; 5/acre) in this size class, with the individuals apparently distributed more widely than the previous size class (Relative Frequency = 8.3%). The average diameter of these large trees is 46.3 cm dbh (18.2 in), producing a more significant contribution to the size class basal area (Relative Basal Area = 9.7%) than would be expected based on the stem density. A stand table shows 8 stems/ha in the 40.0--60.0 cm dbh class and 1 stem/ha in the greater than 60.0 cm dbh class, making a species basal area of 2.53 m^2/ha (11.0 ft^2/acre)

(Table 7). Slight increases in the relative density (3.4%) and the relative frequency (8.3%), plus a more substantial increase in the relative basal area (9.7%) result in a larger importance value (21.4) than found in the previous size classes (Table 5).

West-facing Study Area

The west-facing study area is situated on a steep slope (mean slope = 51%), virtually a topographic mirror-image of the east-facing unit. In terms of species composition and species importance, however, this area is considerably different than its sister study area. The tree species found on this unit include Douglas-fir, ponderosa pine, subalpine fir, lodgepole pine, and Rocky Mountain juniper (Js) (Juniperus scopulorum sarg.). Douglas-fir is the only tree species of major importance in any size class, except for lodgepole pine in the large tree size class. Since west-facing slopes are regarded as warmer, less mesic sites, one might anticipate a greater importance of such species as ponderosa pine and Rocky Mountain juniper on this area.

The density of the large trees on this site is 662 large trees/ha (267/acre). These stems have an average dbh of 27.4 cm (10.8 in), which results in 39.25 m^2/ha (170 ft^2/acre) of basal area (Table 8). The basal area of this size class accounts for 97% of the total basal area of the site, which is 40.30 m^2/ha (175.5 ft^2/acre).

The small trees on this site have a density of 331 stems/ha, only half that of the large trees. These trees average 6.4 cm dbh and contribute 1.05 m^2/ha of basal area to the unit, which is less than 3% of the total basal area (Table 8).

Table 8. Phytosociological Summary--West-facing Slope.

	Density		Frequency		Basal Area		Importance Value	
	Absolute #/ha	Relative %	Absolute %	Relative %	Absolute m^2/ha	Relative %	Absolute	Relative %
Douglas-fir								
Seedlings	3501	100	18.8	100	--		200	100
Saplings	50	100	6.3	100	--	--	200	100
Trees <10cmdbh	330	99.7	100	98.8	1.05	99.9	298.3	99.4
Trees ≥10cmdbh	622	94.1	100	85.1	37.74	96.2	275.3	91.8
Ponderosa Pine								
Trees ≥10cmdbh	2	0.3	1.3	1.1	0.3	0.8	2.1	0.1
Subalpine Fir								
Trees ≥10cmdbh	2	0.3	1.3	1.1	0.02	0.1	1.4	0.5
Lodgepole Pine								
Trees ≥10cmdbh	35	5.3	15.0	12.8	1.19	3.0	21.1	7.0
Rocky Mt. Juniper								
Trees <10cmdbh	1	0.3	1.3	1.2	.01	0.1	1.7	0.6
Total								
Seedlings	3501	--	18.8	--	--	--	--	--
Saplings	50	--	6.3	--	--	--	--	--
Trees <10cmdbh	331	--	100	--	1.05	--	--	--
Trees ≥10cmdbh	662	--	100	--	39.25	--	--	--

Reproduction is plentiful within this study area, with seedlings being numerous (3501 seedlings/ha; 1417/acre) but not frequent (Frequency = 18.8%). Saplings are not abundant with a density of only 50 stems/ha (20/acre), nor are they frequent, being estimated to occur on only 6.3% of the study area.

Douglas-fir

Douglas-fir is the only species represented in the seedlings size class and as such is responsible for all 3501 seedlings/ha. These seedlings were found on 18.8% of the sample plot (Frequency = 18.8%). Field observations show obvious patches of regeneration. Since the species is the only one present in the size class, it assumes an importance value of 200 (Table 8). Douglas-fir is also the only species present in the sapling size class, constituting all 50 stems/ha. The saplings appear to be associated with the scattered patches of regeneration where, despite their larger size, these individuals may be the same age as the many seedlings associated with them. The indices of aggregation suggest substantial contagion of Douglas-fir seedlings on this slope. Values of zero for Douglas-fir saplings however, indicate a virtually random distribution. Decreases in David and Moore's (I) and Lloyd's ($\overset{*}{m}$) of 15X the seedling values may indicate substantial amounts of density dependent mortality (Table 9).

Douglas-fir also dominates the small tree size class on this unit, accounting for 99.7% of the small trees. These individuals are widely distributed in the study area (Frequency = 100%) and account for 99.9% of the basal area. The high values for relative

Table 9. Indices of aggregation for the seedling and sapling populations on the west-facing study area on Section 31.

	David and Moore's Index of Disperson (I)	Lloyd's Index of Clumping ($\overset{*}{m}$)	Lloyd's Index of Patchiness ($\overset{*}{m}$)/m
Seedling	14.4	15.5	14.1
Sapling	0.0	0.0	0.2

density, relative frequency, and relative basal area combine to produce an importance value of 298.3 for Douglas-fir in this size class (Table 8).

Douglas-fir is somewhat less important in the large tree size class with an importance value of 275.3 (Figure 4). The density of the species in this case is 622 large trees/ha (251/acre), which represents 94.1% of the stems in the size class. These individuals occur with a frequency of 100% and are thus found throughout the unit. The average diameter of the stems in this size class is 27.7 cm dbh (10.9 in) and the majority (≃ 67%) of the stems lie between 10.1--30.0 cm dbh. The number of individuals declines in the large diameter size classes, but 5% of the individuals are greater than 50.1 cm dbh (20 in) (Table 10). The numerous individuals in the large diameter size classes contribute substantially to the size class basal area of 37.74 m^2/ha (164.39 ft^2/acre) and relative basal area of 96.2% (Table 8).

Rocky Mountain juniper

Rocky Mountain juniper occurs only in the small tree size class where it is not important (IV = 1.7). These infrequent individuals (Frequency = 1.3%) are generally found near rock outcrops in this area, with birds possibly being responsible for seed dissemination. The density of the species is only 1 small tree/ha, and the species contribution to the size class basal area is negligible (Table 8).

Lodgepole pine

Lodgepole pine is present only in the large tree size class. The species may be considered significant when postulating the past dynamics of this stand, but it is not really important to present

Figure 4 . Importance Values, West-facing Slope.

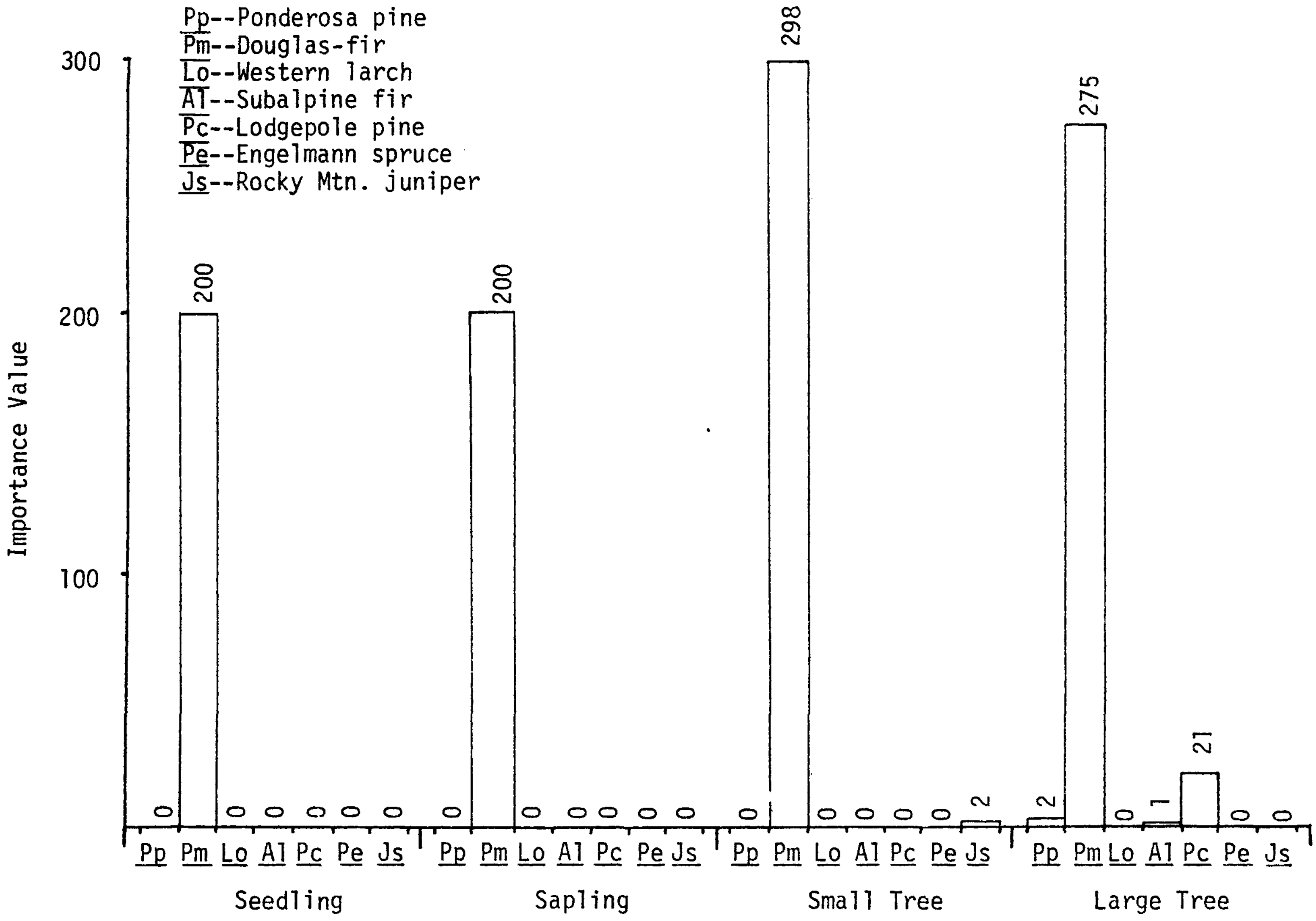


Table 10. Stand table of number of stems/ha on the west-facing study area in nine successive size classes.

Stand Table

Size Class	Total	Pm	Pp	Lo	Al	Pc	Pe	Js
Seedlings^{x}	3,501	3,501	0	0	0	0	0	0
Saplings$^{\Delta}$	50	50	0	0	0	0	0	0
1.0-10.0 cm dbh	330	329	0	0	0	0	0	1
10.1-20.0	323	304	0	2	17	0	0	0
20.1-30.0	161	143	0	0	9	0	0	0
30.1-40.0	83	83	0	0	0	0	0	0
40.1-50.0	62	60	2	0	0	0	0	0
50.1-60.0	21	21	0	0	0	0	0	0
60.1 +	12	12	0	0	0	0	0	0

[x] less than 1.0 meters tall

[Δ] greater than 1.0 meters tall, but not greater than 1.0 cm dbh

structure (IV = 21.1). The relatively few individuals (Density = 35 large trees/ha) present are widespread (Frequency = 15%). Stems of this species average 20.8 cm dbh (8.2 in) and are concentrated in the 10.0--30.0 cm dbh class (Table 10). The species basal area is 1.19 m^2/ha (5.18 ft^2/acre), only 3.0% of the basal area of the size class. Although the relative density and relative basal area, 5.3% and 3.0% respectively, are very small, lodgepole pine's higher relative frequency (12.8%) is responsible for more than half of its importance value (Table 8).

Ponderosa pine

Occasional ponderosa pine are found in the large tree size class. These few individuals (2 large trees/ha) are large, with an average diameter of 43.7 cm dbh (16.2 in). Their low frequency (1.3%) (0.30 m^2/ha; 1.30 ft^2/acre) and density result in an importance value of only 2.1.

Subalpine fir

Subalpine fir is found on the lower portion of the study area as the creek bottom is approached. The few individuals (2.0 large trees/ha) appear scattered. The trees are not large, all of them being between 10.1 and 20.0 cm dbh, and the species importance value is 1.4.

South-facing Study Area

Any description of the vegetation within the south-facing study area should include reference to the more complex physiography of this unit compared to the other three. The slope of the area is not homogeneous; the upper portion of the unit is bench-like (mean slope = 27%), while the lower portion slopes steeply into the creek bottom (mean slope = 60%). Field observations indicated that these two topographic situations might support different community structures. Therefore, after a brief summary of the unit as a whole, a more detailed analysis of each topographic subunit is presented.

A total of four tree species are found throughout the study area. These species are Douglas-fir, ponderosa pine, lodgepole pine, and Rocky Mountain juniper. Southerly aspects are generally the warmest and driest; the relatively more xeric species such as ponderosa pine and Rocky Mountain juniper should be expected to reach their maximum importance in this particular unit. Douglas-fir is, however, the dominant tree species in the area.

The overall density of large trees in the area is 272 large trees/ha (110/acre) (Table 11). Individuals on this unit have the largest average diameter (35.9 cm dbh (14.1 in)) of any unit and account for 27.66 m^2/ha (120.48 ft^2/acre) of basal area. The trees in this major size class are distributed throughout the range of the dbh classes, with 15% of the stems >50.1 cm dbh (Table 12).

The density of the small tree size class is only 81 small trees/ha. These stems average 5.9 cm dbh and contribute .23 m^2/ha of basal area to the unit total of 27.89 m^2/ha.

Reproduction is not abundant on the area. Saplings are scarce (50 saplings/ha) and these stems are not widely distributed (Frequency = 6.3%). In some instances they are intermixed with seedling patches. Although seedlings are more plentiful (796 seedlings/ha, 322/acre)

Table 11. Phytosociological Summary--South-facing Slope (Whole unit)

	Density		Frequency		Basal Area		Importance Value	
	Absolute #/ha	Relative %	Absolute %	Relative %	Absolute m^2/ha	Relative %	Absolute	Relative %
Douglas-fir								
Seedlings	796	100	7.5	100	--	--	200	100
Saplings	50	100	6.3	100	--	--	200	100
Trees <10cmdbh	79	96.3	100	87.9	0.22	95.7	279.8	93.3
Trees ≥10cmdbh	259	95.0	100	25.42	85.1	91.9	272.0	90.7
Ponderosa Pine								
Trees <10cmdbh	1	1.6	5.0	4.4	.01	1.0	7.0	2.3
Trees ≥10cmdbh	13	4.7	16.3	13.8	2.23	8.1	26.6	8.9
Lodgepole Pine								
Trees ≥10cmdbh	1	0.3	1.3	1.1	0.01	.01	1.4	0.5
Rocky Mt. Juniper								
Trees <10cmdbh	2	2.2	8.8	7.7	0.01	3.3	13.2	4.4
Total								
Seedlings	796	--	7.5	--	--	--	--	--
Saplings	50	--	6.3	--	--	--	--	--
Trees <10cmdbh	82	--	100	--	.23	--	--	--
Trees ≥10cmdbh	273	--	100	--	27.66	--	--	--

Table 12. Stand table of number of stems/ha on the south-facing study area in nine successive size classes.

Stand Table

Size Class	Total	*Pm*	*Pp*	*Lo*	*Al*	*Pc*	*Pe*	*Js*
Seedling[x]	796	796	0	0	0	0	0	0
Sapling[Δ]	50	50	0	0	0	0	0	0
1.0-10.0 cm dbh	82	79	1	0	0	0	0	2
10.1-20.0	99	93	5	0	0	1	0	0
20.1--30.0	45	44	1	0	0	0	0	0
30.1-40.0	49	47	2	0	0	0	0	0
40.1-50.0	38	37	1	0	0	0	0	0
50.1-60.0	25	23	2	0	0	0	0	0
60.1 +	17	14	3	0	0	0	0	0

[x] less than 1 meter tall

[Δ] greater than 1 meter tall, but not greater than 1.0 cm dbh their frequency is not high either (7.5%). By observation, there appear to be two distinct types of seedling distributions. On the bench seedlings appear scattered, but on the steeper subunit the seedlings appear contagiously distributed.

Bench subunit

The bench-like area seems to be the better site of the two subunits. Both Douglas-fir and ponderosa pine are found in this upper unit, though Douglas-fir is by far the more important (Figure 5). The density of large trees in this subunit is 667 large trees/ha (270/acre). Douglas-fir accounts for 654 large trees/ha, while ponderosa pine is responsible for only 14 large trees/ha. The large trees average 27.7 cm dbh (10.9 in) and constitute 40.41 m^2/ha (176.02 ft^2/acre) of basal area (Table 13). Individual Douglas-fir stems average 25.0 cm dbh with 76% of the stems falling between 10.1--30.0 cm dbh. The remaining trees are found in all of the larger dbh classes; 5% of the large trees are 50.1 cm dbh or larger (Table 14). Douglas-fir has a basal area of 34.27 m^2/ha which is 84.8% of the subunit total for large trees. Ponderosa pine average 74.7 cm dbh, nearly three times that of Douglas-fir, and tend to be concentrated within two specific dbh classes. About one half of the stems fall in the 30.1--40.0 cm dbh class, while the other half fall in the > 60.1 cm dbh class (Table 14). Because of the low species density, the basal area of ponderosa pine is only 6.14 m^2/ha (26.74 ft^2/acre), about 15% of the total for this size class (Table 13). Douglas-fir is widely distributed (Frequency = 100%), but ponderosa pine is not frequent (8.3%). The relative importance of the two species in this size class is clearly illustrated

Figure 5. Importance Values, South-facing Slope (Bench Subunit).

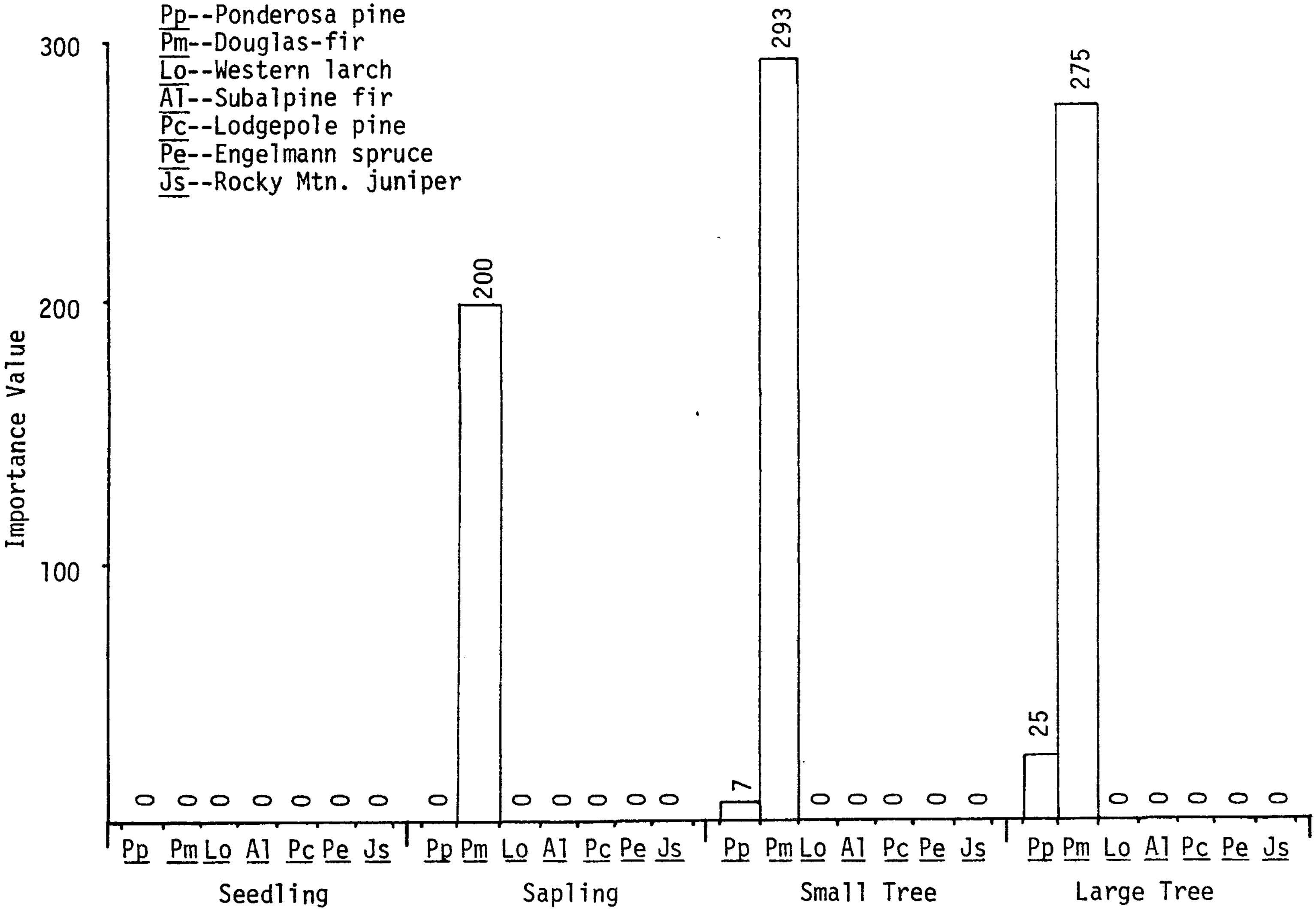


Table 13. Phytosociological Summary--South-facing Slope (Bench unit).

	Density		Frequency		Basal Area		Importance Value	
	Absolute #/ha	Relative %	Absolute %	Relalive %	Absolute m^2/ha	Relative %	Absolute	Relative %
<u>Douglas-fir</u>								
Saplings	30	100	12.5	100	--	--	200	100
Trees <10cmdbh	265	99.0	100	96.0	0.83	97.9	292.9	97.6
Trees ≥10cmdbh	654	97.9	100	92.3	34.27	84.8	275.0	91.7
<u>Ponderosa Pine</u>								
Trees <10cmdbh	3	1.0	4.2	4.0	0.02	2.1	7.1	2.4
Trees ≥10cmdbh	14	2.1	8.4	7.7	6.14	15.2	25.0	8.3
<u>Total</u>								
Saplings	30	--	12.5	--	--	--	--	--
Trees <10cmdbh	268	--	100	--	.84	--	--	--
Trees ≥10cmdbh	667	--	100	--	40.41	--	--	--

Table 14. Stand table of number of stems/ha on the south-facing study area in nine successive size classes. (Bench subunit)

Stand Table

Size Class	Total	*Pm*	*Pp*	*Lo*	*Al*	*Pc*	*Pe*	*Js*
Seedling[x]	0	0	0	0	0	0	0	0
Sapling[Δ]	30	30	0	0	0	0	0	0
1.o-10.0 cm dbh	268	265	0	0	0	0	0	0
10.1-20.0	368	368	0	0	0	0	0	0
20.1-30.0	132	132	0	0	0	0	0	0
30.1-40.0	97	90	7	0	0	0	0	0
40.1-50.0	35	35	0	0	0	0	0	0
50.1-60.0	21	21	0	0	0	0	0	0
60.1 +	14	7	7	0	0	0	0	0

[x] less than 1.0 meters tall

[Δ] greater than 1.0 meters tall, but not greater than 1.0 cm dbh

by their importance values. Douglas-fir has an importance value of 275 and ponderosa pine has a much smaller value of 25.0, of which 15.2 units are dependent on the large average size of the few stems.

There are 268 small trees/ha averaging 5.2 cm dbh on this upper subunit. Collectively these stems constitute .84 m^2/ha (3.66 ft^2/acre) of basal area. Again, the only species found in this size class are Douglas-fir and ponderosa pine (Table 13). Douglas-fir accounts for 99% of the small trees in the subunit, as well as 99% of the small tree basal area. Douglas-fir is also widely distributed (Frequency = 100%), contributing to its importance value of 292.9. Ponderosa pine is a relatively insignificant species in this size class (IV = 7.1). The species is represented by 3 small trees/ha, although their average size (9.2 cm dbh), exceeds that of Douglas-fir by 3.0 cm. Nevertheless, the relative basal area of ponderosa pine within this size class is only 2.1 and its frequency is 4.2%.

Plants in the smallest two size classes are very scarce on the bench subunit. Only 30 saplings/ha are found in the area, all of which are Douglas-fir. These stems are, by observation, scattered throughout the area (Frequency = 12.5%). Indices of aggregation indicate that Douglas-fir saplings are nearly randomly distributed (Table 15). No seedlings were sampled within this subunit and very few were observed.

Slope subunit

The slope subunit is characterized by a steep slope and generally thin soils. The canopy of the area is more open than on the upper subunit, as illustrated by a reduced density to 261 stems/ha (105 stems/acre, all stems > 1.0 cm dbh) (Table 16).

Table 15. Indices of aggregation for the seedling and sapling populations on the south-facing (bench subunit) study area on Section 31.

	David and Moore's Index of Dispersion (I)	Lloyd's Index of Clumping ($\overset{*}{m}$)	Lloyd's Index of Patchiness ($\overset{*}{m}$)/m
Seedling	none	--	--
Sapling	0.0	0.0	0.5

Table 16. Phytosociological Summary--South-facing Slope (Slope subunit)

	Density		Frequency		Basal Area		Importance Value	
	Absolute #/ha	Relative %	Absolute %	Relative %	Absolute m^2/ha	Relative %	Absolute	Relative %
Douglas-fir								
Seedlings	796	100	10.7	100	--	--	200	100
Saplings	20	100	3.6	100	--	--	200	100
Trees <10cmdbh	55	95.1	100	84.8	0.14	94.5	274.4	91.5
Trees ≥10cmdbh	192	93.8	100	82.4	22.74	93.4	269.5	89.8
Ponderosa Pine								
Trees <10cmdbh	1	1.8	5.4	4.5	<.01	0.5	6.8	2.3
Trees >10cmdbh	12	5.8	19.6	16.2	1.58	6.5	28.5	9.5
Lodgepole Pine								
Trees >10cmdbh	1	0.4	1.8	1.5	0.01	<.01	2.0	0.6
Rocky Mt. Juniper								
Trees <10cmdbh	2	3.1	12.5	10.5	0.01	5.0	18.8	6.3
Total								
Seedlings	796	--	10.7	--	--	--	--	--
Saplings	20	--	3.6	--	--	--	--	--
Trees <10cmdbh	58	--	100	11	.15	--	--	--
Trees >10cmdbh	205	--	100	--	24.34	--	--	--

The density of large trees in this subunit is 204 large trees/ha (82 large trees/acre), each with an average diameter of 38.9 cm dbh (15.3 in). The stems in this major size class constitute 24.34 m^2/ha (106.02 ft^2/acre) of basal area.

Douglas-fir accounts for 192 large trees/ha or 93.8% of the stems in the size class. The average diameter of Douglas-fir trees is 38.8 cm dbh. These stems are distributed throughout all of the dbh classes, although numbers decrease slightly in dbh classes > 50.1 cm dbh. Twenty percent of the large trees are, however, 50.1 cm dbh or larger (Table 17). Douglas-fir constitutes 93.4% of the size class basal area (Basal Area = 22.74 m^2/ha). Large Douglas-fir stems are found near every sample point (Frequency = 100%). Douglas-fir's importance in this size class is depicted by its importance value of 269.5 (Figure 6). The density of ponderosa pine is 12 large trees/ha accounting for 5.8% of the stems in the large tree size class. The diameter of these individuals is relatively large, each stem averaging 40.9 cm dbh. These stems are found throughout the dbh range of the size class, with some concentration within the 10.1--20.0 cm dbh class. Thirty-three percent of the ponderosa pine are larger than 50.0 cm dbh (Table 17). Although the average diameter of the stems is large, the low density of the species leads to a basal area of 1.58 m^2/ha, only 6.5% of the size class total. Individuals of this species are not encountered as frequently as those of Douglas-fir, occurring at only 19.6% of the points sampled (Table 16). The importance value of ponderosa pine, 28.5, is considerably less than that of Douglas-fir in this subunit.

Table 17. Stand table of number of stems/ha on the south-facing study area in nine successive size classes. (Slope subunit)

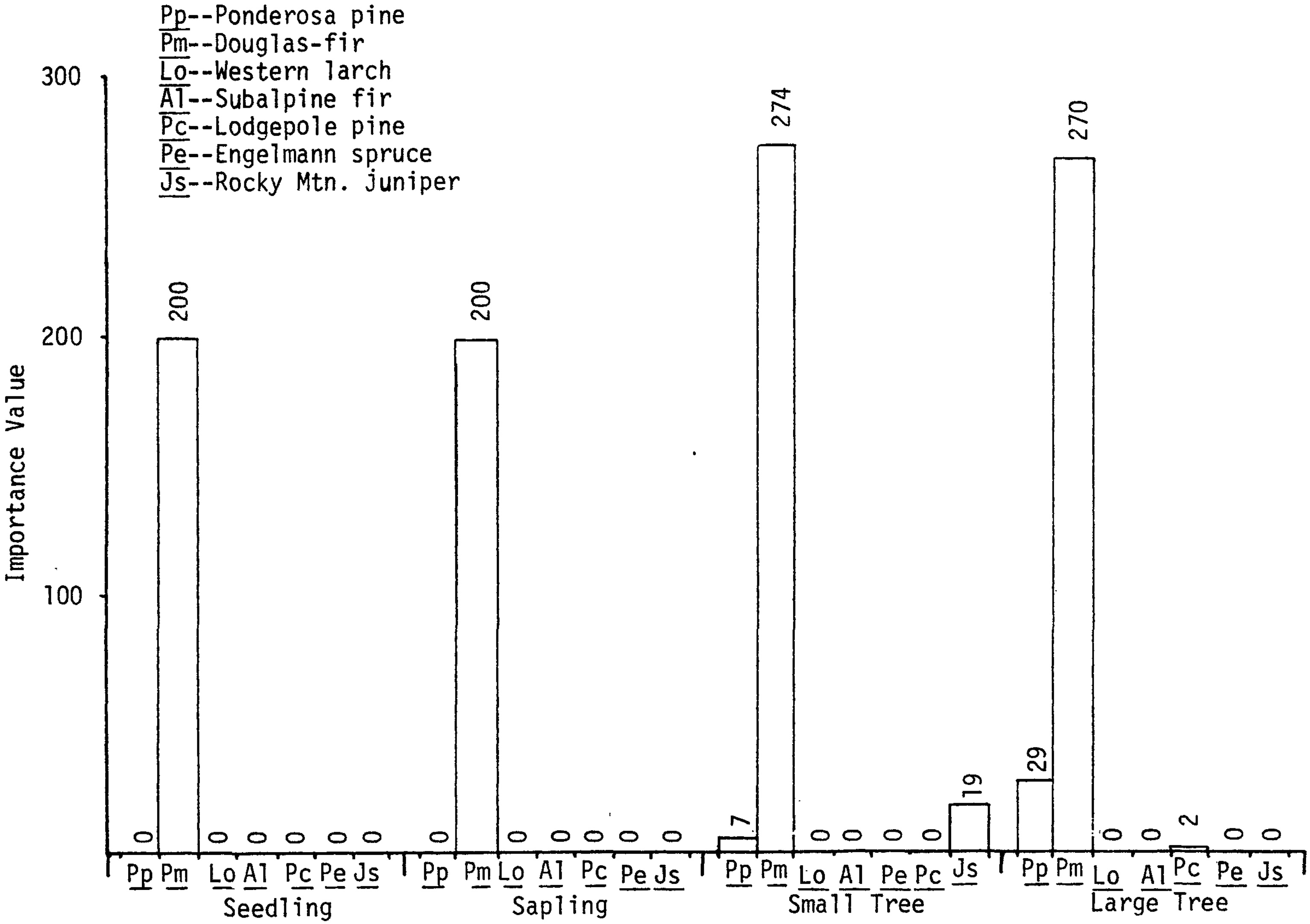
Stand Table

Size Class	Total	Pm	Pp	Lo	Al	Pc	Pe	Js
Seedling[x]	796	796	0	0	0	0	0	0
Sapling[Δ]	20	20	0	0	0	0	0	0
1.0-19.0 cm dbh	58	55	1	0	0	0	0	2
10.1-20.0	58	51	5	0	0	1	0	0
20.1-30.0	31	30	1	0	0	0	0	0
30.1-40.0	39	38	1	0	0	0	0	0
40.1-50.0	37	36	1	0	0	0	0	0
50.1-60.0	24	22	2	0	0	0	0	0
60.0 +	16	15	2	0	0	0	0	0

[x] less than 1.0 meters tall

[Δ] greater than 1.0 meters tall, but not greater than 1.0 cm dbh

Figure 6. Importance Values, South-facing Slope (Slope Subunit).



The density of small trees in this subunit is low (57 small trees/ha) and they constitute .15 m^2/ha of basal area, only 0.6% of the total basal area of the subunit. Douglas-fir comprises 95% of the stems in the size class and is found throughout the entire subunit (Table 16). Ponderosa pine is not as important in this size class as in the large tree size class (IV = 6.8). Only one small tree/ha of the species is estimated to occur in the subunit.

Rocky Mountain juniper appears in this subunit, particularly in relation to the more frequent rock outcrops found in this area. Although the appearance of the juniper is interesting, the species is not important. Only 2 small trees/ha are found, with a species basal area contribution of 0.01 m^2/ha. The frequency of Rocky Mountain juniper is, necessarily, not high (Frequency = 12.5%). The low relative values for density, frequency and basal area result in an importance value of only 18.8.

Reproduction is more abundant in this subunit than on the bench subunit. Seedlings have an overall density of 796 stems/ha all of which are Douglas-fir. Seedling frequency of 10.7% may indicate a contagious seedling pattern. The density of saplings is low, with only 20 saplings/ha found within the subunit. Douglas-fir is again the only species represented in the size class. The frequency of these Douglas-fir saplings is low, with saplings found in only 3.6% of the plots sampled. Aggregation indices suggest a clumped distribution of Douglas-fir seedlings. David and Moore's (I) and Lloyd's ($\overset{*}{m}$) indicate a moderately contagious seedling population with values of 3.5 and 3.9 respectively. Aggregation indices, with values near zero, indicate a virtually random distribution of Douglas-fir saplings. Death of seedlings potentially due to density dependent factors may be illustrated by the 3.5X reduction in sapling values for David and Moore's (I) and Lloyd's ($\overset{*}{m}$) from seedling values (Table 18).

Age Structure and Relevant Growth Relationships

General Age Structure

A comprehensive analysis of the age structure and relevant growth relationships is paramount to the understanding of the vegetation dynamics of an area. The age structures of the trees on each of the study areas differ (Table 19). There appears to be a greater difference between the age structures of the trees found on the north and south sides of Washoe Creek than among the three study areas found on the south side.

The forest stands within the three study areas on the south side appear to have originated about 240 years ago (Table 19). The age structure of the trees on the west-facing study area, however, is quite different from that found on either the east- or north-facing slopes. Within this unit, one relict individual was 359 years old. The next oldest tree aged was 232 years old, leaving a gap of nearly 130 years in which no individuals were recorded. In the eighty-year period between 150 and 230 years ago, 56 percent of the trees sampled became established. This peak period of tree establishment on this west-facing slope began about a decade later than on either the east- or north-facing slopes. The establishment of individuals apparently declined for several decades, with another peak occurring between 100

Table 18. Indices of aggregation for the seedling and sapling populations on the south-facing (slope subunit) study area on Section 31.

	David and Moore's Index of Dispersion (I)	Lloyd's Index of Clumping ($\overset{*}{m}$)	Lloyd's Index of Patchiness ($\overset{*}{m}$)/m
Seedling	3.5	3.9	10.9
Sapling	0.0	0.0	0.3

Table 19. The number of sample trees which became established during respective decades, by study area, on Section 31.

Age	Study Area North	East	West	South
0-9	0	0	0	0
10-19	4	2	7	1
20-29	4	6	2	1
30-39	3	3	1	2
40-49	3	7	0	5
50-59	5	4	1	2
60-69	6	4	2	4
70-79	5	1	0	1
80-89	3	2	2	3
90-99	3	1	1	3
100-109	2	0	5	6
110-120	0	1	5	3
120-129	0	0	2	9
130-139	0	2	2	5
140-149	0	0	1	8
150-159	0	2	3	6
160-169	1	1	5	3
170-179	1	2	8	8
180-189	2	6	6	1
190-199	2	4	7	2
200-209	15	7	5	
210-219	6	9	5	
220-229	4	8	3	
230-239	3	3	1	
350-359			1	
380-389				1
390-399				1
	n = 72	n = 75	n = 75	n = 75

and 120 years ago. Since that period tree establishment has been less abundant, but generally continuous. A new group of individuals became established between 10 and 20 years ago; however, these stems are still small and may not become members of the overstory community, eventually succumbing to various sorts of environmental stress. No trees less than 10 years old were encountered in the sample.

The age structure of the trees found on the east-facing slope is different from that found immediately across the draw on the west-facing slope (Table 19). No relict individuals were found on this unit, the oldest tree aged being only 239 years old. Fifty percent of the individuals sampled became established in the 60-year period between 180 and 240 years ago. The next 110 year period shows a general reduction in the establishment of stems. Within this time period no more than two individuals appear per decade and in most cases one or no individuals represent respective decades. The establishment of trees increased again about 60 years ago, with a large influx of individuals occurring during the following 50 years. This latest influx accounted for 32% of the sampled individuals. Few individuals were found to be < 20 years old and no stems < 10 years old were found.

The trees on the north-facing unit exhibit an age structure very similar to that found on the east-facing unit (Table 19). No relict individuals were found; the oldest individual aged was 230 years old. Thirty-seven percent of the individuals sampled became established in the 40 year period between 200 and 240 years ago. Establishment declined sharply in the next three decades and apparently ceased altogether in the following 50 year period, i.e. 110-160 years ago.

The establishment of trees appears to have resumed about 100 years ago and has proceeded continuously until 10 years ago. No stems were found to be < 10 years old.

One might anticipate a different age structure among the trees on the south-facing slope (Table 19), as this unit is separated from the other three areas by a major stream barrier. Two relict individuals were sampled, one 383 and the other 390 years old. The next oldest tree aged was 196 years old. The establishment of trees appears to have been slow on this site, not beginning in earnest until about 190 years ago. The beginning of this establishment influx occurred about 50 years after apparently similar events on the east- and north-facing unit, and follows the initial establishment influx on the west-facing slope by about 40 years. The establishment of trees on the south-facing slope continued through time with perhaps the major influx occurring between 80 and 180 years ago. Seventy-three percent of the stems sampled on this unit became established during this 100 year period. The last 40 year period shows a declining number of individuals becoming established and no sample individuals were < 10 years old.

The age structure of all four study areas is presently uneven-aged. To delimit respective age structures further would probably result in labels such as irregularly uneven-aged or even-aged groups (Baker, 1950). However, our present understanding of spatial pattern and past history of disturbance within the stands prohibits using such labels with confidence.

Crown Class Age Structure

One approach to describing the age structure of the various tree strata is to compare the ages of the defined crown classes. Although the particular crown classification system used was developed for even-aged stands, the crown classes effectively describe the relative position of the tree's crown with respect to other crowns in the area. In this case, we are interested in determining the age structure of the various relative canopy heights within and between study units. For subsequent analyses stems considered relicts are not included in the age data.

Within the north-facing unit, no significant difference occurs at a .95 level of confidence between the mean age of the dominant and codominant crown classes (Figure 7). The mean age of the dominants is 210 years and that of the codominants is 208. Individuals sampled from the intermediate crown class are significantly younger (P = .95) than either the dominants or codominants with a mean age of 145 years. The suppressed trees within this unit are much younger than any of the higher crown classes, exhibiting a mean age of 50 years (Table 20). The greatest variation within a particular crown class occurs in the intermediate crown class, where stems between 58 and 230 years old were observed. The ranges of ages encountered within the dominant and codominant crown classes is smaller, including stems between 200 and 236 years old and between 176 and 228 years old, respectively. The sampled suppressed stems ranged in age between 13 and 99 years. Based on the ages of the crown classes, at least 3 age classes are apparent (Figure 7).

Figure 7. Crown class age structure for Douglas-fir stems on the north-facing slope.

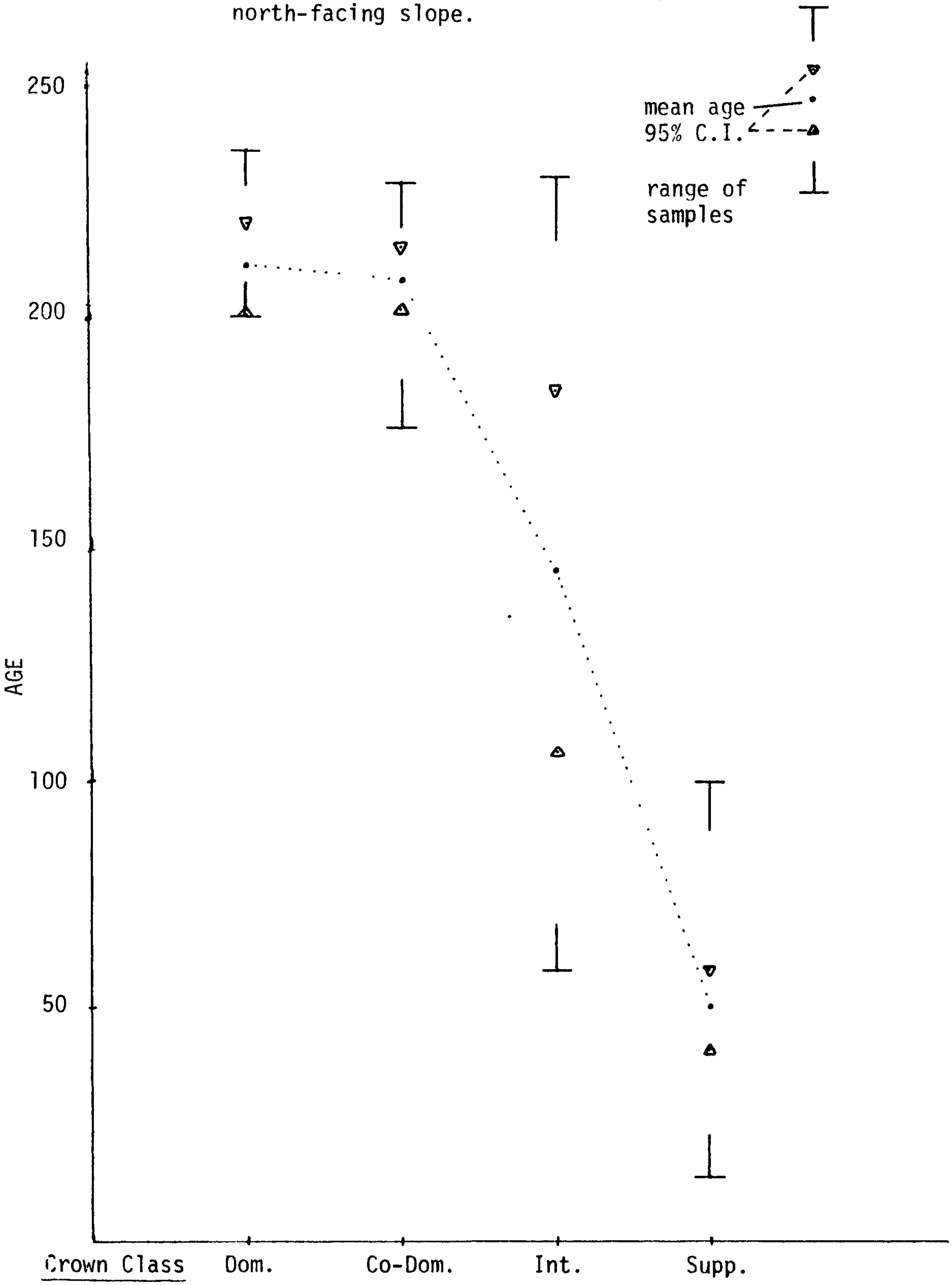


Table 20. Mean age of sampled stems by crown class and study area, using a 95% confidence interval. Values in parentheses indicate number of trees sampled, all of which were Douglas-fir.

Crown Class	Dominant	Codominant	Intermediate	Suppressed
Study Area (Aspect)		Age (Years)		
North	210±11(6)	208±7(13)	145±39(12)	50±9(31)
East	221±8(8)	214±8(14)	169±28(12)	71±18(36)
West	216±8$^{\Delta}$(8)	186±9(11)	172±13(16)	94±18(37)
South	167±17*(6)	164±9(15)	136±8(13)	104±15(22)

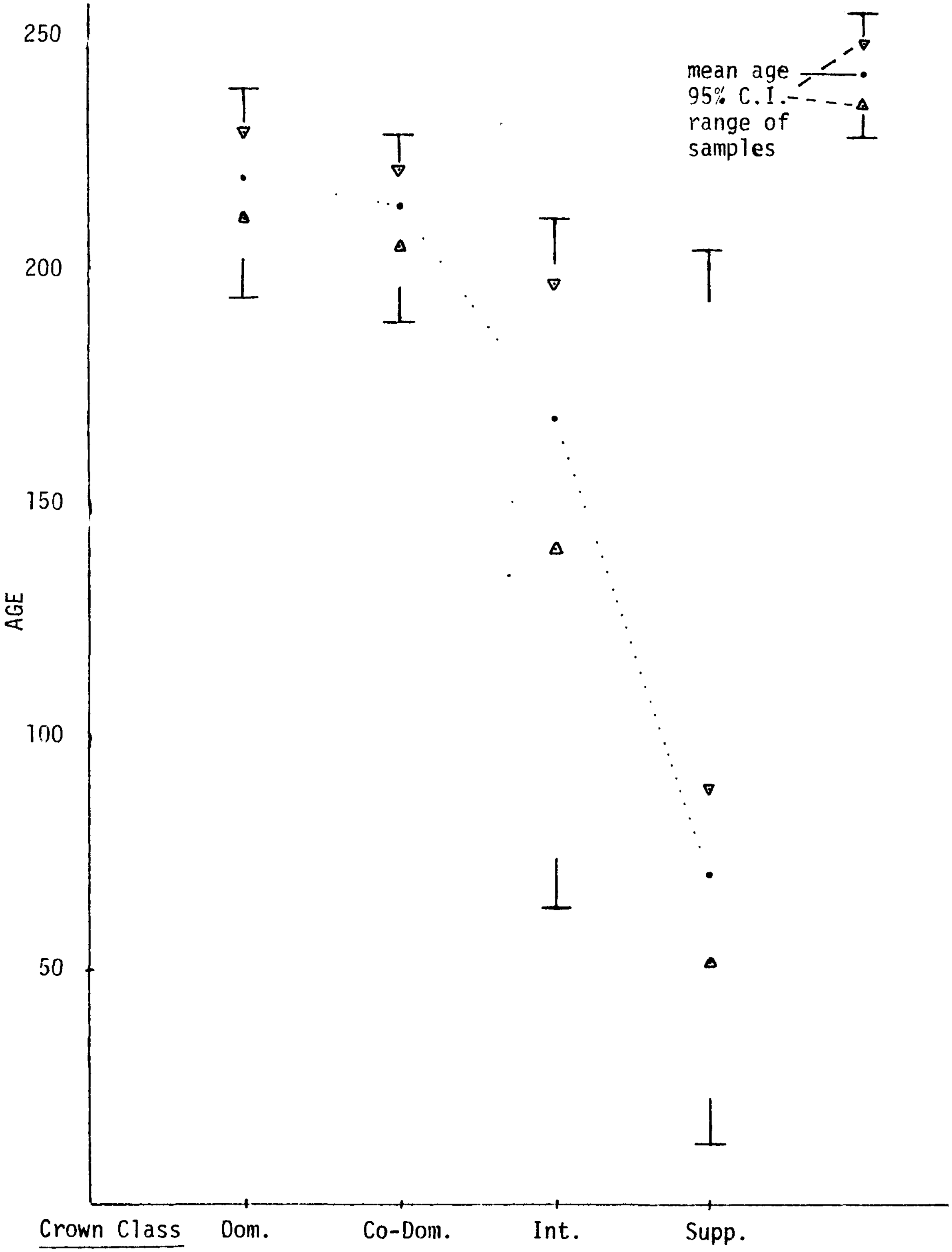
$^{\Delta}$ does not include a relict stem 359 years old.

* does not include two relict stems, 383 and 390 years old.

On the east-facing slope the dominant and codominant crown classes are also essentially the same age with mean ages of 221 years and 214 years old, respectively. The intermediate stems are again significantly younger at a .95 level of probability than either of the dominant crown classes as illustrated by a mean age of 169 years. With a mean age of 71 years, the suppressed stems are significantly younger (P = .95) than stems in the previously mentioned crown classes (Table 20). Within this unit, the greatest range in ages occurs within the suppressed crown class where stems between 13 and 205 years old are encountered. The intermediate stems also vary widely in age, ranging between 63 and 212 years. The dominants and codominants have much smaller ranges, including stems between 195 and 240 years and between 190 and 230 years old, respectively (Figure 8). Based upon the ages of the crown classes, at least three age classes are evident on this exposure, a result similar to that on the north-facing slope.

Within the west-facing study area, the mean ages of the dominant and codominant individuals are significantly different at the .95 level of probability. Although confidence intervals nearly overlap, the mean age of the codominants (196 ± 9 years old) is signficantly lower than the mean age of the dominants (216 ± 9 years old) (Table 20). The intermediate individuals are significantly younger (P = .95) than the codominants, exhibiting a mean age of 172 years. The mean age of the individuals within the suppressed crown class is 94 years, significantly lower (P = .95) than the mean age of the intermediates. On the west-facing slope the greatest range of ages is encountered within the suppressed crown class where stems range in age from 19 to 192 years.

Figure 8 . Crown class age structure for Douglas-fir stems on the east-facing slope.



The range of ages becomes increasingly smaller as we approach the dominant crown class. Intermediates range in age between 107 and 205 years old, codominants range between 169 and 220 years of age, and dominants range between 199 and 234 years of age (Figure 9). Thus, no less than 4 different age classes are apparent using this type of analysis.

Within the south-facing study area the dominant and codominant crown classes are essentially the same age (Figure 10) since there is no significant difference between their respective mean ages of 167 years and 164 years (Table 20). However, the intermediate stems are significantly younger (P = .95) than either of the dominant crown classes with a mean age of 136 years. In turn, the suppressed stems are significantly younger (P = .95) than the intermediate stems, as illustrated by a mean age of 104 years. The range of ages encountered within crown classes is generally smaller on this unit, with the suppressed stems exhibiting the greatest range, i.e., 30 to 150 years old. The intermediates range in age between 107 and 157 years old, codominants between 137 and 193 years old, and dominants range between 138 and 185 years old. At least three age classes are apparent on this unit (Figure 10).

The mean age of the dominants within all three units on the south side of Washoe Creek is essentially the same at about 215 years (Table 20). The mean age of the dominants on the north side of the creek, i.e., south-facing study unit, is 167 years or nearly 50 years younger than those sampled south of the creek. A similar difference exists in the codominant crown class, but the mean ages of these stems on all units decline slightly.

Figure 9. Crown class age structure for Douglas-fir stems on the west-facing slope.

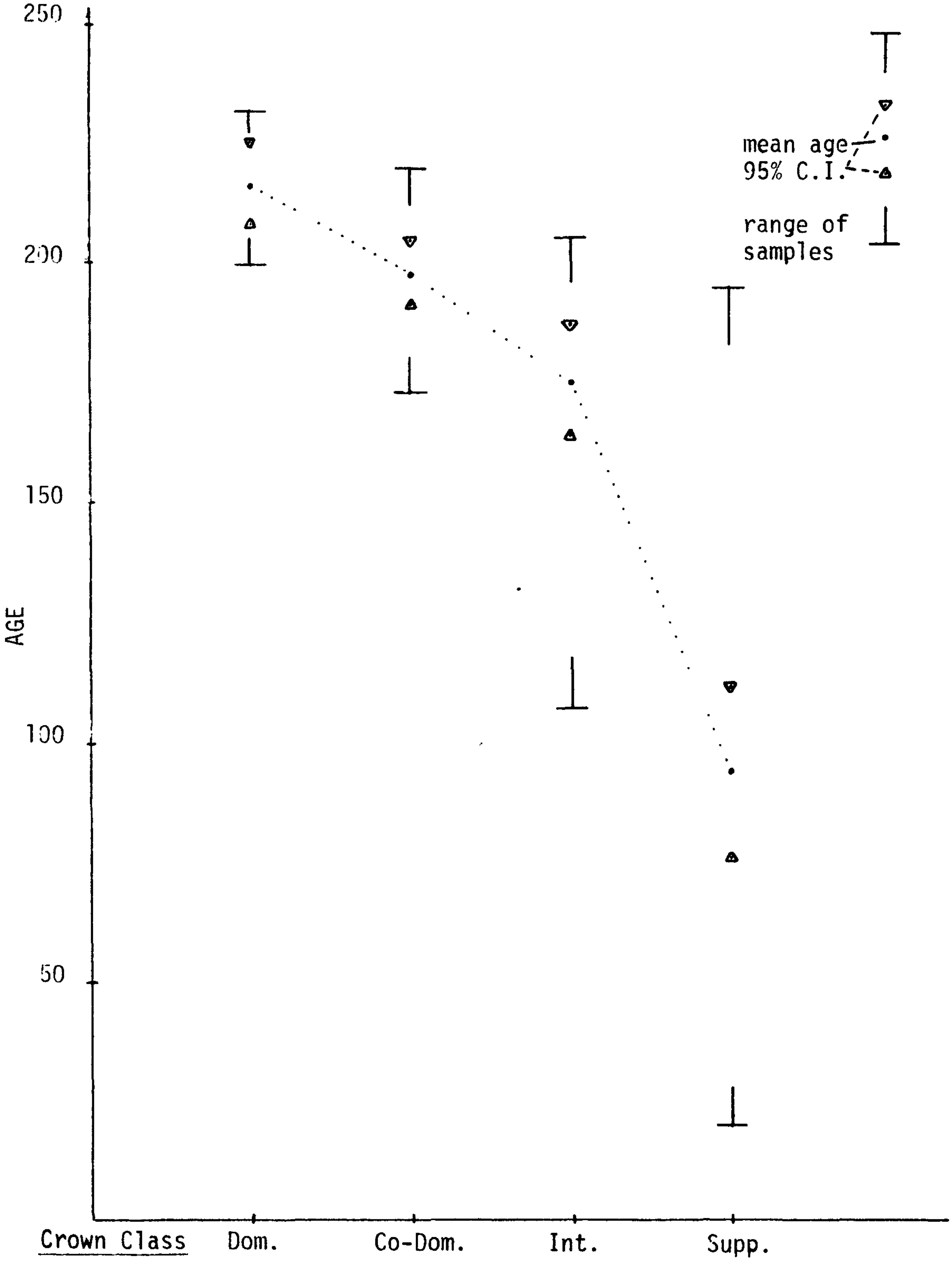
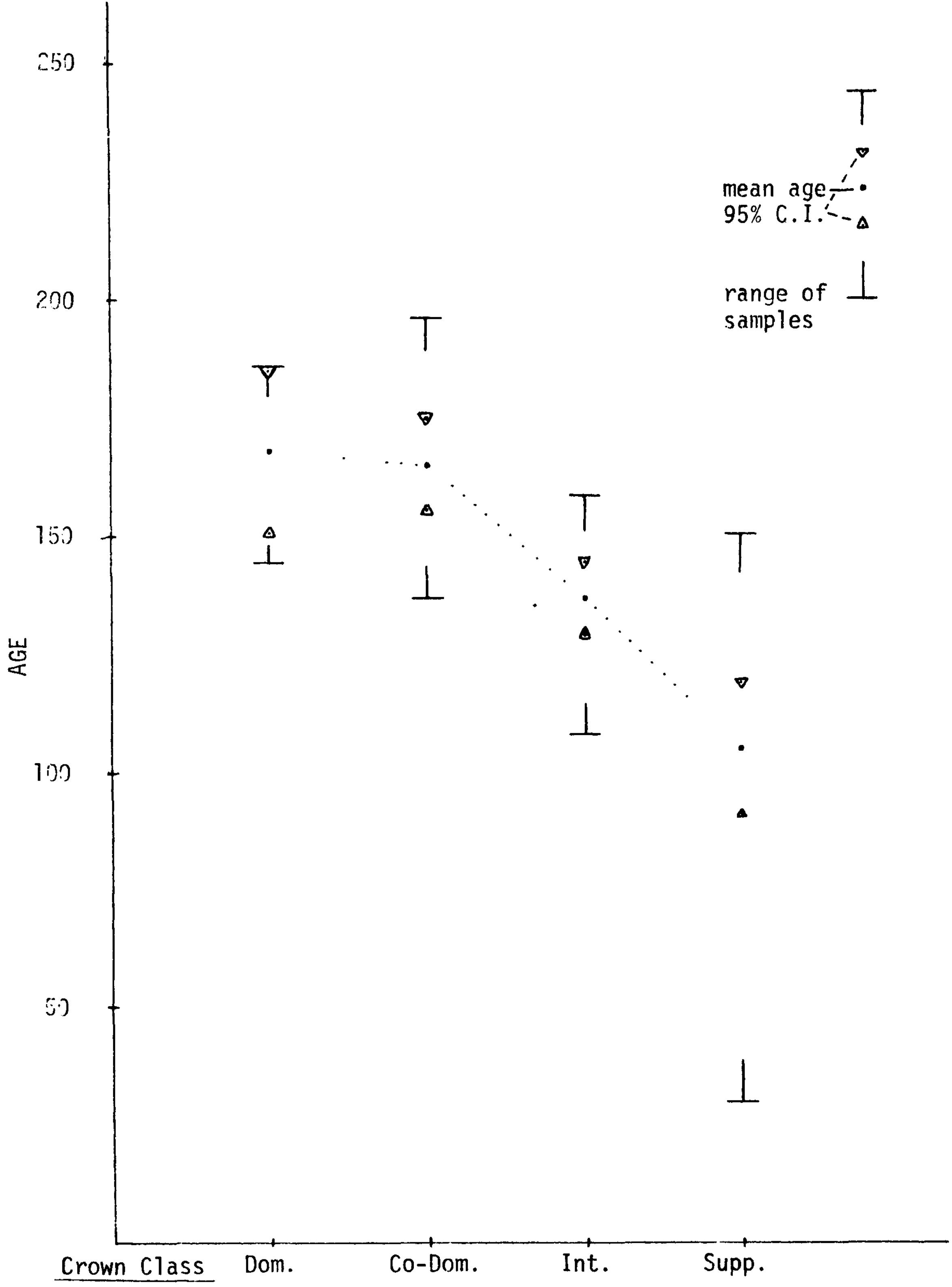


Figure 10. Crown class age structure for Douglas-fir stems on the south-facing slope.



It is interesting to note the differences in mean age between the different crown classes within the various study areas (Figures 7, 8, 9, 10). The north-facing slope has the largest difference in mean age between dominants and suppressed crown classes. The mean age of the dominants is among the highest, but the mean age of the suppressed individuals is the lowest found on any of the sites. The difference between these two mean ages decreases through the east-, west-, and south-facing study areas. Within the south-facing unit, the difference between these mean ages decreases to 63 years, while the comparable value on the north-facing area is 160 years.

Diameter-Age Relationships

An analysis of the diameter-age relationships within a stand of trees is imperative to a thorough understanding of stand dynamics and prudent silvicultural management. In each study area, trees sampled throughout the range of diameter (breast height) classes were used to develop some feeling for the diameter-age relationships.

On the south-facing slope, the large trees are generally the oldest; however, the small trees are not necessarily young (Figure 11). A breaking point is apparent within the 41-50 cm dbh class (Table 21). Trees larger than 50 cm dbh are at least 170 years old. In diameter classes less than 50 cm dbh, the range of ages encountered within a particular 10 cm diameter class broadens. The broadening effect is most noticeable in the smaller size classes where the range of ages encountered in the 0-10 cm dbh class includes stems between 45 and 152 years old. The upper limit of diameter growth for Douglas-fir on this site

Figure 11. Diameter-age relationships for sampled stems on south-facing study area in Section 31.

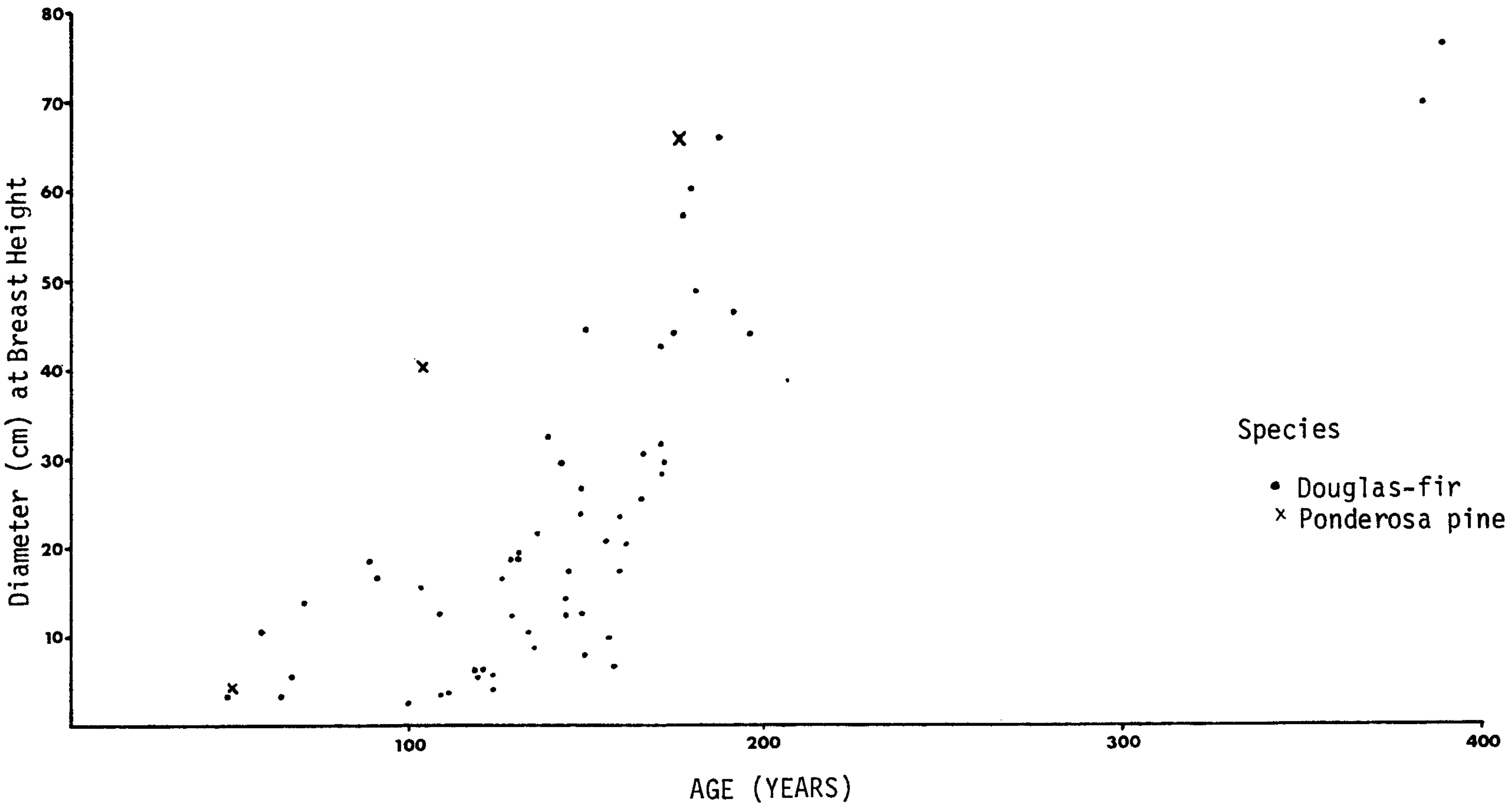


Table 21. Range of ages encountered within dbh size classes on four study areas in Section 31.

DBH (cm)	North-facing Slope	East-facing Slope	West-facing Slope	South-facing Slope
0-10	30-97 years	30-202	52-202	45-152
10-20	55-227	85-217	104-207	55-157
21-30	97-227	190-221	186-230	133-170
31-40	198-232	208-228	180-219	137-167
41-50	185-197	215-223	191-218, 355	107-192
51-60	205-220	220-238	210-214	174
61-70	197	--	--	173-184
71-80	222-235	--	--	383-390

might be illustrated by the two relict individuals which are 383 and 390 years old, and 70 cm and 75 cm dbh respectively. Ponderosa pine may be subject to approximately the same upper diameter limits, but appears to grow more rapidly than Douglas-fir. One of the few ponderosa pine aged was already 40 cm dbh at 105 years of age.

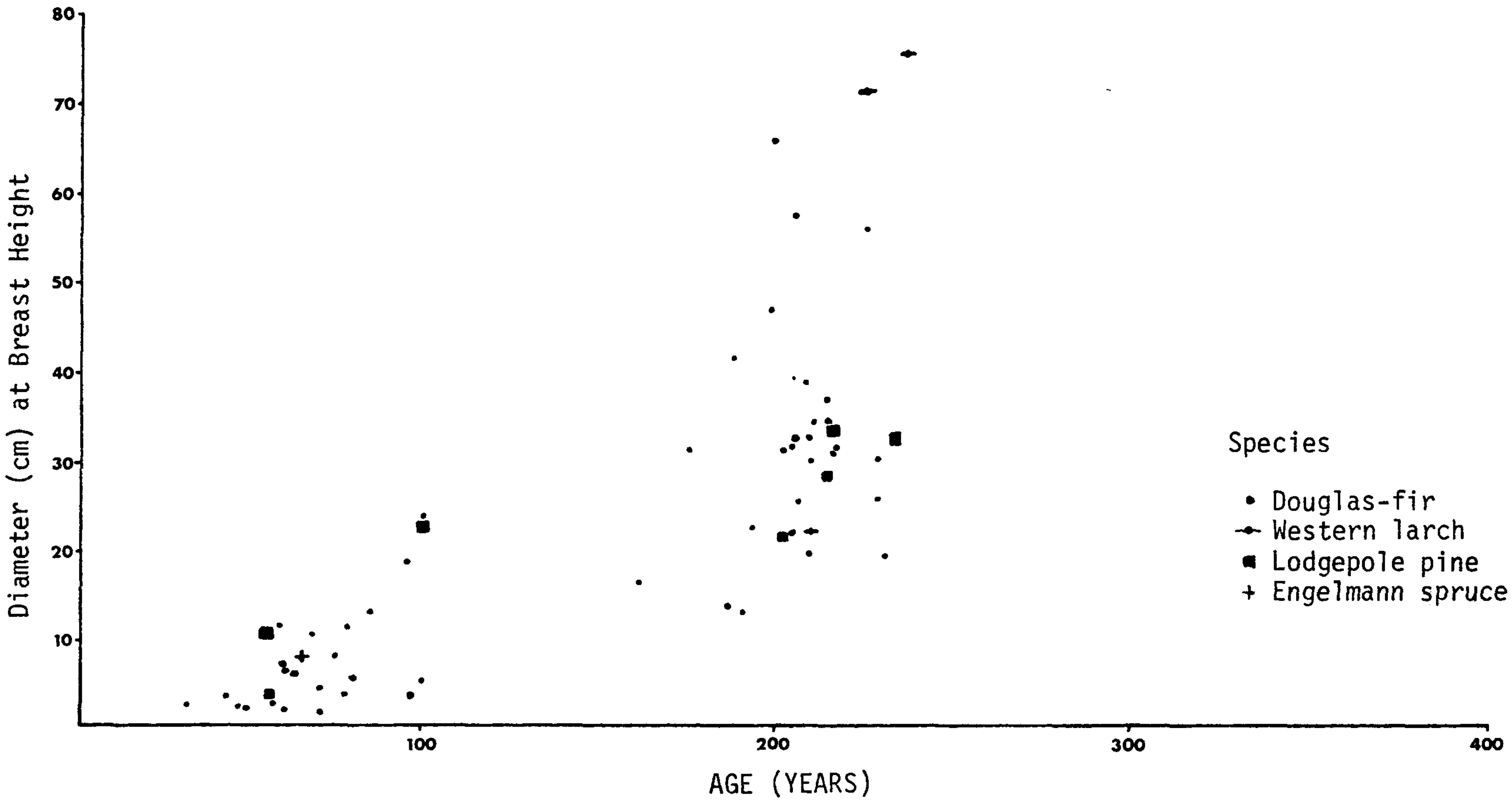
Transposing the analysis and looking at the range of diameters found within 20 year age classes another dimension is apparent (Table 22). Viewing stems ranging in age class from 41-60 years through 101-120 years old, we notice a fairly constant dbh range for the sampled individuals (Figure 11). The dbh range of these stems falls consistently between 2 and 20 cm dbh, with one 41 cm dbh ponderosa pine the exception. Within the age classes between 121 and 160 years old, the lower limits of the dbh range rise only slightly but the upper bound begins to increase more quickly. With increasing age beyond 160 years the lower diameter limit of each 20 year age class increases dramatically but the upper limit begins to stabilize at about 65 cm dbh. Stems sampled which are between 181 and 200 years old ranged in diameter from 44 to 65 cm dbh.

The diameter-age relationships developed from the sample trees on the north-facing study area may suggest a more even-aged stand than found on the south-facing slope (Figure 12). Sample stems in the 0-10 cm dbh class are generally younger than the larger stems, but a considerable range of ages is encountered in the smaller size classes (Table 21). Within this dbh class the range of ages encountered includes stems between 30 and 100 years of age. The dbh class between 11 and 30 cm dbh may be viewed as a transition size. Within this 11-30

Table 22. Range of diameters (dbh) encountered within 20 year age classes on four study areas in Section 31.

Total Age (Years)	North-facing Slope	East-facing Slope	West-facing Slope	South-facing Slope
20-40	2.5 cm	2-6	--	--
41-60	.5-12	1-7	5.5	3.5-11
61-80	2-11	2-9	1-2	4-14
81-100	3.5-23	3-13	1-3	2-18.5
101-120	--	3	1-10.5	4-41
121-140	--	3-13	3-16.5	7.5-33
141-160	--	5-14	3-18	6.5-44
161-180	16.5	4-13	4-19.5	26-65
181-200	13-65	7-26.5	7-47	44-65
201-220	21-57	7-54	9.5-58.5	--
221-240	19-75	25-56	29	--
340-360	--	--	49	--
380-400	--	--	--	69-76

Figure 12. Diameter-age relationships for sampled stems on north-facing study area in Section 31.

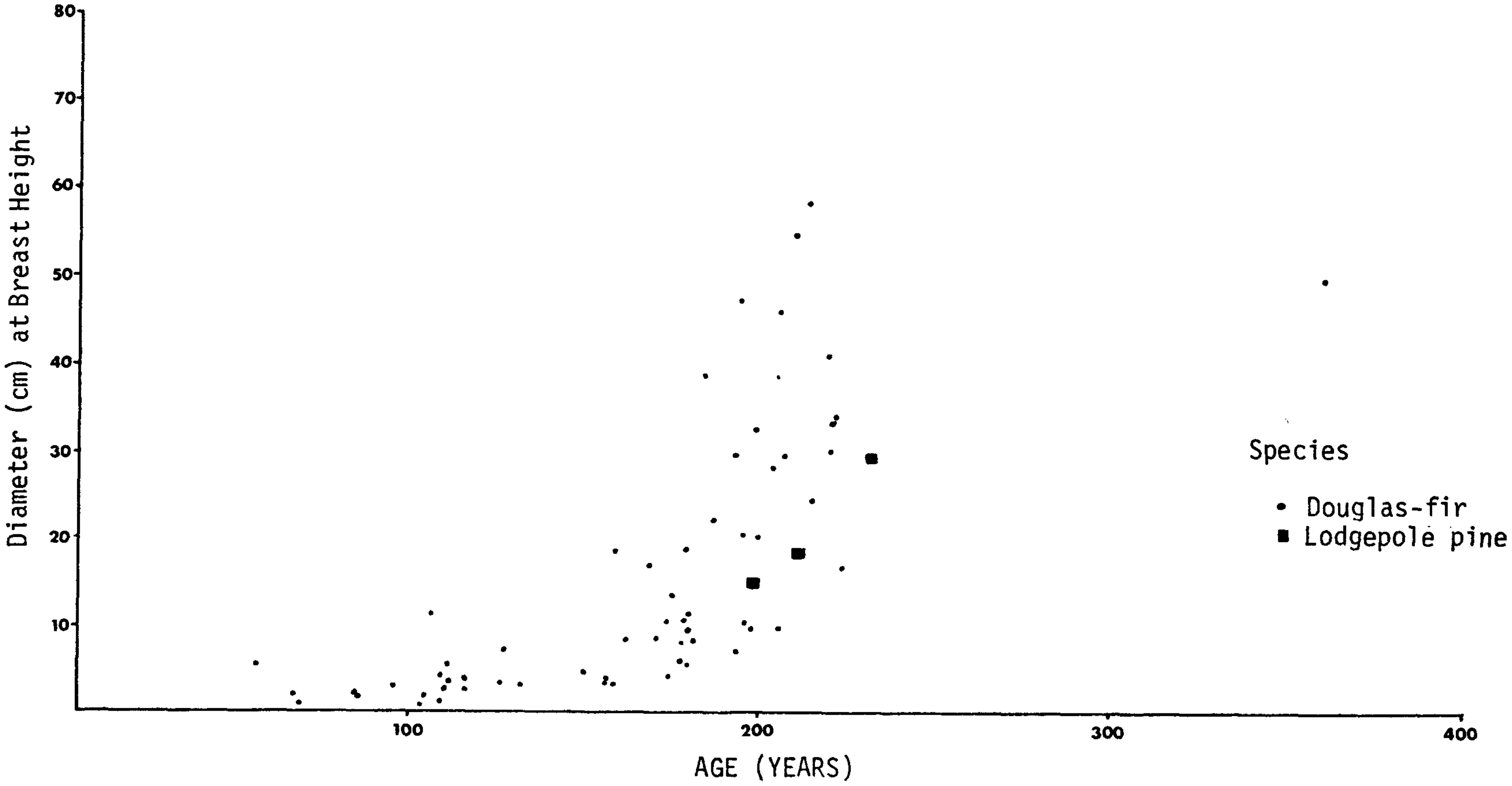


cm dbh class, stems between 55 and 227 years old are encountered. Beyond 30 cm dbh the stand is quite even-aged. Within these larger size classes the lower bound of ages encountered increases to the point where virtually no sampled stems are less than 200 years old and the upper bound is about 235 years old.

Considering the distribution of tree diameters within 20 year age classes (Table 22), the dearth of sampled stems between 100 and 160 years of age is immediately apparent (Figure 12). In the younger age classes, noteably between 21 and 100 years old, we see a range of diameters with a fairly constant lower limit but a steadily increasing upper bound with increasing age. The lower limit in this case fluctuates very near to 2 cm dbh, with the upper limit increasing from 11 cm to 23 cm dbh. In these younger age classes, lodgepole pine appears to be a vigorous component of the stand, even in view of its generally acknowledged shade-intolerance. Following the 60-year break in ages encountered, all successive 20-year age classes include a wide range of diameters. The 181-200 year old age class includes diameters ranging from 13-65 cm dbh and the 221-240 year old age class includes diameters ranging between 19-75 cm dbh.

The diameter-age relationships found within the west-facing study unit indicate the largest trees are generally the oldest, but the smaller trees are not necessarily the youngest (Figure 13). The variability of ages encountered within the smaller dbh classes is large. For example, within the 0-10 cm dbh class stems are encountered between 52 and 202 years old. Beyond 21 cm dbh the age range within

Figure 13. Diameter-age relationships for sampled stems on west-facing study area in Section 31.



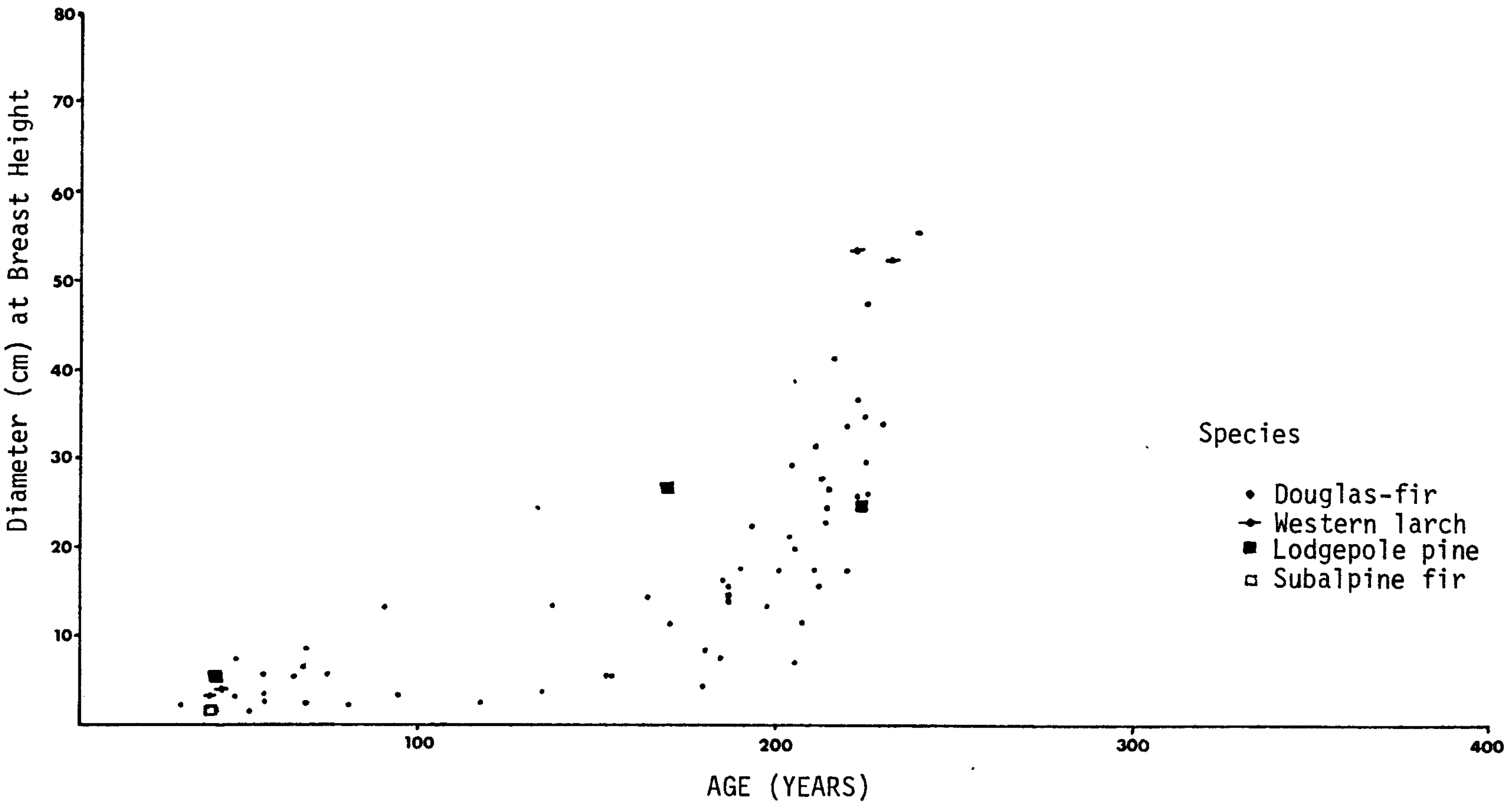
the respective 10 cm dbh classes is essentially the same, 190-230 years old. The one relict on this study area was 355 years old and 49 cm dbh.

Within respective 20 year age classes stems < 10 cm dbh are found in virtually every age class between 51 and 220 years old. Beyond 160 years of age, the upper bound of the diameter range increases substantially, but the lower bound rises only slightly. Within the 201-220 year age class, the range of diameters includes stems between 9 and 59 cm dbh. Within age classes beyond 220 years, the lower bound rises significantly but the upper bound remains in the vicinity of 50 cm dbh.

The diameter-age relationships developed from the sampled stems on the east-facing study area are similar, in different ways, to those of both the west-facing slope and the north-facing slope. The larger trees are old, but the smaller trees vary a great deal in age (Figure 14). In the 0-10 cm dbh class the sampled stems range in age between 30 and 202 years old. Among stems larger than 20 cm dbh, the lowest age encountered rises to 185 years, the highest age to 238 years.

An examination of the various 20 year age classes indicates a very slow increase in the lower bound of diameters encountered with increasing age (Table 22). Stems sampled in 201-220 years old age-class range in size from 7-54 cm dbh. Not until the 221-240 year age-class is any appreciable increase in this lower bound noted. The upper range of diameters encountered increases more quickly, making particularly large gains in the 181-220 years old and 201-220 years old age classes (Figure 14).

Figure 14. Diameter-age relationships for sampled stems on east-facing study area in Section 31.



Height-Age Relationships; Site Index

The relationship between the heights and the ages of the trees within a stand is important both in understanding stand dynamics and in predicting the productive potential of the site. The relative position of various tree species and specific individuals within the canopy can be useful in deciphering past stand development, as well as for predicting the future stand species composition and structure. The productive potential of an area is estimated by determining the average site index of the area. Site indices were developed by determining the height and age of a sample of trees in dominant and codominant positions in the canopy and estimating a site index for each tree sampled. The mean value of these individual estimations is used as an approximation for the site index at base age 50 years (Brickell, 1968).

The range of ages encountered within the various 7.6 m (25 feet) height classes on the north-facing slope indicate that trees less than 7.6 m feet tall are less than 100 years old (Table 23). Trees between 7.6 m and 24.4 m tall may belong to either of two age ranges, one ranging between 50 and 100 years old and another ranging between 160 and about 225 years old. Part of the reason for the extended range of ages in the height classes around 22.9 m (75 feet) is the apparently faster height growth of lodgepole pine and Engelmann spruce (Figure 15). For Douglas-fir, trees greater than 15.2 m (50 feet) tall are generally 190 years old or more. Western larch is the tallest tree species found in the study area.

Trees less than 50 years old are short, i.e. generally less than 3.9 m (10 feet) tall (Table 24). Within the 51-100 year old age class,

Table 23. Age range encountered within 7.6 m (25 feet) height classes, by study area,on Section 31.

Height Class	North-facing Slope	East-facing Slope	West-facing Slope	South-facing Slope
0-7.6 m	20-95 (years)	20-180	19-190	30-155
7.6-15.2	55-70, 160-190	45-205	100-210	105-190
15.2-22.9	80-90, 170-225	180-225	160-225, 355	106-185
22.9-30.4	190-225	210-240	175-215	140-175, 383, 390
30.4-38.1	190-220	210-225	--	160-185

Figure 15. Height-age relationships for sampled stems on north-facing study area in Section 31.

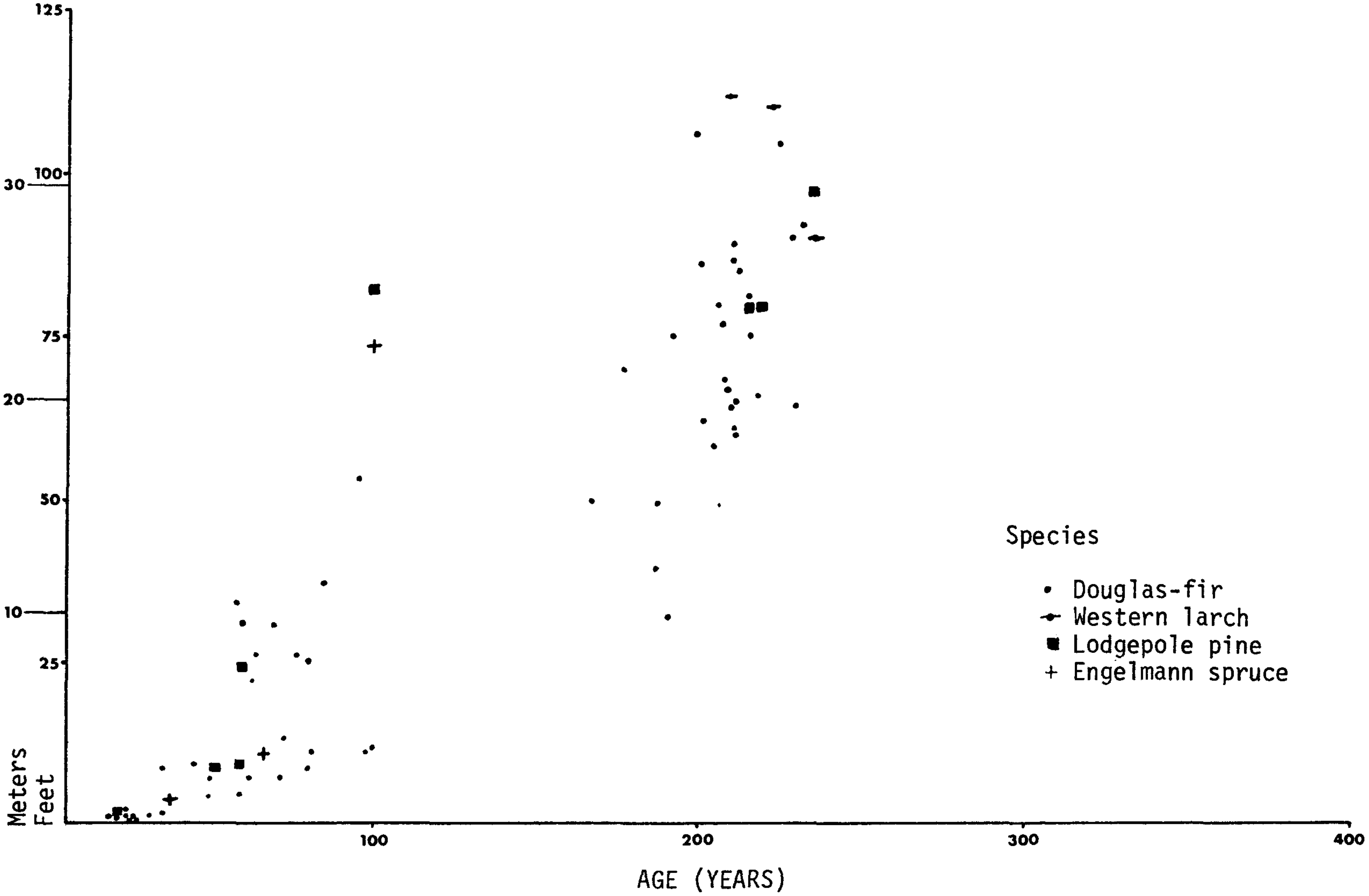


Table 24. Height range (m) encountered within 50 year age classes, by study area, on Section 31.

Age Class (Years)	North-facing Slope	East-facing Slope	West-facing Slope	South-facing Slope
0-50	0.3-21.3 m	0.3-7.9 m	0.3-0.6 m	0.3-4.6 m
51-100	1.5-24.4	1.5-9.7	1.5-3.7	1.5-7.3
101-150	--	2.4-11.3	1.5-12.2	2.4-24.4
151-200	9.2-33.5	5.5-22.9	1.8-26.5	2.4-36.6
201-250	18.3-35.1	9.2-37.8	14.9-27.1	2.4-36.6
350-400	--	--	20.7	24.4-27.4

stems 1.5 to 24.4 m are encountered, with the tallest individuals being lodgepole pine and Engelmann spruce. No trees were encountered in the 101 to 150 year age class, but within the 151-200 year age class Douglas-fir ranged in height from 9.2 to 33.5 m (110 feet) tall. Several species were found within the 200-250 year age class, with heights ranging from about 18.3 to 35.1 m tall (Figure 15).

The site index for Douglas-fir on this study area is 15.8 m (52 feet). This figure is based upon the average site index of 18 dominant and codominant individuals (Table 25). Indices based on each individual range between 12.2 and 21.3 m at 50 years. The mean age of the stems used in this site index determination is 209 years old with a 95% confidence interval of ± 5.83 years.

The east-facing study unit has height-age character similar to the north-facing slope, except that the 60 year gap in ages encountered on the north-facing slope is not apparent (Figure 16). Stems < 7.6 m tall range from about 20 years to 180 years old, with most of stems in the younger end of this range (Table 23). Stems between 7.6 and 15.2 m (50 feet) tall are in the same range (45 to 205 years old), but most of these stems are near 200 years of age. Trees greater than 15.2 m (50 feet) tall have a smaller range of ages, 180 to 240 years old, and several species are represented. In trees beyond 22.9 m (75 feet), the range of sample ages is limited to between 210 and 240 years old.

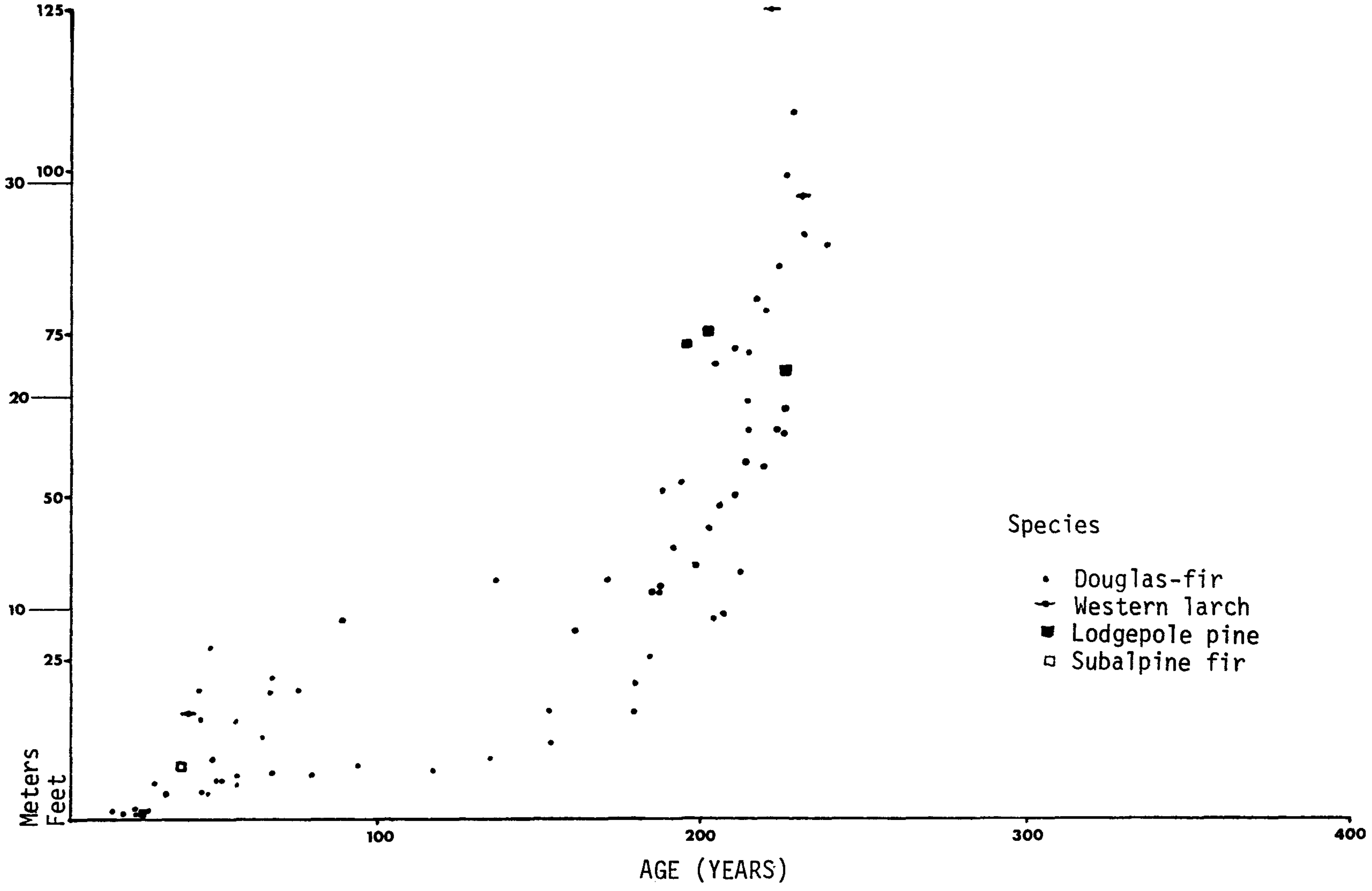
Upon examination of 50 year age classes, it is apparent that the younger trees are generally shorter, ranging in height between 0.3 (1 foot) and 7.0 m (Table 24). Both the lower and upper bounds of this height range increase slowly through the 101-150 year age class where

Table 25. Site indices for 18 Douglas-fir trees on the north-facing study area. The average site index for the study area is the mean site index for these individual stems, with base age 50 years (Brickell, 1968).

Height	Age (Years)	Crown Class	Site Index
23.5 m	216	dominant	15.2 m
28.1	231	dominant	18.3
32.3	200	dominant	21.3
26.5	208	dominant	17.9
24.7	213	dominant	15.8
18.9	201	codominant	12.2
18.6	208	codominant	12.2
19.5	208	codominant	12.2
19.8	209	codominant	12.2
21.3	176	codominant	14.0
22.9	215	codominant	14.9
20.7	207	codominant	13.4
25.6	209	codominant	17.1
24.4	204	codominant	15.8
27.4	228	codominant	18.3
25.9	212	dominant	17.1
31.7	223	codominant	18.6
26.2	200	dominant	17.4

Average Site Index = 15.8 m (52 feet).

Figure 16. Height-age relationships for sampled stems on east-facing study area in Section 31.



the range of heights encountered falls between 2.4 and 11.3 m. Within the 151-200 year age class the lower bound increases by 3.0 m (10 feet), but the upper bound doubles, widening the range of heights encountered to between 5.4 and 22.9 m (75 feet). Similar increases occur in the 201-250 year age class, where the heights encountered range between 9.2 and 37.8 m.

On the east-facing slope the site index for Douglas-fir is based upon 22 sample trees. The estimated site index of 14.3 m (47 feet) is an average of individual indices ranging between 9.3 and 22.0 m (Table 26). The average age of the trees sampled is 218 years with a 95% confidence interval of ± 4.5 years.

The height-age character of the west-facing study area differs distinctly from that recognized on the north- and east-facing slopes (Figure 17). Height growth appears suppressed on this unit, as many trees have subsisted at heights below 7.6 m (25 feet) for up to 200 years (Table 23). Between 7.6 and 15.2 m (50 feet) in height, sampled stems range in age between 100 and 210 years old, with the majority of the individuals between 150 and 200 years old. Trees greater than 15.2 m (50 feet) tall range in age between 160 and 225 years old, with one relict Douglas-fir only 19.8 m (65 feet) tall despite being 355 years old.

Stems which are less than 50 years old are short, averaging < 1 m in height (Table 24). Sample individuals between 51 and 100 years old are somewhat taller, ranging in height from 1.5-3.0 m. A few stems between 101 and 150 years of age are greater than 7.6 m (25 feet) in height, but the majority of the individuals sampled range between

Table 26. Site indices for 22 Douglas-fir trees on the east-facing study area. The average site index for the study area is the mean site index for these individual stems, with base age 50 years (Brickell, 1968).

Height	Age (Years)	Crown Class	Site Index
21.9 m	214	dominant	14.3 m
19.5	214	dominant	12.2
22.9	203	dominant	14.9
18.9	193	codominant	12.2
21.0	224	dominant	13.4
16.8	214	codominant	10.1
18.3	213	codominant	11.6
19.2	225	codominant	12.2
21.3	204	dominant	13.7
15.2	210	codominant	9.2
16.5	219	codominant	9.8
26.8	239	dominant	18.0
29.3	231	dominant	19.8
23.7	218	codominant	15.2
21.9	209	codominant	14.0
18.0	224	codominant	11.3
24.4	217	dominant	15.8
18.3	223	codominant	11.6
27.4	230	codominant	18.3
30.2	224	dominant	20.1
25.9	221	codominant	17.1
32.9	226	cominant	21.9

Average Site Index = 14.3 m (47 feet).

2.1 and 6.1 m (20 feet) tall. A wide range of heights exists among stems between 151 and 200 years old, as these individuals range between 2.1 and 22.4 m tall. All sampled stems 200 years old are at least 15.9 m tall, the tallest being about 26.8 m (Figure 17).

The average site index for Douglas-fir on a west-facing study area is 12.8 m (42 feet) (Table 27). In this case, the average site index is based upon 20 sample trees, ranging in individual indices from 8.5 to 18.3 m (60 feet) at 50 years. Excluding the 355 year old relict reduces the average age to 201 years old with a 95% confidence interval of ± 7.46 years.

The height-age relationships found on the south-facing slope are similar to those encountered on the west-facing slope, but the stand age is about 50 years younger on the south-facing slope (Figure 18). Sample stems up to 7.6 m (25 feet) tall range between 39 and 155 years old (Table 23). The ages encountered for individuals between 7.6 and 15.2 m (50 feet) tall range between 100 and 150 years. A similar age range is encountered for stems between 15.2 and 22.9 m (75 feet) tall, but the stems are concentrated between 125 and 175 years of age. Stems greater than 22.9 m (75 feet) tall generally range between 149 and 185 years old. The two relict Douglas-fir are about 27.4 m (90 feet) tall and are 383 and 390 years old.

Stems less than 50 years old range in height between 0.3 and 4.6 m (15 feet) (Table 24). The lower bound of heights encountered increases slowly throughout the older age classes, but the upper bound rises quickly. The range of heights encountered in the 151-200 year age class include stems between 2.4 and 36.6 m (120 feet) tall.

Figure 17. Height-age relationships for sampled stems on west-facing study area in Section 31.

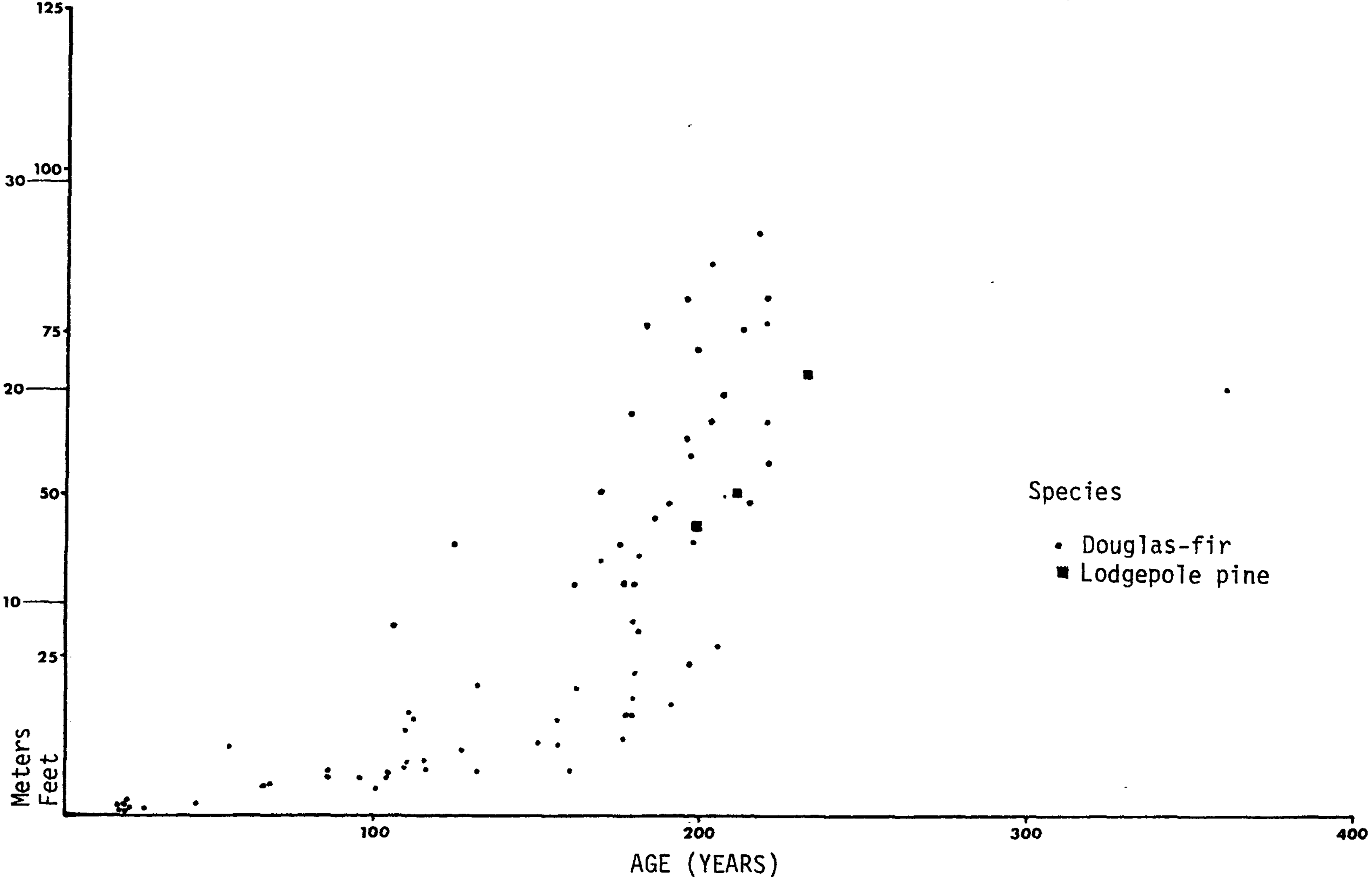
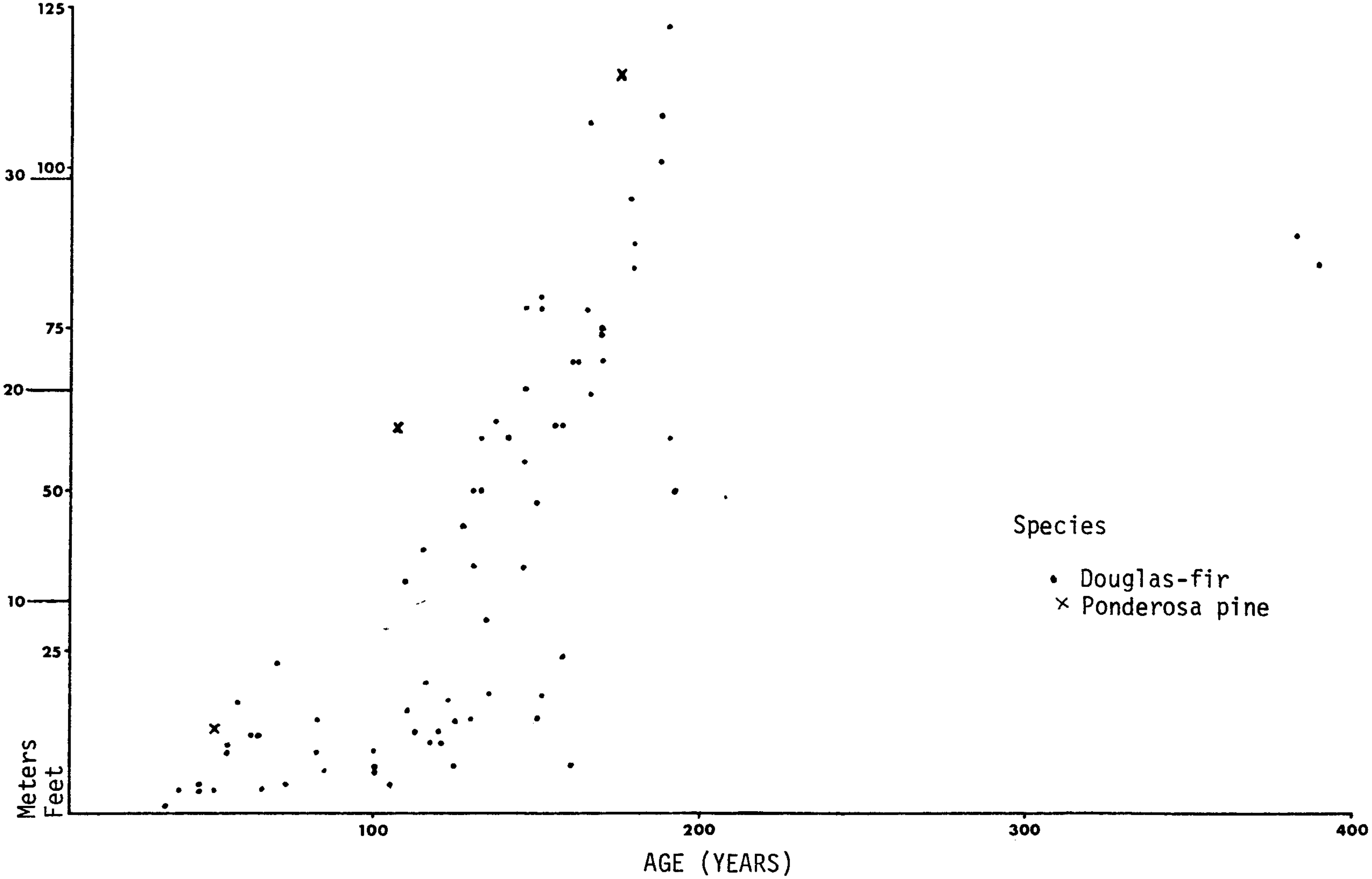


Table 27. Site indices for 22 Douglas-fir trees on the west-facing study area. The average site index for the study area is the mean site index for these individual stems, with base age 50 years (Brickell, 1968).

Height	Age (Years)	Crown Class	Site Index
19.8 m	206	codominant	12 m
18.9	178	codominant	12.2
14.6	200	codominant	8.5
14.6	213	codominant	8.5
18.6	203	codominant	11.9
16.5	220	codominant	9.8
17.1	196	codominant	10.4
15.2	169	codominant	9.2
21.9	199	dominant	14.3
18.6	220	dominant	11.9
20.1	359	dominant	12.5
25.9	204	dominant	17.1
15.2	221	dominant	15.8
15.2	194	codominant	15.8
22.9	212	dominant	14.9
23.2	182	codominant	15.2
23.2	219	codominant	14.9
27.4	216	dominant	18.3
17.9	194	codominant	11.0
18.6	177	codominant	11.9

Average Site Index = 12.8 m (42 feet)

Figure 18. Height-age relationships for sampled stems on south-facing study area in Section 31.



The site index for Douglas-fir on this study area is 15.5 m (51 feet). This estimation is an average of 20 individual indices ranging from 11.9 to 20.7 m at 50 years (Table 28). Excluding the two relict stems, the average age of the sampled stems is 164 years with a 95% confidence interval of ± 9.12 years.

Radial Growth

Annual Rate of Radial Growth

With due respect to the effects of stand density, the rate of diameter growth of trees within a stand is often used as in indicator of stand vigor at a given point in time. The use of 10 year periodic annual incremental growth rates from the various crown classes may be useful in comparing the vigor of the tree strata of a study area. However, these 10 year incremental analyses are not ideal as short-term declines or increases in the radial growth may be obscured within a 10-year average. Due to time limitations, complete analyses of radial growth rates throughout the life of the stand have not been completed. However, even limited analyses indicate that radial growth rates vary considerably within the areas. No simple or obvious pattern in the radial growth rates of individual stems through time was observed. A cursory examination of the data suggests that environmental conditions may be more important in influencing the growth rate of a particular individual than stem age or crown class, although the latter parameters do appear to influence the relative growth rates of individuals within the study area. In order to generally compare the present vigor of trees in each study area, a comparison was made using the last 10 year and

Table 28. Site indices for 22 Douglas-fir trees on the south-facing study area. The average site index for the study area is the mean site index for these individual stems, with base age 50 years (Brickwell, 1968).

Height	Age (Years)	Crown Class	Site Index
17.9 m	140	codominant	11.9 m
18.3	156	codominant	11.9
18.3	158	codominant	11.9
22.9	181	dominant	15.2
30.8	198	dominant	20.7
20.1	135	codominant	13.1
25.9	390	dominant	17.4
21.3	169	codominant	14.0
21.3	169	codominant	14.0
23.7	163	codominant	15.8
22.6	170	codominant	15.2
25.6	178	dominant	16.8
22.9	170	codominant	15.2
32.6*	174	codominant	21.6
32.9*	196	codominant	21.9
37.2*	190	codominant	24.4
29.0	179	codominant	19.5
23.7	148	codominant	15.8
27.1	383	dominant	18.3
26.8	178	dominant	18.0
24.4	149	dominant	16.2
18.3	105	codominant	12.5
23.7	144	dominant	15.8

Average Site Index = 15.5 m (51 feet)

*Not included in average because of location in what appears to be a considerably more mesic microsite than is representative of the area as a whole.

the previous 10-year periodic annual incremental growth rates for representatives from the dominant, codominant, and intermediate crown classes on each site (Table 29).

Using a .95 level of confidence, the last 10-year periodic annual radial growth rates encountered within each study area are observed to be significantly different from the growth rates of the previous 10 years in three cases. Within the south-facing study area, the average growth rate of the individuals in the intermediate crown class is significantly lower in the last decade than during the previous one. On the north-facing study area, the average growth rate of sampled stems in both the codominant and intermediate crown classes is significantly lower in the last decade than in the previous one. Similar trends occur for all crown classes within all of the study areas, but no other significant differences occur at a .95% level of confidence.

The radial growth rate for the last 10 years is not great on any of the study areas (Table 29); the average for the dominant trees on all sites is .044 cm/yr or 58 rings/inch. A similar figure for codominant individuals is .048 cm/yr or 53 rings/in. The average radial growth rate for intermediate individuals on all areas is .042 cm/yr or 61 rings/inch. The mean growth rate for dominant individuals on the south-facing unit is significantly greater (P = .95) than for similar individuals on the west-facing unit. The only significant difference occurring within the codominant crown class at this level of confidence is between the radial growth rates for the individuals within the west-, south-, and north-facing units. The growth rate of the codominants on the west-facing unit (.032 ± .010 cm/yr) is significantly slower (P = .95) than that found for similar individuals on the north-facing unit

Table 29. Periodic annual radial growth rates for last two decades, by crown class and study area, using a 95% confidence interval. Values in parentheses indicate number of stems sampled, all of which were Douglas-fir.

Crown Class	Dominant	Codominant	Intermediate
Study Area			
	Periodic Annual Radial Growth Rate (last 10 yrs.; cm/yr)		
North (aspect)	.045±.032(6)	.060±.012(13)	.059±.037(12)
East	.046±.018(8)	.047±.012(14)	.059±.018(12)
West	.035±.006(8)	.032±.010(11)	.024±.007(16)
South	.051±.012(8)	.052±.014(15)	.025±.006(13)
	Periodic Annual Radial Growth Rate (previous 10 yrs.; cm/yr)		
North (aspect)	.068±.040(6)	.089±.019(13)	.093±.004(12)
East	.067±.024(8)	.063±.023(14)	.069±.015(12)
West	.040±.008(8)	.045±.013(11)	.035±.011(16)
South	.065±.020(8)	.-62±.014(15)	.049±.015(13)

(.060 ± .012 cm/yr) and on the south-facing unit (.052 ± .014 cm/yr). Within this crown class, the north-facing slope apparently has the highest rate of growth followed by the south-, east-, and west-facing slopes in descending order. The radial growth rates of intermediate individuals on the south (.025 ± .006 cm/yr) and west-facing (.024 ± .007 cm/yr) slopes are significantly lower than those found on the east-facing (.059 ± .018 cm/yr) and north-facing (.059 ± .037 cm/yr) slopes.

The last 10 year periodic annual incremental growth rates indicate no significant difference (P = .95) between the three crown classes on the north-facing unit. The growth rate of the dominants is modest in comparison to the other areas, but the codominant crown class is the fastest growing of any of the areas. The growth rate of the intermediate individuals is high compared to other units. Within the east-facing unit there is again no significant difference between the radial growth rates of any of the respective crown classes (P = .95). When compared to other study areas, the growth rate of the dominants is moderately high as is the growth rate of the codominant crown class. The intermediate individuals in this area have the highest growth rate of any of the study areas. The rates of radial growth evident on the west-facing slope show the dominant stems to be growing significantly faster than intermediate stems, with the rates of growth for all crown classes consistently the lowest of any of the study areas. Finally, within the south-facing unit, the rate of radial growth found in the intermediate crown class is significantly less than that found in the dominant and codominant crown classes at the 95% level of confidence.

The dominant individuals on the area are the fastest growing, in diameter, of all dominants in any of the units. The codominant individuals are also growing comparatively well, but are bettered slightly by the codominants found on the east-facing slope. The intermediate individuals are relatively slow growing when compared by intermediate individuals on other slopes in Section 31.

Seasonal Pattern of Radial Growth

No statistical analysis of the radial growth rates as indicated by the band dendrometers have been attempted as a limited number of bands survived the summer intact. On the south-facing slope only 6 out of 12 bands remained functional, while 6 out of 11 survived on the north-facing slope. On the west- and east-facing slopes, 4 out of 9 and 5 out of 9 bands survived within the respective study areas.

The dendrometers were affixed to determine the timing and periodicity of diameter growth on each study area; however, the incremental growth rates indicated by the dendrometers fall well within the range of radial growth rates encountered in the analysis of the increment cores and cross-sections. Last year's radial growth rates for the banded trees ranged from .004 cm/yr (628 rings/inch) to .105 cm/yr (24 rings/inch).

Although variation in the growth rates of the banded trees is large, some indications of specific patterns in the timing of diameter growth are apparent. Figures 19 and 20 illustrate the average daily incremental growth rate and total cumulative growth respectively for representatives of the "better" Douglas-fir found on each unit. Trends are similar between units (Figure 19), however banded individuals on

Figure 19. Average daily radial growth rates per observation period for faster growing Douglas-fir stems from each study area in Section 31.

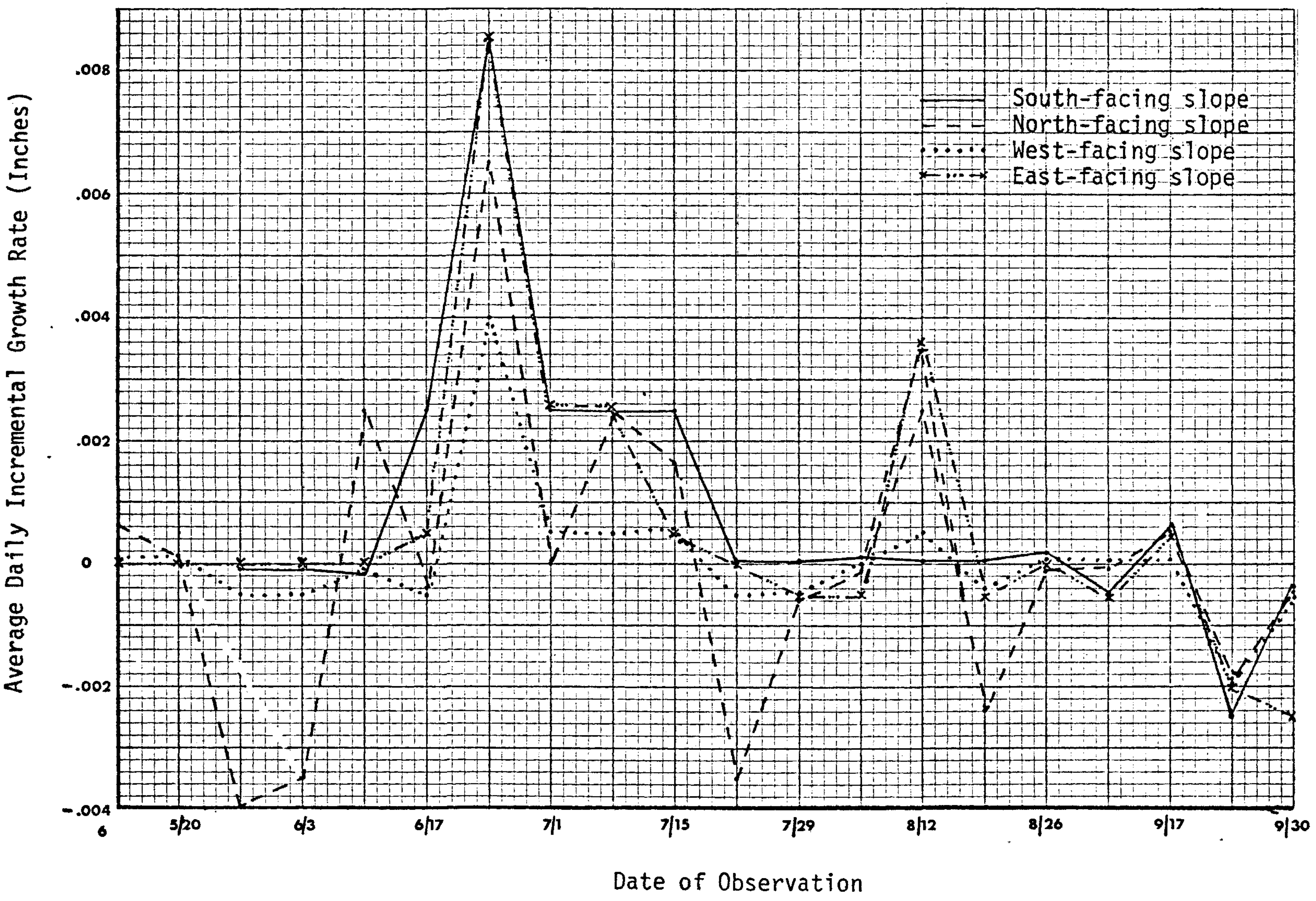
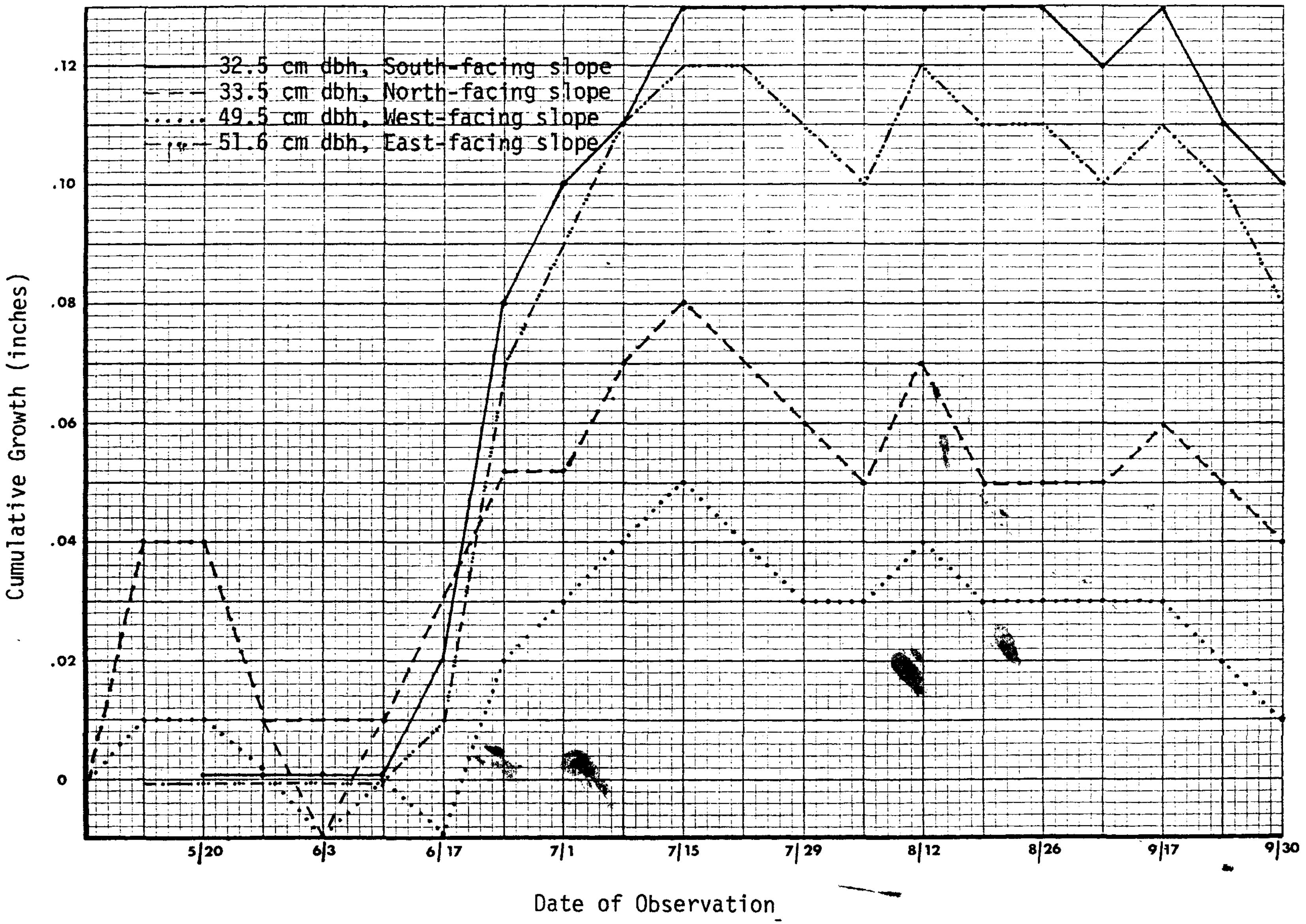


Figure 20 . Cumulative radial growth for Douglas-fir stems representing respective aspect units.



the north-facing unit exhibited greater fluctuations in daily growth rates than banded trees on the other three study areas.

Some banded individuals showed a decrease in diameter in late May and early June while most showed no change during this period. In any case, virtually all trees began to increase in diameter by June 17 and many by June 10 (Figures 19 and 20). The greatest daily incremental growth rate occurred between June 17 and June 24. Beyond that date all trees declined in growth rate, but most continued to amass additional cumulative diameter growth.

It is impossible to determine the length of the growing season by this method of measurement as a strong correlation exists between apparent diameter growth and summer storms which occur during particular observations periods. Examples of this correlation are illustrated during observation periods ending August 12 and September 17, within which heavy preciptiation occurred. A reduction in the incremental growth observation period following the one in which the storm occurred. It is also interesting to note that the circumference of sample trees is continually declining through the last observation period (Figure 20). It is important to determine if dehydration is taking place due to a dry fall or if assumed diameter growth earlier in the summer is really a swelling of a tree due to increased moisture in the stem during active photosynthetic and transpirational periods.

Observations were made comparing the timing of phenological characteristics such as floral development and bud burst to the initiation of diameter growth at breast height. Western larch leafed out the earliest of any of the species banded, having completed bud burst by June 3 on the north-facing unit in the overstory. Western larch does not conform to the previously discussed pattern of diameter growth. A slight amount of shrinkage was evident during the observation period in which the bud burst occurred. Because of its deciduous nature, western larch must expend energy to achieve bud burst and obtain a new photosynthetic surface through which additional energy may be obtained for diameter growth. For this reason, the maximum daily incremental growth rate for western larch did not occur until the observation period between July 8 and July 15, two weeks following the peak of Douglas-fir and lodgepole pine.

Lodgepole pine bud burst and shoot elongation began during the observation period between May 27 and June 3 and six inch elongation of the candle was common by June 17. The period of maximum daily incremental growth rate occurred during the observation period between June 17 and June 24.

For Douglas-fir, floral development began in the overstory about June 1. Vegetative bud burst occurred during the observation period between June 24 and July 1. The initiation of floral development coincided with a general shrinkage in the diameter of the banded trees. The observation period in which bud burst occurred followed the period of maximum daily incremental growth rate by one week. Daily incremental growth rates were lower during this period of bud burst.

Chapter 5

DISCUSSION

Reproduction of Inland Douglas-fir

Forest managers must be concerned with the perpetuation of forests following disturbance, regardless of the origin of the pertubation. Information gathered in this study begins to decipher the reproductive strategy of inland Douglas-fir in several naturally developed, successionally-advanced forest communities. Potentially, increased knowledge of the ecology of a species may supplement the development of silvicultural programs directed at regenerating commercially harvested areas.

Although information regarding the reproductive strategy of interior Douglas-fir in unmanaged situations is unavailable, several investigators have studied the regeneration process in commercially harvested areas and have reported on factors affecting Douglas-fir regeneration (Roe, 1951; Roeser, 1924; Steele and Pierce, 1968; Hatch and Lotan, 1969). Factors which seem to be most critical in the regeneration of a site following disturbance include an adequate seed source, a suitable seedbed, and an environment amenable to seedling germination and establishment (Smith, 1962; Baker, 1950).

In general, an adequate seed source is not reported to be a problem in inland Douglas-fir. In Montana, Douglas-fir is rated as a prolific seeder, producing good or fair cone crops 58% of the time through an extended observation (Fowells, 1965). Fowells reported seed dissemination up to 80.5 m (4 chains) from uncut timber averaging 30.5 m (100 feet) tall. Steele and Pierce (1968) determined that adequate seed dissemination was possible up to 305 m (1000 feet) from a seed source in western Montana. In some cases, however, insects or disease may influence the vigor of potential seed trees causing reduced production of viable seed over an extended period of time. Hatch and Lotan (1968) reported the possible influence of the spruce budworm in reducing seed availability in central Montana.

The condition of the seedbed is probably the most discussed factor when reproductive successes or failures are analyzed. Foresters believe the seedbed is a factor over which they may have considerable control. Researchers have reported on a wide variety of seedbeds, with the greatest concern usually expressed over the reduction of injury by heat or by frost. Cochrane (1969) reported the probability of seedling injury by heat or frost depends upon the temperature variation at the soil surface. He states that the color of the soil surface may be overemphasized and that the thermal properties of the soil or soil covering, e.g. litter or mulch, are more important in influencing surface temperature variation. Many types of mulch or litter act to increase surface temperature variation by lowering the thermal contact coefficient and the conductivity coefficient of the soil surface material. A widening range of soil surface temperatures may ultimately include temperatures injurious to seedlings by either frost or heat. Cochrane also contended that moist mulches are effective due to the amount of heat dissipated via high rates of evaporative heat flux. Hallin (1968) reported that seedlings could withstand a lethal temperature (138°F) for 1 hour in peat moss and 4 hours in yellow mineral soil.

Herman ahd Chilcote (1965) determined coastal Douglas-fir germinated best on a black, charcoal seedbed; gradually decreasing germination percentages were noted on ash resulting from a heavy burn, mineral soil, and undisturbed seed beds. They stressed the importance of light shade in promoting seedlings survival.

Boe (1948) suggests that successful germination of Rocky Mountain Douglas-fir is possible in duff if it is kept moist; however, he states that a mineral surface is best. Boe stressed the importance of light shade for the initial survival and establishment of the seedlings. While studying western larch--Douglas-fir forests in western Montana, Roe (1951) found that mineral soil is the most effective seedbed for Douglas-fir. He stated that established seedlings do best in full sunlight. Roe indicated that tall shrubs were most detrimental to Douglas-fir seedlings, but that low shrubs were less a hindrance and acted to increase the competitive advantage for Douglas-fir over western larch. According to Fowells (1965), inland Douglas-fir establishment is improved by partial shade and the presence of litter, if the litter is kept moist. He also states that dark colored soils or blackened soils are unfavorable because they create high surface temperatures. In central Montana, Hatch and Lotan (1969) discovered that Douglas-fir seedling stocking levels were best on undisturbed seedbeds or those covered with logging slash. They stressed the importance of litter in conserving soil moisture, reducing herbaceous vegetation, and protecting the seed from rodents and birds. Ryker and Potter (1970) also determined that shade encourages the establishment of Rocky Mountain Douglas-fir seedlings. These researchers attributed deaths not necessarily to high soil temperatures, but rather to a metabolic imbalance caused by internal moisture stress. They concluded that shading reduced leaf temperatures, reduced water loss and resultant moisture stress, and increased net photosynthesis. Inland Douglas-fir in the southwestern United States is noted to need shade for successful seedling establishment, although overhead light is important for further seedling development (Jones, 1971; Krauch, 1956).

Factors Controlling Reproduction on Section 31

Although it is impossible to develop a complete reproduction model for Douglas-fir at this time, personal observations have been made regarding the reproductive strategy of the species throughout an environmental gradient on Section 31.

The south- and west-facing slopes appear to be severe for seedling establishment. On the bench subunit of the south-facing slope reproduction is sparse. Virtually all of this subunit is a *Pseudotsuga menziesii*--*Calamagrostis rubescens* habitat type (Pfister, et al., 1974). Pinegrass (*Calamagrostis rubescens*) is a sod-forming grass that is frequently noted as reducing seedling success on cutover areas in western Montana, and this species may be limiting seedling establishment in the virgin stand. The bench area also supports a generally closed canopy which may effectively reduce sunlight penetration to the forest floor. Regeneration, when present, often occurs in conjunction with some type of minor disturbance, e.g. uprooted trees, which probably reduce understory competition for soil moisture and may increase available light. Some seedlings were observed within undisturbed Calamagrostis rubescens in microsites where competition for soil moisture is probably less severe, e.g. draw bottoms.

On the slope subunit of the south-facing area, where greater numbers of Douglas-fir reproduction are observed, understory vegetation appears more sparse and the canopy is not closed. The habitat type for this subunit is generally Pseudotsuga menziesii--Symphoricarpos albus (Pfister, et al., 1974). Small seedling clumps are found toward the lower portions of the canopy openings. The insolation on this steep slope appears intense, so shading may be important in seedling establishment. The understory in these openings is not generally lush, and is dominated by Symphoricarpos albus or Agropyron spicatum. Adequate amounts of mineral soil are generally present but moisture stress due to higher soil surface temperatures is expected to be limiting.

Reproduction on the west-facing slope may be limited by biological competition. Large portions of the area are a Pseudotsuga menziesii--Calamagrostis rubescens habitat type with smaller portions classified as Pseudotsuga menziesii--Symphoricarpos albus and P. menziesii--Xerophyllum tenax. The Douglas-fir--pinegrass areas generally lack seedlings; areas with the understory dominated by snowberry and Xerophyllum tenax seem to support greater numbers of seedlings. Seedlings are evident near microsites where rock outcrops occur.

Because the study area lies within a steep, narrow drainage, the soil surface temperatures probably do not reach the extremes expected on the south-facing slope.

The north- and east-facing slopes have abundant seedlings under fairly closed canopies. The major habitat types on these areas include P. menziesii--Xerophyllum tenax, P. menziesii--Vaccinium globulare, and Abies lasiocarpa--Linnea borealis. Seedling germination and establishment does not seem to be greatly restricted on these aspects; however, seedlings may depend upon a canopy opening and adequate sunlight for further development.

In summary, physical factors limiting regeneration are clearly apparent only on the slope subunit of the south-facing study area. This limitation is due to the potential heat injury caused by high soil surface temperatures. On this harsh site, the position of the seed with regard to soil moisture stress may be most critical in determining the future development of the individual. Too much shade is generally not a problem in these areas; once the stem becomes established there are few abiotic obstacles to prevent the full development of the individual. Understory competition for available soil moisture and overstory shading are expected to be more ubiquitous as limits to seedling success. The sod-forming grass Calamagrostis rubescens is probably very important in limiting seedling establishment; the effects of low shrubs such as Symphoricarpos albus and Vaccinium globulare are more difficult to ascertain, particularly because they occur on areas with more favorable moisture regimes. Seedlings are also evident within patches of Xerophyllum tenax. On the north- and east-facing slopes, where large numbers of seedlings are found, shade may be a limiting factor in the continued development of an established individual. A canopy opening created by the death of a dominant tree may be key to the continued development of stems in areas where seed source and seedling establishment seem assured.

Spatial Distribution of Seedlings and Saplings

All of the seedling populations and several of the sapling populations are apparently contagiously distributed (Table 30). Cole (1946) included as potential reasons for contagious results the heterogeneity of the study area, incorrect sample size, attractive forces which lead to the formation of familial groups or adaptive aggregations, and the production of offspring in groups rather than singly. Brown (1954) suggests individuals tend to be grouped because of coppice reproductive systems or by design of the sexual reproduction process. Whittaker (1975) listed three reasons for aggregated populations including (1) dispersal mechanisms from parent individuals, (2) differences in environmental conditions, i.e. microclimatic differences which may preclude individuals from some locations or encourage establishment in others, and (3) species interrelations.

Microclimatic factors are probably most important in controlling the initial survival of seedlings and hence the seedling distribution on any site. Microclimate is also a controlling factor in sapling distributions, particularly for less tolerant species which require more light for successful development past the seedling stage.

Table 30. Indices of aggregation for the seedling and sapling populations on Section 31.

	David and Moore's Index of Dispersion (I)	Lloyd's Index of Clumping ($\overset{*}{m}$)	Lloyd's Index of Patchiness ($\overset{*}{m}$)/m
North-facing Slope			
Seedling	15.9	20.4	4.5
Sapling	5.1	7.4	3.1
East-facing Slope			
Seedling	9.9	15.1	2.9
Sapling	2.5	3.0	5.9
West-facing Slope			
Seedling	14.4	15.5	14.1
Sapling	0.0	0.0	0.2
South-facing Slope			
Bench Subunit			
Seedling	none	--	--
Sapling	0.0	0.0	0.5
Slope Subunit			
Seedling	3.5	3.9	10.9
Sapling	0.0	0.0	0.3

On the north-facing study area, microclimatic conditions favor seedling establishment. Density dependent mortality may be prevalent, but the favorable environment acts to reduce competitive stress. On the east-facing slope, microclimate is also favorable for seedling establishment. However, the influence of a more severe environment, combined with density dependent mortality increase the patchiness of the sapling size class. On the west-facing slope seedling establishment is limited to favorable microsites as evidenced by increased patchiness and, if allowance is made for lower seedling density, the higher values of the clumping indices. Environmental stress apparently becomes very limiting as the aggregation indices suggest that density dependent mortality is high. Successful saplings are individuals that (1) are able to withstand rigorous competitive pressure and/or (2) exist on isolated favorable microsites. On the south-facing slope, microclimate conditions are harsh enough to severely limit initial seedling survival. Lloyd's ($\overset{*}{m}$) is probably low because the harsh microsite conditions reduce the number of co-occupants possible in a clump. Density dependent mortality of seedlings is likely reduced simply because fewer individuals become established initially.

Hypothesized Developmental Patterns for Non-catastrophically Disturbed Old-growth Stands Dominated by Douglas-fir

Any attempt to ordinate the respective study areas in regard to apparent available soil moisture would probably result in identifying the south-facing unit as the warmest and driest, with the west-facing, east-facing, and north-facing units identified as increasingly cool and moist. Within the south-facing unit, the more gently sloping bench subunit can be considered less harsh environmentally than the slope subunit. In view of the proposed environmental framework, it is important to observe the community dynamics and present stage of stand development of the study areas along this gradient.

The north-facing slope is an uneven-aged stand, approaching the all-aged condition, except for an apparent 50-year period in which no trees became established (Table 19). The size class density distribution indicates a slightly unbalanced stand (Figure 21) (Leak, 1964). The main stand establishment phase lasted 40 years and, following this period, few individuals became established for the next 100 years. Seedling establishment again proceeded vigorously about 100 years ago and has continued since. Given a site suitable for seedling establishment following some major disturbance, a heavily stocked stand of Douglas-fir, western larch, and lodgepole pine could have evolved to preclude light penetration to the forest floor, effectively prohibiting seedling development. Once stand development had advanced to the point where the canopy had raised enough to allow greater diffuse light penetration to the forest floor and occasional dominant stems began to lose vigor creating additional canopy openings, seedling establishment commenced again (Bray, 1956). As additional overstory trees become overmature and a greater portion of the canopy begins to break up, the developing, but probably suppressed understory trees may be released (Marks, 1974; Day, 1972). If no major disturbance occurs which starts the process of stand development anew, this proposed developmental scheme may become

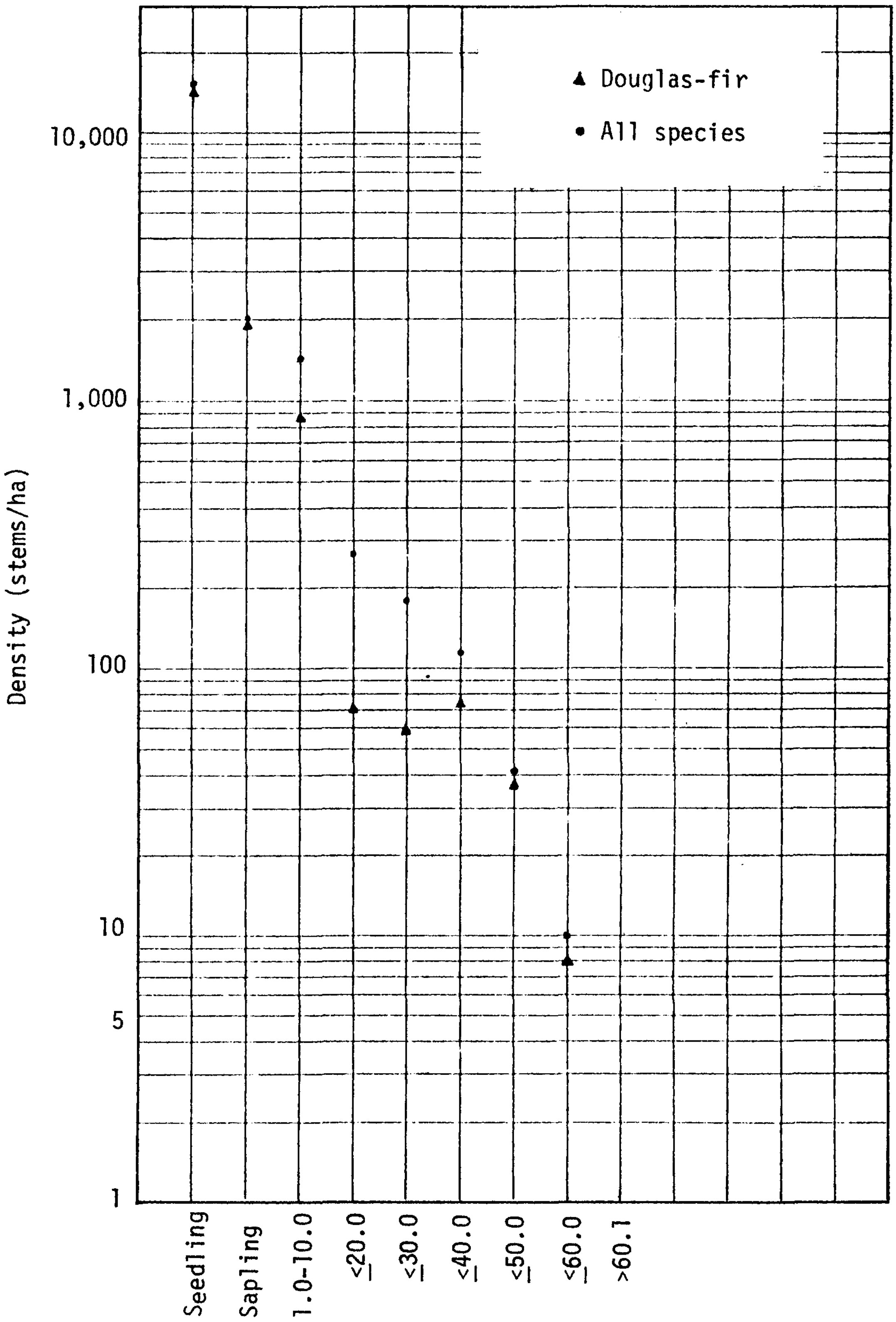


Figure 21. Size class density distribution, north-facing slope.

cyclic in nature, depending upon a rather rapid breakup of the canopy as senescence is reached.

The east-facing study area appears to have had a developmental pattern quite similar to that found on the north-facing slope, varying slightly in timing and speed of development. The age structure again appears to be nearly all-aged (Table 19), but deviates from the expected balanced size class distribution (Figure 22). Table 19 indicates a 60 year stand establishment phase followed by a 110-year period in which very little stem establishment occurred. Seventy years ago seedling establishment again began and has continued until the present.

The west-facing study area appears to have lagged behind the north- and east-facing units in the timing of developmental events. The stand is uneven-aged with an unbalanced size class distribution (Figure 23). The initial stand establishment phase lasted 130 years, with stem establishment being greatly reduced since that time (Table 19). The currently reduced number of saplings may indicate a canopy which is still effectively preventing light penetration to the forest floor. However, it has been 100 years since the main stand establishment phase ended and perhaps the stand is currently maturing developmentally to the point where there is enough light for seedling germination and development beneath the canopy.

Age structural evidence indicates that the south-facing slope is an uneven-aged stand (Table 19). Stand development began as much as 60 years following the other three units already described. The main establishment phase proceeded more slowly taking 140 years before stem establishment dropped off. Only during the last 40 year period has stem

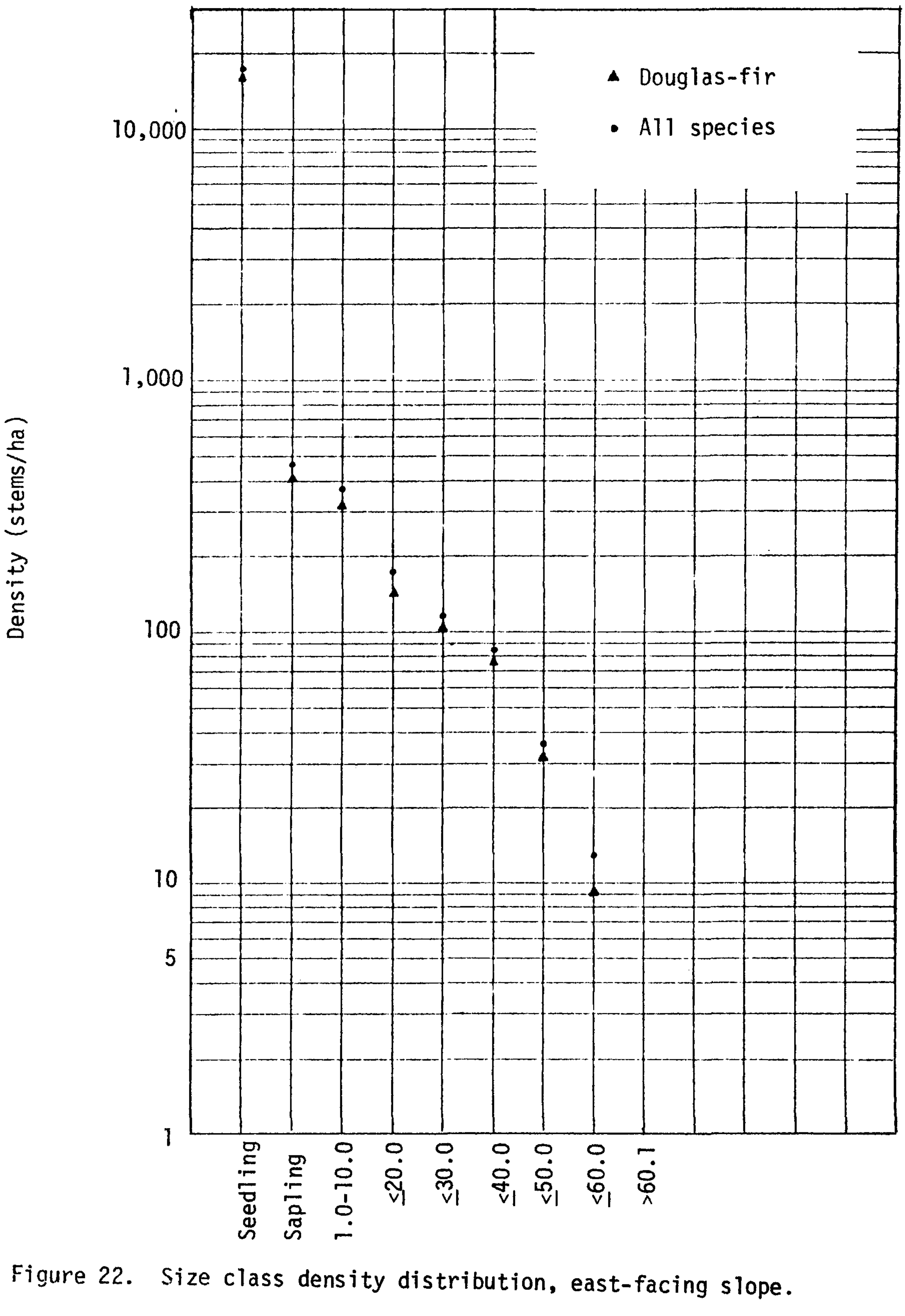


Figure 22. Size class density distribution, east-facing slope.

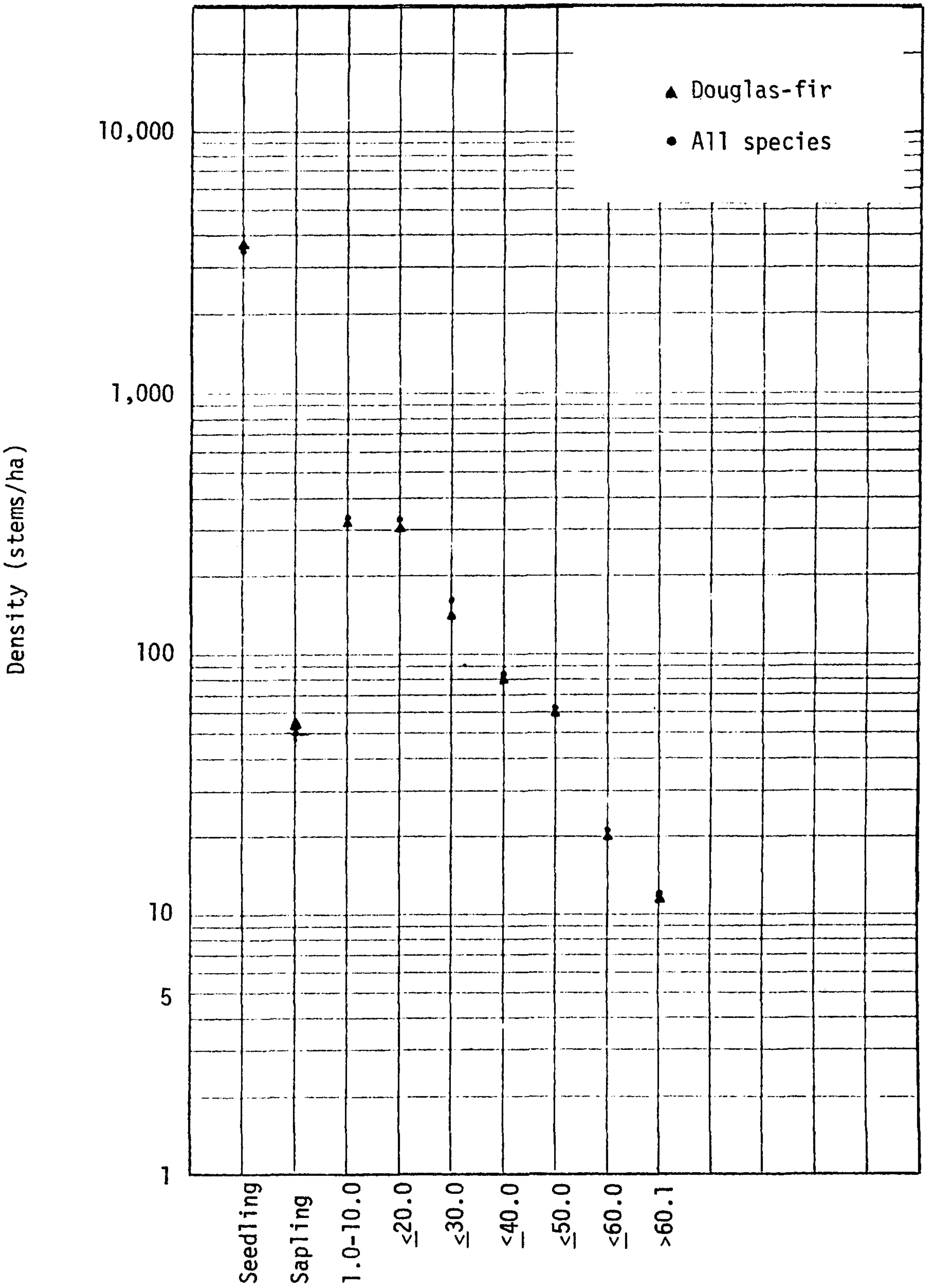


Figure 23. Size class density distribution, west-facing slope.

establishment been consistently reduced (Table 19). On the bench subunit in particular, where seedlings and saplings are scarce, the canopy may be too dense for seedling establishment and development. This dearth of reproduction creates an unbalanced stand structure (Figure 24). On the slope subunit, the previously proposed scheme for stand development may not be applicable. Under the harsh environmental conditions present on the slope, it is unlikely that a tightly closed canopy will ever occur. Openings are constantly available for seedling establishment. An examination of the stand table (Table 17) for this subunit shows a rather uniform distribution of individuals throughout all dbh classes, perhaps indicating a slow, but constant input of individuals into the community. The size class density distribution is slightly unbalanced due to the low number of saplings (Figure 25).

Although many similar developmental trends are apparent within four areas studied, it is interesting to note the differences in the timing and the speed of development throughout the environmental gradient. Initial stand establishment apparently occurs most quickly on the moister, cooler sites while establishment and canopy closure proceed more slowly on progressively warmer, drier sites, to the point where canopy closure may never occur. The stand differentiation process is also shorter on the progressively moister sites.

Non-catastrophically initiated community dynamics appear dependent on some form of gap-phase replacement. Canopy openings seem to be necessary for the establishment of regeneration or the continued development of advanced reproduction. The size of these openings and their frequency is dependent upon the nature of the community and on the

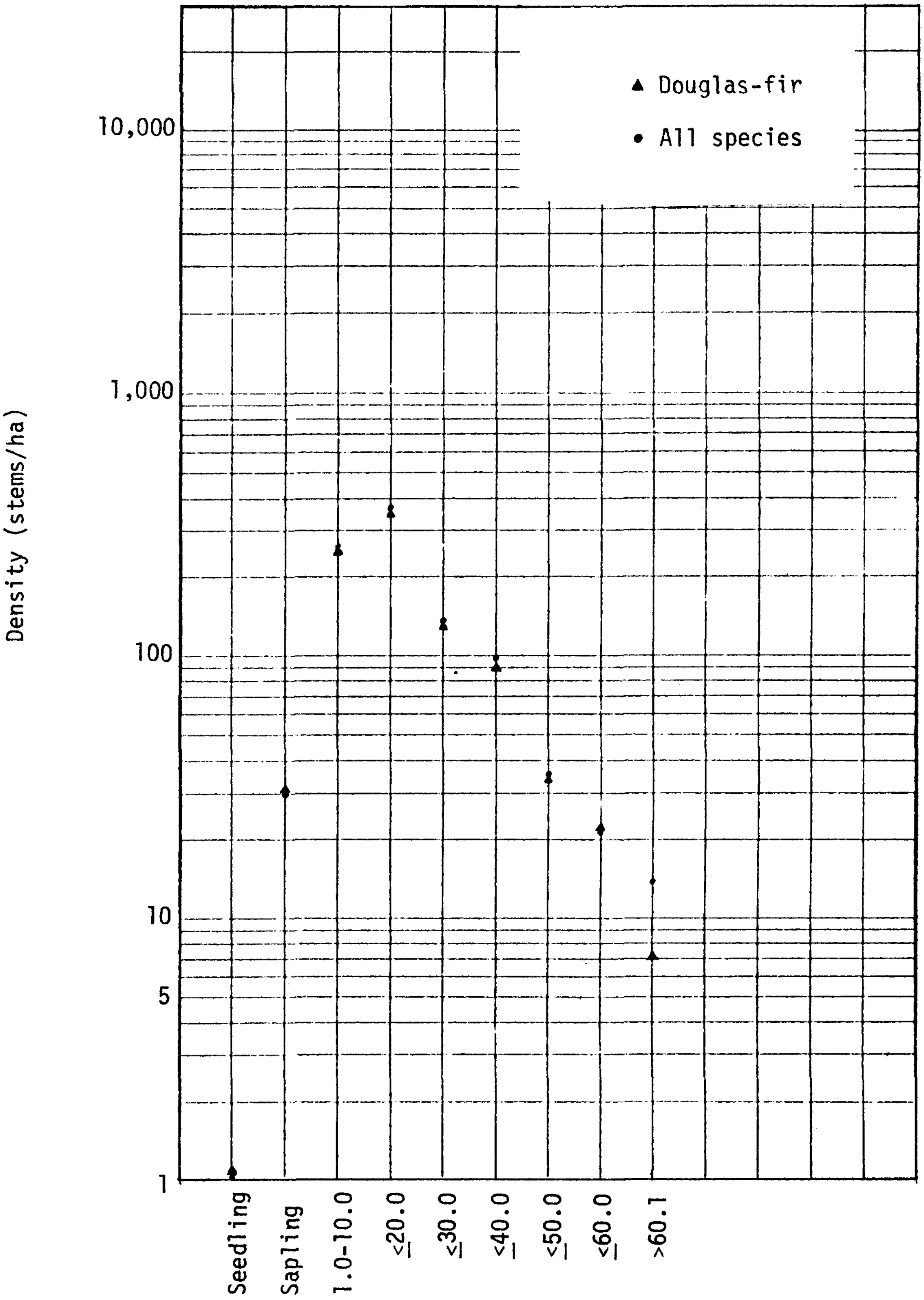


Figure 24. Size class density distribution, south-facing slope, bench subunit.

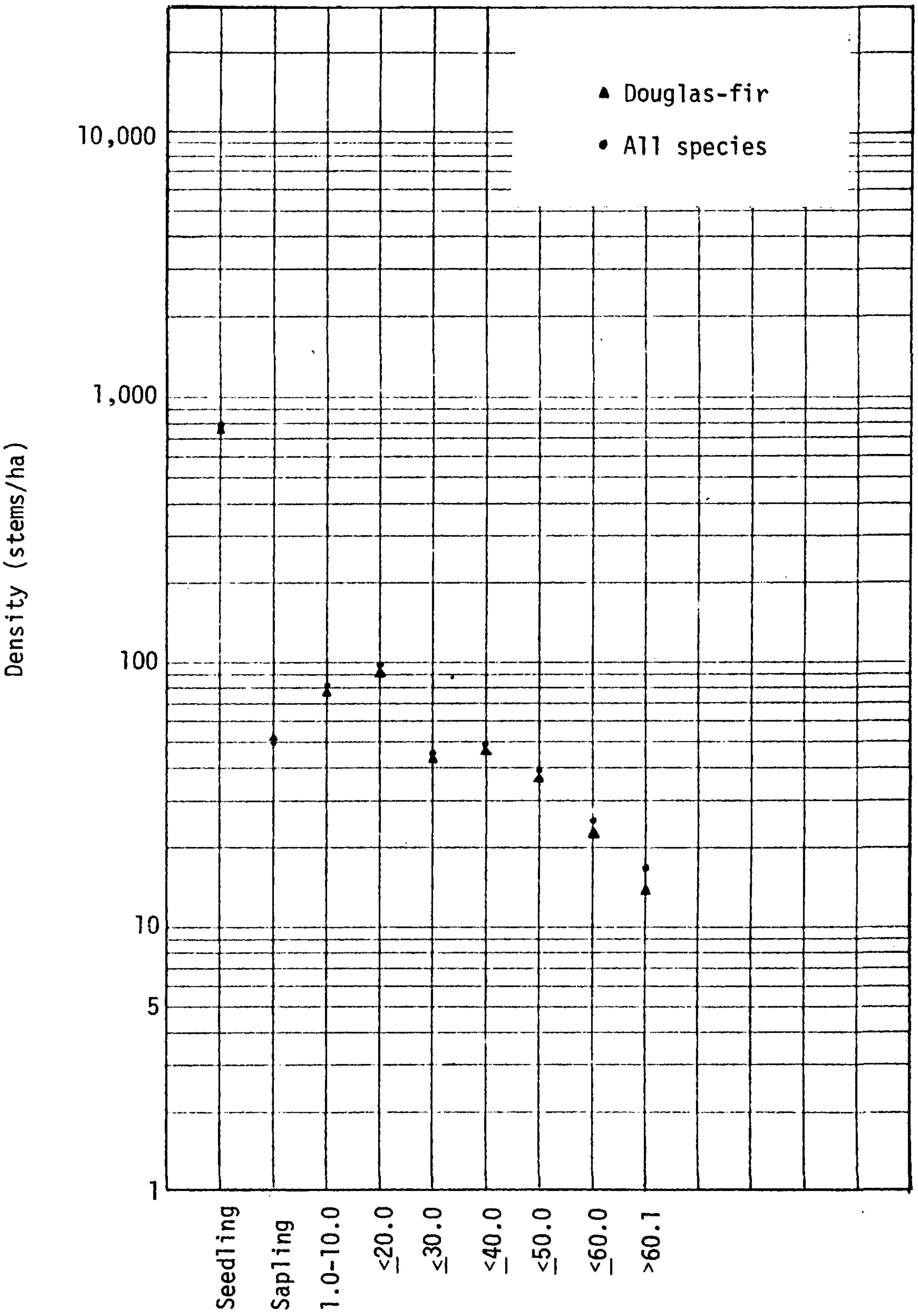


Figure 25. Size class density distribution, south-facing slope, slope subunit.

abiotic environment in which it exists. Openings vary in size from small openings created by the death of one or several dominant individuals to larger openings created by the death of many dominant trees. Openings of varying sizes may result from harsh abiotic environments or small-scale allogenic or autogenic disturbance, e.g. fires, endemic insect populations, and windthrow. The age structure of the canopy and relative longevity of the species comprising the canopy are important in determining the frequency of openings and their size when they do occur (Jones, 1945).

Harsh sites, where canopy closure is not observed, always contain canopy openings although these are likely spatially shifting in time (Watt, 1947). The environment in which this smaller-scale gap-phase system operates seems to inhibit large influxes of individuals into the community at one time, but promotes an all-aged structure in which small numbers of individuals are continually entering the community.

Communities occupying more favorable sites may be perpetuated by a combination of small, frequent openings and less frequent, but larger-scale canopy break up. More favorable sites tend to support a more even-aged canopy initially, which is frequently made up of several species. The various species in the canopy may have different longevities, a situation which encourages the creation of small openings as the shorter lived species lose vigor. Reproduction is able to become established in these small openings, but is likely to be suppressed as the remaining dominant trees fill in the gaps by branch growth. Once canopy breakup begins to occur, the rate of the process generating small gaps increases rapidly due to the increased exposure of the residual stand (Day, 1972;

Baskerville, 1965), effectively creating larger openings which (1) induce increased regeneration and (2) release advanced regeneration. If the shorter-lived species are reduced to a minor component of the stand, future replacement behavior may become increasingly dependent on the smaller scale, single tree type of replacement.

This proposed gradual decreasing of gap size would be expected to produce a more all-aged canopy as stand development proceeds.

Neither of these stand perpetuation theories have included the role of major allogenic influence. In the northern Rocky Mountains it is unrealistic to preclude catastrophe from the system (Daubenmire, 1969). On drier and warmer sites, occasional fires may reduce understory competition from grasses or shrubs, assisting tree regenerative processes. Fire, however, does not fit as nicely into the cyclic pattern envisaged for the cooler, moister sites as it would probably first kill the advanced reproduction hypothesized as necessary to the cycle. Fires in these environments may be more catastrophic, tending to set the community back further in the successional sequence. In fact, evidence may suggest such a large-scale catastrophe on the entire south side of Washoe Creek, initiating present stand development about 240 years ago. Due to the occasional relict stems nearly 400 years old on the south-facing slope, it is more difficult to envision any catastrophic event setting the stand back very far successionally in the last several hundred years.

Chapter 6

SUMMARY

Each of the four study units represents a different position along an environmental gradient from cool, moist to warm, dry within a limited elevation range. The three theoretically most mesic study areas, the north-facing, the east-facing, and the west-facing units are found on the south side of a major stream barrier, separating them from the warm, dry south-facing unit. Age structural analyses show that the three study stands on the south side of Washoe apparently originated following some large scale disturbance about 240 years ago. The south-facing study stand, however, appears to be younger, originating some 200 years ago.

The species composition and stand structure found on each of the four study sites are different. The north-facing community has the greatest tree species diversity including Douglas-fir, ponderosa pine, western larch, subalpine fir, lodgepole pine, and Engelmann spruce. The density of all stems > 1 cm dbh is high (Table 31) and constitutes 34.9 m^2/ha of basal area. The density of stems >10 cm dbh is 630 stems/ha, constituting 32.56 m^2/ha of basal area. Although the density of large stems is high, as is the basal area of these stems, large trees on the west- and south-facing (bench) slopes are more dense and constitute more basal area. A large number of seedlings (15,319 seedlings/ha) and saplings (2,019 saplings/ha) contribute to the north-facing area's

Table 31. Total density, frequency, and basal area for four study areas on Section 31.

	North-facing Unit	East-facing Unit	West-facing Unit	South-facing Unit	
				Bench	Slope
Density (stems/ha)					
Seedlings	15,319	17,258	3,501	0	796
Saplings	2,019	477	50	30	20
Trees <10cmdbh	1,414	387	331	268	58
Trees >10cmdbh	630	426	662	667	205
Frequency (percent)					
Seedlings	66.3	72.5	18.8	--	10.7
Saplings	62.5	25.0	6.3	12.5	3.6
Trees <10cmdbh[1]	100	100	100	100	100
Trees >10cmdbh[1]	100	100	100	100	100
Basal Area[2] (m^2/ha)					
Trees <10cmdbh	2.35	0.82	1.5	0.84	0.15
Trees >10cmdbh	32.56	26.03	39.25	40.41	24.34
Site Index (m)	15.6	14.3	12.8	15.5	

[1] By nature of the point-quarters sampling method, trees are forced to have 100% frequency.

[2] By definition, seedlings and saplings have no basal area.

almost balanced diameter distribution, suggesting an uneven-aged stand (Leak, 1964). Douglas-fir, lodgepole pine, and subalpine fir appear to be reproducing successfully on this study area. Age structural information also indicates uneven-aged stand structure. Even though the stand is uneven-aged, caution is urged in predicting age based on height and particularly diameter as the height and diameter of stems varies considerably in some age classes. The site index on this slope for Douglas-fir, 15.6 m (51 feet), is the highest found on any study area.

The east-facing tree community is also diverse, including Douglas-fir, western larch, subalpine fir, lodgepole pine, and Engelmann spruce. The density of stems > 1 cm dbh is 849 stems/ha, which constitute a basal area of 26.84 m^2/ha. The density of stems > 10 cm dbh is 426 stems/ha, with these stems constituting virtually all of the basal area (Table 31). Although seedlings are abundant (17,268 seedlings/ha), the saplings are not dense. The lower number of saplings (477 saplings/ha) combines with other factors to create a slightly unbalanced diameter distribution; however, age structural information suggests an uneven-aged stand structure. Douglas-fir, lodgepole pine, western larch, and Engelmann spruce appear to be reproducing successfully on this study area. Caution is again urged in predicting age based on height or diameter as the age of stems varies considerably, particularly within smaller size classes. The site index for Douglas-fir on this slope is 14.3 m (47 feet).

Many tree species were found on the west-facing slope, but the diversity of species within size classes is reduced. Douglas-fir, ponderosa pine, subalpine fir, lodgepole pine, and Rocky Mountain juniper are found on the site. The density of all stems > 1 cm dbh is 992 stems/ha, constituting 40.30 m^2/ha of basal area. Stems > 10 cm dbh have a density of 662 stems/ha and constitute most of the basal area (Table 31). The number of seedlings and saplings is low, but the sapling to seedling density ratio is about equal to that found on the east-facing slope. Douglas-fir is the only species reproducing successfully on this slope. In any case, the size-class distribution is unbalanced (Leak, 1964) and age structural data suggest an uneven-aged stand. A wide range of ages is encountered within smaller dbh and height classes. The site index for Douglas-fir on this slope is 12.8 m (42 feet).

On the south-facing slope two communities are apparent. On the less steep, bench subunit, Douglas-fir and ponderosa pine are found. The density of stems > 1 cm dbh is 935 stems/ha, constituting 41.25 m^2/ha of basal area. The majority of these stems are greater than 10 cm dbh and combined with an average diameter of 19.6 cm dbh, constitute 40.41 m^2/ha of basal area. No seedlings and few saplings were encountered in sampling (Table 31). The slope subunit has a greater tree species diversity including Douglas-fir, ponderosa pine, lodgepole pine, and Rocky Mountain juniper. The density of stems > 1 cm dbh is reduced to 261 trees/ha which constitute only 24.49 m^2/ha of basal area. Small numbers of seedlings and saplings cause an unbalanced size class distribution (Table 31). Sampling for age structure combined both subunits and suggests an uneven-aged structure. Trees between 10 and 20 cm dbh range in age between 55 and 160 years old, while stems less than 25 feet tall range between 30 and 155 years old. The combined site index for this study area is 15.2 m (50 feet), almost as high as that found on the north-facing slope.

Stand development apparently has occurred most quickly on the cooler, moister sites, taking progressively longer on the warmer and drier sites. Complete stand development, in terms of a closed canopy, may never occur on the warmest, driest site. Stand differentiation following full canopy closure also appears to proceed more quickly on the cooler, moister sites.

In the stands where canopy closure occurs relatively quickly, the canopy may be even or one-storied in structure. Within these well-stocked more even-aged canopies, the stems are forced to compete for light and consequently differentiation should be rapid, permitting diffuse side-light to reach the forest floor sooner than if the canopy is several storied. Canopies which take longer to fill in may acquire a several storied structure. If stand establishment is spread over a longer period of time, differentiation pressures may not be great until younger stems begin competing with older stems for canopy positions. Once light is again available on the forest floor, a new reproductive phase can begin. If no major disturbance occurs which sets the system back to the initial establishment phase, this advanced regeneration may release following any breakup of the original canopy.

If canopy closure never occurs, a continuous gap-phase system of stand perpetuation is probable. The environment is harsh on these sites, but necessary shade for seedling survival may be provided by residual trees. The uneven-aged structure probably reduce the probability of mass mortality, unless large-scale allogenic perturbation occurs.

Tree species which are capable of being perpetuated over long periods of time on a given catastrophically undisturbed site are generally termed climax. This perpetuation process requires that a species is capable of successfully reproducing under the environmental conditions found within the stand. Successful reproduction must be viewed as more than the presence of seedlings. The individuals must have the ability to survive environmental conditions present in the understory. If saplings are known to be vigorous, then the number of saplings within an area is a better indicator of successful reproduction.

Douglas-fir has the ability to reproduce successfully on all sites studied, genuinely earning the title of a climax tree species within this elevational range. Subalpine fir is regenerating successfully only on the north-facing slope, but is not presently important in this community. Lodgepole pine appears to be reproducing successfully on both the north- and east-facing slopes. Although the species is not important, it apparently is a member of the climax community on the cooler, moister sites at this elevation. Engelmann spruce and western larch seems to be reproducing successfully on the east-facing slope. Both of these species generally require sunlight for successful establishment. Due to the great longevity of these two species, it is likely that occasional openings in successionally mature stands may be regenerated with either of these species and they may remain as minor components of climax stands in spite of their intolerance (Sterns, 1951).

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