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Title: AGE STRUCTURE AND SPATIAL PATTERN OF OLD-GROWTH PONDEROSA PINE IN PRINGLE FALLS EXPERIMENTAL FOREST, CENTRAL OREGON

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The dynamics of stands in old-growth ponderosa pine (Pinus ponderosa) forests on the eastern flank of the central Oregon Cascades are investigated. Age structure and spatial pattern of ponderosa pine within the Pringle Falls Experimental Forest Research Natural Area coupled with the fire history of the area aid in interpreting stand development.

Two 1.0-ha permanent reference stands were established in the Pinus ponderosa/Purshia tridentata-Ceanothus velutinus/Stipa occidentalis community type. Age data were taken from 294 Pinus ponderosa and 223 Pinus contorta ≥10 cm dbh, and 98 Pinus ponderosa and 57 Pinus contorta <10 cm dbh. Spatial dispersion of trees within identifiable age cohorts was tested using Morisita's Index. The historical development of both stands since 1500 is examined using a chronosequence of the location of stems of known ages. Associations using chi-square tests are examined for the identified cohorts of both species.

Both reference stands are composed of three identifiable age cohorts. Comparison of the age data with a fire history of the Pringle Falls Experimental Forest indicates that periods of increased fire activity correspond to periods of decreased survivorship in both stands. Regeneration of Pinus ponderosa and Pinus contorta on both stands since the turn of the century, in the absence of fire, indicates that successful regeneration within these stands is not as dependent on fire-prepared mineral seedbed as is regeneration in pine stands in the Southwest.

Trees on both stands in all three cohorts occur in clumps ranging from 25-3500 $m^2$. Distribution within the clumps is aggregated as well, with small, usually even-aged clusters of trees being a common component of the larger aggregations.

Two scales of pattern are identified in both stands. High mortality during periods of increased fire activity produce long-term temporal and coarse-grained spatial patterns of the broad age cohorts. Fine-grained spatial and shorter temporal patterns result from contemporaneous reproduction in small areas. Chi-square associations indicate that the spatial and temporal patterns of the older cohorts have been maintained in the stands for the last 250 years. Fire exclusion has caused a deterioration in both types of patterns.

A fire regime that includes frequent (7-20 years) low-intensity burns must be introduced to these stands if the desired goal is to maintain patterns characteristic of the primeval forest. Furthermore, rare fires that are either larger or hotter must be periodically included in the fire regime if coarse-grained spatial and long-term temporal patterns are to be maintained.

# Age Structure and Spatial Pattern of Old-Growth Ponderosa Pine in Pringle Falls Experimental Forest, Central Oregon

by

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Typed by Tawny Blinn for Robert J. Morrow

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This thesis is dedicated to the memory of Marion Hobbs, a man unlike any other I have ever known. His strength was in his wisdom.

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# AGE STRUCTURE AND SPATIAL PATTERN OF OLD-GROWTH PONDEROSA PINE IN PRINGLE FALLS EXPERIMENTAL FOREST, CENTRAL OREGON

## INTRODUCTION

The age structure of a present population may mirror past population dynamics. For example, present age structure may reflect changes in recruitment and mortality (Hibbs 1979). Analysis of these kinds of changes utilizes survivorship curves, originally described by Deevey (1947). This analysis, which identifies age-specific events that alter rates of natality and mortality, have been discussed in detail by Jones (1945), Henry and Swan (1974), Goff and West (1975), and Hett and Loucks (1976). Discussions of natural history characteristics and disturbance histories and their relationship to age and size distributions have focused on many forest types: striped maple (Hibbs 1979), balsam fir and eastern hemlock (Hett and Loucks 1976), pin cherry (Marks 1974), Douglas-fir (Tesch 1981, Means 1981, 1982), spruce-fir (Hanley et al. 1975), lodgepole pine (Despain 1983), and mixed hardwoods (Schmelz and Lindsey 1965). Disturbances, such as hurricanes, insect infestations, logging, and grazing, have been investigated with respect to stand structure and age-size distributions. In western forests, fire is considered to be the major disturbance agent influencing stand dynamics.

## Age Structure Research in Western North American Ponderosa Pine Forests

Within western coniferous forests, many investigations have dealt with the determination of fire frequencies (Keen 1937, McBride and Laven 1976, Arno and Sneck 1977, Van Wagner 1978, Kilgore and Taylor 1979, Yarie 1981, Means 1982, McCune 1983, Arno and Petersen 1983) and have examined successional changes related to fire (Show and Kotok 1924, Johnson and Smathers 1976, Parsons and DeBennedetti 1979, McNeil and Zobel 1980, Bonnicksen and Stone 1981, Martin 1982, Means 1982, Mandany and West 1983). Investigations dealing with fire history and/or stand dynamics of ponderosa pine forests have been conducted throughout much of the species' range, including Arizona (Pearson 1923, Cooper 1960, 1961, Dieterich 1980, White 1985), California (Vale 1977, Kilgore and Taylor 1979, Martin and Johnson 1979, McBride and Jacobs 1980, Warner 1980), Colorado (Laven et al. 1980, Knowles and Grant 1983), Montana (Arno 1980, McCune 1983), and Utah (Mandany and West 1983).

Working in the pumice zone of central Oregon, Keen (1937) examined both climatic data and growth characteristics of ponderosa pine forests using tree-ring analysis. In a study of climatic cycles in eastern Oregon, Keen (1937) also described periods of high fire activity within the region. Weaver (1943, 1947, 1959, 1961), on occasion using tree-ring analysis, carried Keen's work further within central and southern Oregon pine forests, with studies of fire histories, particularly within the Warm Springs Indian Reservation. Weaver's dendrochronological sample sizes were small, however, and much of his work described in detail the compositional and structural changes of pine forests as a result of fire exclusion initiated near the turn of the century. In the same area, Soeriaatmadja (1966) calculated mean fire-return intervals within the ponderosa pine zone along a moisture gradient.

In the most comprehensive work to date dealing with ponderosa pine, Cooper (1960, 1961) not only described the natural history of ponderosa pine in the Southwest but thoroughly analyzed its age and size distributions. Results revealed an unbalanced age distribution characteristic of ponderosa pine forests in which distinguishable age cohorts are created by disturbance events followed by pulses of recruitment.

It has long been recognized that a conspicuous feature of ponderosa pine forests is the grouped arrangement of the trees. Early settlers encountering these forests provide vivid descriptions of pine forests composed of distinct tree groups, each consisting of a number of trees similar in size and apparent age. Although Weaver (1943) gave excellent structural descriptions of both mature and younger stands, Cooper (1960, 1961) was the first to critically examine and quantify structure of the groups and examine their mode of origin. Using the contiguous quadrat analysis proposed by Greig-Smith (1952), Cooper described stand structure in terms of spatial pattern and identified several scales of pattern typical of ponderosa pine forests of the Southwest. West (1964, 1969), working on the eastern flank of the central Oregon Cascades, quantified similar spatial patterns using both nested quadrat and distance analysis to compare structure of pine forests in the Pacific Northwest with those in Arizona. Similarities in pattern and scale were observed, even from areas having rather different fire regimes.

West (1964, 1969), however, collected only a limited amount of age-class data, the majority of which was restricted to reproduction-size classes. Cooper's (1960, 1961) mensurational analyses were conducted over fairly large areas utilizing age-size relationships requiring a fair amount of synecological stratification. Use of age-size correlations to determine tree age may introduce significant inaccuracies to age-structure analysis (Means 1982, Viers 1982, Stewart 1984). Within Crater Lake National Park, Mastrogiuseppe (1982) prepared age distributions for stands of ponderosa pine, also based on age-size correlations.

## Objective

The objective of the present study is to examine the structural characteristics of old-growth ponderosa pine forests within the Pringle Falls Experimental Forest in Deschutes National Forest, central Oregon. Detailed age distributions obtained by coring all trees $\geq$10 cm dbh on two 1.0-ha reference stands are used to test the hypothesis that old-growth ponderosa pine forests are composed of identifiable age cohorts. Although this characteristic has been described by Weaver (1943), Cooper (1960, 1961), West (1964, 1969), and Agee (1981), it has never been rigorously tested in the Pacific Northwest for mature age classes. A second hypothesis, that trees of similar ages in old-growth ponderosa pine forests are spatially clumped, is tested using large-scale computer-generated stem maps of the reference stands and Morisita's (1959) Index of Dispersion. Coupling accurate age structure and spatial patterns with the fire history of the Pringle Falls Experimental Forest prepared by Bork (1985) provides an opportunity to discuss many of the processes shaping the structure of pine forests in the region.

# STUDY AREA

Pinus ponderosa[1] occurs in extensive pure stands in 9 of the 15 physiographic and geologic provinces described by Franklin and Dyrness (1973). Pringle Falls Experimental Forest lies at the center of the western edge of the High Lava Plains Province in the Mount Mazama (Crater Lake) pumice zone in south-central Oregon (Franklin et al. 1972). These pumice-derived soils, in spite of low fertility, support fine stands of ponderosa pine (Hermann 1970). Although pure stands of ponderosa pine are found within the Lava Plains Province, lodgepole pine (Pinus contorta) is often a major associate within the Province.

The 470-ha Pringle Falls Research Natural Area (RNA), located in the Pringle Falls Experimental Forest in the Deschutes National Forest, was established in 1936 to preserve an example of the topographically related mosaic of lodgepole pine and ponderosa pine forests characteristic of the Mount Mazama pumice zone (Franklin et al. 1972).

The eastern block of the RNA containing the study sites is dominated by old-growth ponderosa pine (>250 years old) and characterized by a highly stratified multi-aged canopy composed of lodgepole and ponderosa pine. The subclimax status of ponderosa pine forests is maintained by fire on sites with enough moisture

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[1] Plant nomenclature follows Hitchcock and Cronquist, Flora of the Pacific Northwest, 1973.

to support more tolerant species such as Pinus contorta, Abies grandis, Abies concolor, and Pinus lambertiana (Fowells 1965, Martin et al. 1976, Minore 1979). A general successional sequence tied directly to frequent low-intensity fires promotes ponderosa pine regeneration, with lodgepole pine occurring as a persistent seral species (Martin 1982, Volland 1982).

The eastern block of the RNA is located on a gently undulating lava plain at the base of two basaltic cinder cones. Elevation of the study plots ranges between 1350-1370 m (Fig. 1).

Soils are predominantly an intergrade of Lapine and Shanahan series, Typic Cryorthents that developed in dacite pumice originating from the eruption of Mount Mazama, c. 6,500 years B.P., and Newberry Crater, c. 2000 B.P. (Barrett 1982). Pumice averages 83 cm deep and overlays sandy loam paleosols. Bedrock depth is 61-152 cm and is Pleistocene basaltic and basaltic andesite lava (Larsen 1976, Volland 1982).

A modified continental climate prevails. Climatic data from Wickiup Reservoir, 3 km west of the study site, indicate average annual precipitation of 520 mm, 85 percent of which falls between October 1 and April 30, primarily as snow. A snowpack occurs from January to March and often reaches 600 mm (Barrett 1982). Precipitation for June through August averages 58 mm and occurs primarily as high-intensity convectional storms. One- to three-month droughts are common during the summer months. Within the Pringle Falls area, mean annual temperatures are between 5.4-9.9°C, with the average July-August temperature between

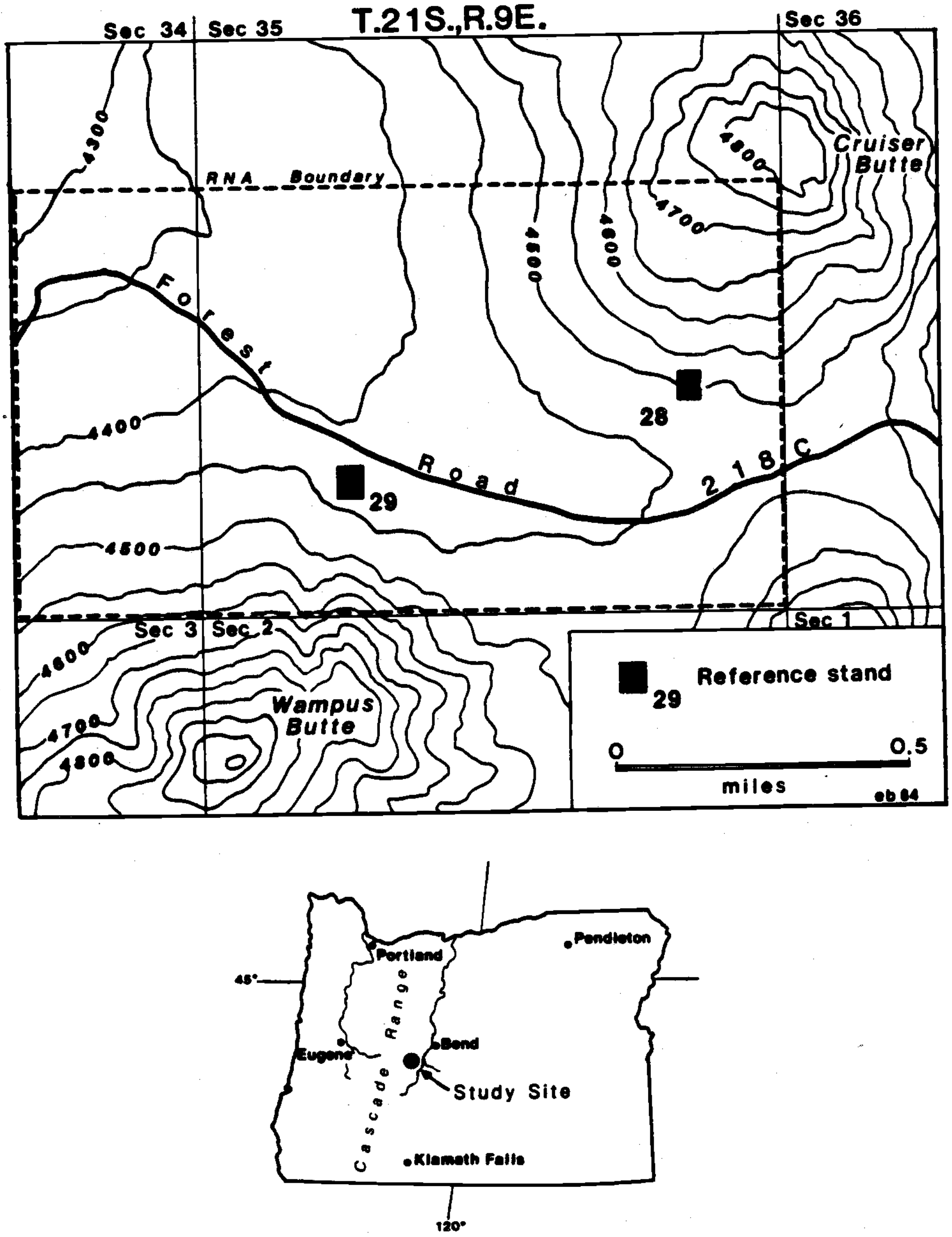

Figure 1. Study site with Reference Stands 28 and 29 located in the eastern block of the Research Natural Area, Pringle Falls Experimental Forest

16.7-20.9°C. Occasional frosts may occur throughout the year (Franklin et al. 1972, Hatton 1977, Barrett 1979).

The study area is dominated by ponderosa and lodgepole pine. Understory vegetation is mainly antelope bitterbrush (*Purshia tridentata*), snowbrush (*Ceanothus velutinus*), greenleaf manzanita (*Arctostaphylos patula*), and occasionally golden chinkapin (*Castanopsis chrysophylla*). Scattered Ross sedge (*Carex rossii*), broadpetal strawberry (*Fragaria virginiana platypetala*), squirreltail (*Sitanion hystrix*), western needlegrass (*Stipa occidentalis*, yarrow (*Achillea millefolium lanulosa*), and pinedrops (*Pterospora andromedea*) are the most common herbs. These forests are classified as ponderosa pine/bitterbrush-snowbrush/needlegrass community type (Volland 1982) or as ponderosa pine/snowbrush-bitterbrush community type (Franklin and Dyrness 1973).

Within the RNA, fire exclusion since ca. 1915 has been the major de facto perturbation. There is no record or physical evidence of salvage logging (Frewing and Barrett, 1983 personal communication). Limited transhumant grazing continued until 1961 but was excluded from Reference Stand 28 beginning in 1936.

# METHODS

## Stand Selection

Two stands were located in the Pringle Falls RNA to approximately coincide with the area of Bork's (1985) fire-history study permitting interpretation of age structures. Bork's study sites were located between 1-3 km to the northeast of the RNA. Stands were located within the RNA because it had been free from anthropogenic disturbances since its establishment in 1936. Evidence for the absence of disturbance is based on examination of archival material and discussion with Barrett and Frewing (1983 personal communication) at the Bend Silviculture Laboratory.

Location of permanent reference stands employed the following criteria:

- greater than 80 percent ponderosa pine in the canopy;
- a minimum of 75 old-growth (>250 years old) ponderosa pine per hectare;
- plant associations on each site as similar to each other as possible according to the associations described by Volland (1982);
- no evidence of major anthropogenic disturbances; and
- no evidence of major fires since 1910.

For the purpose of stand selection, a tree was determined to be "old-growth" based on: (1) diameter greater than 45 cm dbh (preliminary corings indicated trees this size were usually

>250 years old), (2) deep furrows between lighter colored bark plates, and (3) flat or rounded crowns (Keen 1943).

## Field Methods

One 1.0-ha (100x100 m) stand was established at two selected sites. Reference stand 28 (RS28) was created within a permanent sample plot originally surveyed in 1936. The 1936 plot was a 10-acre site that was fenced to ". . . furnish an ungrazed area in the nearly pure Ponderosa Pine Type for observing ecological changes and plant development under natural conditions" (Plot Survey Form 1936). Reference stand 29 (RS29) was situated 1 km to the southwest of RS28.

The reference stands were gridded to 25x25 m and 5x5 m cells using techniques described by Hawk et al. (1979). Iron rods were placed at all 25x25 m corners as permanent markers. All live stems ≥10 cm dbh were numerically tagged. Within each 5x5 m cell, all tagged individuals were mapped by species, measured for dbh, coded for vigor, classified according to bole and canopy conditions, and examined for evidence of disturbance using the methods of Hawk et al. (1979). Downed wood ≥10 cm dbh was also mapped. All live trees ≥10 cm dbh were increment cored to determine age (years determined by counting annual rings). Trees were cored as close to the ground as possible and height of coring from mineral soil was recorded. Cores were stored in the field in plastic straws according to a method described by Cole (1977). A correction factor was applied in the field to cores that missed tree center. The arc of an annual growth ring on the core was matched by a set of concentric arcs (spaced 1 mm apart) to estimate the shortest distance from the core to the pith. To determine the number of years missing between the core and the pith, this distance was multiplied by the mean number of annual rings per millimeter, calculated from the proximal 25 mm of core, and then added to the core count age. When the distance from the core to the pith was greater than 20 mm, the core was discarded and the tree cored again.

To obtain a measure of the number of years needed to reach core height, limited destructive sampling of seedlings (individuals < breast height (~144 cm)), subsaplings (individuals ≥ breast height but ≤ 5.5 cm dbh), and saplings (individuals > 5.5 cm dbh but < 10 cm dbh) was conducted. Disks of 65 ponderosa pine and 54 lodgepole pine were cut at heights of 3-113 cm above mineral soil. Individual trees were taken from both the center and edges of regeneration patches. Individuals that were not part of dense regeneration patches were also sampled. The location of the regeneration patches ranged from beneath canopy trees to areas without an overstory. Ring-age determined from the disks was later regressed against height to correct for the age of the trees at core-height.

The center four contiguous 25x25 m grid cells within the reference stands were chosen as regeneration subplots. These 0.25-ha (50x50 m) subplots were mapped by species for three size-classes, seedlings (<144 cm tall), subsaplings (≥144 cm but ≤5.5 cm dbh), and saplings (>5.5 cm dbh but <10 cm dbh). The percent cover of each shrub species was estimated to the nearest 5 percent for each 5x5 m grid cell. To improve the interpretation of the age distribution that was truncated by coring only stems ≥10 cm dbh, 155 randomly selected saplings and subsaplings of both species within the reproduction subplots were cored and ages determined.

## Laboratory and Analytical Methods

### Age and Size Structure

The cores were placed in wooden drying racks, air dried for several days, and then glued into the racks for lab analysis. Optimum clarity of annual growth rings was obtained by sanding the increment cores and disks with progressively finer grits on a belt sander. Rings on cores and disks were then counted twice under a binocular microscope.

To check for missing or false rings, a sample of increment cores of various ages was tested by cross-dating against the master chronology of the Pringle Falls Experimental Forest constructed by Bork (1985). The established synchroneity of annual rings for trees in the Experimental Forest was used to determine the accuracy of the core count ages obtained from stems on both reference stands (e.g., Stokes 1980). A subsample of cores <200 years old were in error by <1 percent. For older stems, the error was 2 percent. The total sample of increment cores was not cross-dated to correct for missing and false rings since I judged the small error from these sources would not materially affect the results of the study. Furthermore, Keen (1937) found that false rings were not very common in the Pringle Falls area.

Tree ages were corrected for time to grow to core height in the following manner. A linear regression of the age/height data collected from the destructive sampling disks yielded two equations: lodgepole pine age = 1.94 + .34 ht. ($n = 54$, $r^2 = .7518$, $P < 0.001$) and ponderosa pine age = 2.4 + .2744 ht. ($n = 65$, $r^2 = .8090$, $P < 0.001$). Log transformations of the data, lodgepole pine lnage = .921 ln x - .649 ($r^2 = .8500$, $P < 0.001$) and ponderosa pine lnage = .92 ln x - .812 ($r^2 = .8014$, $P < 0.001$), did not change the correction for years to grow to core height calculated by the linear regressions. Total tree age was determined by adding years to grow to core height to core age.

The age structure of the tree species in each stand was analyzed by preparing age-class histograms depicting the frequency of stems in 20-year age classes beginning at 20 years of age. Twenty year age classes were used to reveal broad patterns of age distribution that may be partially obscured by local events that influence fecundity, establishment, and survival in a single year (Ross et al. 1982). Within the 0.25-ha regeneration subplot of RS28, 67 ponderosa pine saplings were cored and ages determined.

The saplings displayed four age classes between 40-120 years. The percentage of the total number of cored saplings falling into each 20-year age class was then multiplied by the estimated total hectare density of saplings to provide a frequency of ages for stems <10 cm dbh. No seedling or subsapling ponderosa pine was cored within RS28. However, based upon the height/age correlation used to determine core-height age, the percentage of subsaplings within RS29 corresponding to age classes between 40-80 years of age, and ages of ponderosa pine regeneration elsewhere within the Pringle Falls Experimental Forest (5 cm dbh, 3.5 m tall equaling 40-80 years old) described by Barrett (1979), I estimated that the majority of the seedlings and subsaplings were <60 years of age. Within RS28, 18 sapling lodgepole pine were cored and four corresponding age classes, between 20-100 years, were determined. Nine subsapling and 22 sapling ponderosa pine fell into three age classes between 40-100 years of age within RS29. Eight lodgepole pine subsaplings corresponded to two age classes between 20-60 years of age, while 31 saplings fell into three age classes, 40-100 years of age. Thus the age distribution of both tree species represents trees of all size classes (Table 1).

The same analysis was used to determine size structure depicting frequency of stems in 5 cm dbh size classes beginning with seedlings. Size histograms and scattergrams of age versus size were prepared for both species and both reference stands.

Table 1. Number of subsaplings and saplings assigned to 20-year age classes based on a random sample of 155 cored stems taller than or equal to 144 cm and less than 10 cm dbh. Sample taken from 0.25-ha reproduction subplots in RS28 and RS29.

| | | | Stems cored | | | |
|---|---|---|---|---|---|---|
| Plot | Size class | Species | Age class (years) | Number cored | Percent of total cored | Total stems on 1.0-ha plot |
| RS28 | Saplings[1/] | <u>Pinus</u> <u>ponderosa</u> | 40-60 | 4 | 5.9 | 23 |
| | | | 60-80 | 42 | 62.6 | 246 |
| | | | 80-100 | 17 | 25.3 | 99 |
| | | | 100-120 | 4 | 5.9 | 23 |
| | | | All ages | 67 | 100.0 | 392 |
| | | <u>Pinus</u> <u>contorta</u> | 20-40 | 1 | 5.5 | 4 |
| | | | 40-60 | 10 | 55.5 | 44 |
| | | | 60-80 | 6 | 33.3 | 27 |
| | | | 80-100 | 1 | 5.5 | 4 |
| | | | All ages | 18 | 100.0 | 80 |
| RS29 | Saplings | <u>Pinus</u> <u>ponderosa</u> | 40-60 | 4 | 18.1 | 14 |
| | | | 60-80 | 16 | 72.7 | 58 |
| | | | 80-100 | 2 | 9.0 | 7 |
| | | | All ages | 22 | 100.0 | 79 |
| | | <u>Pinus</u> <u>contorta</u> | 40-60 | 15 | 48.3 | 54 |
| | | | 60-80 | 14 | 45.1 | 51 |
| | | | 80-100 | 2 | 6.4 | 7 |
| | | | All ages | 31 | 100.0 | 112 |
| RS29 | Sub-saplings | <u>Pinus</u> <u>ponderosa</u> | 40-60 | 3 | 33.3 | 503 |
| | | | 60-80 | 4 | 44.4 | 672 |
| | | | 80-100 | 2 | 22.2 | 336 |
| | | | All ages | 9 | 100.0 | 1512 |
| | | <u>Pinus</u> <u>contorta</u> | 20-40 | 2 | 25.0 | 115 |
| | | | 40-60 | 6 | 75.0 | 345 |
| | | | All ages | 8 | 100.0 | 460 |

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[1/] Saplings = >5.5 cm dbh but <10 cm dbh and subsaplings = $\geq$144 cm tall but $\leq$5.5 cm dbh.

## Spatial Structure

Computer cartography was used to generate various types of maps needed for data display and analysis. A Fortran program was prepared by Joseph Means of the U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, Corvallis, Oregon, that generated gridded stem maps of both reference stands drawn by species and size class. Throughout this paper, patterns of large or small scale will refer to patterns having a large or small extent. Scale is not to be interpreted geographically with respect to map scale.

To test the departure from a random spatial distribution for different age classes of both lodgepole and ponderosa pine, the data set was analyzed using the Morisita Index (1959), which is analogous to the nested quadrat technique described by Kershaw (1964) and Greig-Smith (1957). Such methodology not only provides information on the dispersion of individuals but also examines the size of the aggregations and the larger patterns that they produce (Bonnicksen and Stone 1981).

The Morisita Index of dispersion was used to examine spatial pattern for three age cohorts determined by the age distribution analysis. Morisita's Index ($I_\sigma$) is calculated as:

$$I_\sigma = q \sum_{i=1}^{q} n_i(n_i-1)/N(N-1)$$

where q = number of quadrats, $n_i$ = number of individuals of the species in the ith quadrat, and N = the total number of individuals in all quadrats. When $I_\sigma = 1.0$, the population is randomly dispersed. Random implies an independent distribution of individuals into quadrats with an equal probability of each individual occurring in any one quadrat. If the index value is >1.0, aggregation is implied. $I_\sigma$ values <1.0 imply an even distribution. The statistical significance of each $I_\sigma$ value >1.0 was tested by an F-test (Morisita 1959). If the number of sampled individuals is small (i.e., <20), $I_\sigma$ values become less reliable; therefore, $I_\sigma$ was computed only for the more abundant age classes of both tree species. $I_\sigma$ was calculated for quadrats of increasing size from 1x1 unit, where each unit was 5x5 m (25 $m^2$). The quadrat sizes analyzed were 25 $m^2$, 100 $m^2$, 225 $m^2$, 400 $m^2$, 625 $m^2$, and so on. For quadrats $\leq$ 10x10 units (2500 $m^2$), the original unit quadrats were grouped into perfect squares, thus avoiding fluctuations in $I_\sigma$ that may result from changes in the shape of the blocks of quadrats (Pielou 1977). Quadrat sizes of 3, 6, 7, 8, and 9 units as perfect squares are not divisible into a 100x100 m plot. In these cases, $I_\sigma$ was calculated from four replications in a manner allowing for coverage of the entire plot. $I_\sigma$ values are an average of the four replications. For quadrat sizes > 10x10 units, $I_\sigma$ was calculated from rectangles; 55x50 m, 60x50 m, 65x50 m, 70x50 m, and so on until two replications of 100x50 were performed (see Williamson 1975, Stewart 1984).

Morisita's Index was chosen for a number of reasons: it is independent of the mean density per quadrat; it does not predispose any type of contagious distribution; and it may give an indication of the intra-clump distribution as well as providing an estimate of clump size (Morisita 1959).

Dot maps of the point positions of trees within the three broad age cohorts by species were used to compare observable patterns with patterns detected by the Morisita Index. Associations between the various age cohorts and species were analyzed using a chi-squared test (Mueller-Dombois and Ellenberg 1974). Maps were drawn for the 20-year age classes depicting the chronological sequence of tree establishment throughout each stand.

# RESULTS AND DISCUSSION

## Stand Description

At the community level, both stands are floristically similar. However, subtle differences in site characteristics have shaped the composition, structure, and dynamics of both stands at the subcommunity level. Broad temporal disturbance histories, particularly fire, are similar for both reference stands. At a finer resolution, however, slight differences in fire regimes may be indicated by comparing both age and size distributions of the two major tree species and spatial patterns of those trees. Collectively, age and size distributions and the associated spatial patterns of stems on the landscape only offer a partial description of the many processes influencing the dynamics of ponderosa pine forests of central Oregon.

The relatively larger number of intermediate canopy class lodgepole pine in reference stand 29 is the major structural difference between the two reference stands (Tables 2 and 3). The high density of larger intermediate canopy class stems is consistent with the recognized role of lodgepole pine as a major seral component within the climax ponderosa pine type (Hansen 1942, Fowells 1965, Volland 1982). The presence of limited true fir regeneration (Abies grandis and Abies concolor) within RS29 and the greater compositional percentage of lodgepole pine suggest that RS29 is slightly more mesic than RS28. The limited number of

Table 2. (A) Stand composition by canopy class. (B) Size distribution of stems within the 50x50 m subplots; seedlings $<$144 cm tall, subsaplings $\geq$144 cm tall and $\leq$5.5 cm dbh, saplings 5.6-10.0 cm dbh.

(A)

REFERENCE STAND CANOPY[1]

| Tree species | Canopy class | | | |
|---|---|---|---|---|
| | Dominant | Co-dominant | Intermediate | Overtopped |
| Reference Stand 28 | | | | |
| <u>Pinus</u> <u>contorta</u> | | 5 | 45 | 16 |
| <u>Pinus</u> <u>ponderosa</u> | 16 | 46 | 67 | 31 |
| Reference Stand 29 | | | | |
| <u>Pinus</u> <u>contorta</u> | | 16 | 108 | 32 |
| <u>Pinus</u> <u>ponderosa</u> | 25 | 55 | 47 | 10 |

(B)

REFERENCE STAND REPRODUCTION SUBPLOTS[2]

| Tree species | Reproduction class | | |
|---|---|---|---|
| | Sapling | Subsapling | Seedling |
| Reference Stand 28 | | | |
| <u>Pinus</u> <u>contorta</u> | 20 | 59 | 108 |
| <u>Pinus</u> <u>ponderosa</u> | 98 | 935 | 875 |
| <u>Abies</u> <u>grandis/</u> <u>contorta</u> | | | 1 |
| Reference Stand 29 | | | |
| <u>Pinus</u> <u>contorta</u> | 28 | 115 | 600 |
| <u>Pinus</u> <u>ponderosa</u> | 20 | 378 | 1864 |
| <u>Pinus</u> <u>lambertiana</u> | 1 | 1 | 4 |
| <u>Abies</u> <u>grandis/</u> <u>contorta</u> | | 1 | 14 |

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[1] Numbers represent number of trees in 1.0 ha.

[2] Numbers represent number of trees in 0.25-ha, 50x50 m subplots.

Table 3. Characteristics of Reference Stands 28 and 29.

| Species | Trees/ha (≥10 cm dbh) | % species composition | Dominant and codominant stems |  |  | %cover |
|---|---|---|---|---|---|---|
|  |  |  | Number | % total stems | % total doms. and codoms. |  |
| STUDY PLOT RS28 |  |  |  |  |  |  |
| TREES |  |  |  |  |  |  |
| *Pinus ponderosa* | 159 | 70.4 | 62 | 27.4 | 92.5 |  |
| *Pinus contorta* | 67 | 29.6 | 5 | 2.2 | 7.4 |  |
| Total | 226 |  | 67 | 29.6 |  |  |
| SHRUBS |  |  |  |  |  |  |
| *Pursia tridentata* |  |  |  |  |  | 31.5 |
| *Ceanothus velutinus* |  |  |  |  |  | 4.4 |
| *Arctostaphylos patula* |  |  |  |  |  | 1.0 |
| STUDY PLOT RS29 |  |  |  |  |  |  |
| TREES |  |  |  |  |  |  |
| *Pinus ponderosa* | 135 | 45.9 | 80 | 27.2 | 83.3 |  |
| *Pinus contorta* | 156 | 53.0 | 16 | 5.4 | 16.6 |  |
| *Abies grandis/ Abies concolor* | 2 | t[1] |  |  |  |  |
| *Pinus lambertiana* | 1 | t |  |  |  |  |
| Total | 294 | 96 | 32.6 |  |  |  |
| SHRUBS |  |  |  |  |  |  |
| *Pursia tridentata* |  |  |  |  |  | 13.9 |
| *Ceanothus velutinus* |  |  |  |  |  | 3.6 |
| *Arctostaphylos patula* |  |  |  |  |  | t |
| *Castanopsis chrysophylla* |  |  |  |  |  | t |

[1] t = trace amount, <5%.

A. grandis and A. concolor following 60-80 years of fire exclusion indicates that succession to these species in the absence of fire will be very slow and may never be complete.

Although both stands have slope gradients of only 5 percent, RS29 located on the northern toe of Wampus Butte probably has a microclimate more favorable to lodgepole pine regeneration; including cooler soils, later spring and earlier fall frosts, and longer duration of snowpack (Minore 1979, Martin 1982). Similarly, being slightly more mesic, RS29 should have had less frequent and less extensive fires that may be evidenced in the age and size structures.

Although both stands are classified as a ponderosa pine/bitterbrush-snowbrush/needlegrass community type (Volland 1982), marked differences in the shrub composition and cover exist. RS28 has greater than twice the percent cover (grand mean) of Purshia tridentata than does RS29 (31.5 vs. 13.9%) (Table 3). This is most likely a result of topo-edaphic variables, primarily greater soil depth to a less permeable soil horizon within RS28, and the physiological characteristics of bitterbrush favoring this species on warmer, drier sites (Mastrogiuseppe 1982, Eddleman, 1985 personal communication). The paucity of snowbrush cover indicates that these sites are marginal for Ceanothus even within the ponderosa pine/bitterbrush-snowbrush/needlegrass association (Volland, 1984 personal communication).

The diameter distribution for both dominant tree species on RS28 and RS29 closely approaches the negative exponential (reverse-J) shape (Figs. 2-5), which is characteristic, although not indicative of an all-aged stand (Meyer 1952, Schmeltz and Lindsey 1965, Lorimer 1980, Means 1982).

Ross et al. (1982) stress that interpretation of population-forming processes based on diameter distribution requires that size is a reasonable estimate of age. Cooper's (1960) work with ponderosa pine forests in Arizona revealed a tremendous variation in diameter within any single age class, which prevented statistically fitting the data to linear or curvilinear regressions. Viers (1982), examining the dynamics of coastal redwood (Sequoia sempervirens) forests, suggested that linear regressions were unsatisfactory for the determination of age from diameter.

Figures 6 and 7 indicate diameter/age relationships for both pine species ($\geq$10 cm dbh) on RS28 and RS29. Although least square regressions resulted in relatively high $r^2$ values for ponderosa pine on both plots, and for lodgepole pine on RS28, these values provide insufficient information necessary for interpretation of age distribution and stand history.

Both Figures 6 and 7 indicate three distinct age cohorts for ponderosa pine and two lodgepole pine age cohorts. Diameter variance is high for both species in all but the youngest stems. When one examines all ages in RS28 and RS29, significant $r^2$ values are obtained. If the relationship between size/age is plotted for the specific cohorts, however, the relationship deteriorates. Within the youngest cohort, there is a very weak

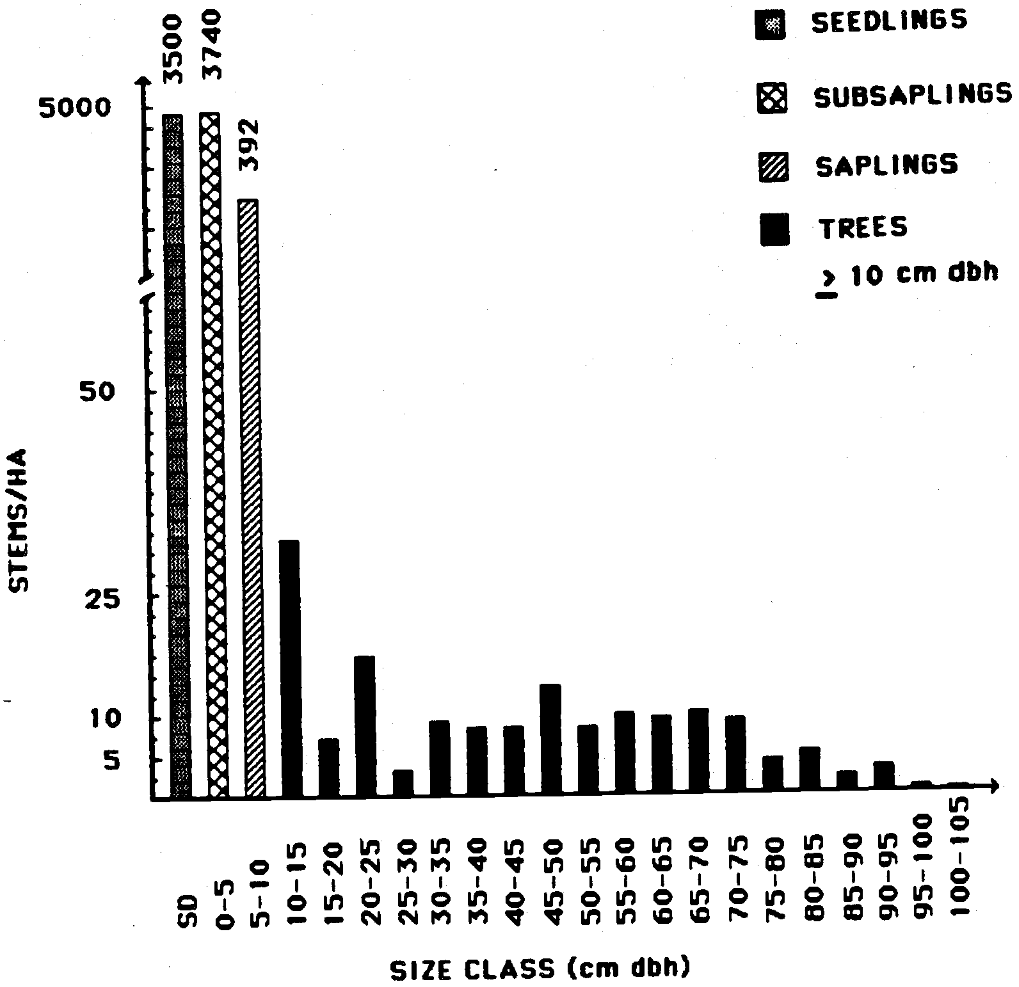

Figure 2. Size-class distribution of Pinus ponderosa in Reference Stand 28. Seedlings (SD)<144 cm tall, subsaplings≥ 144 cm tall and ≤5.5 cm dbh, saplings > 5.5 cm dbh but <10 cm dbh.

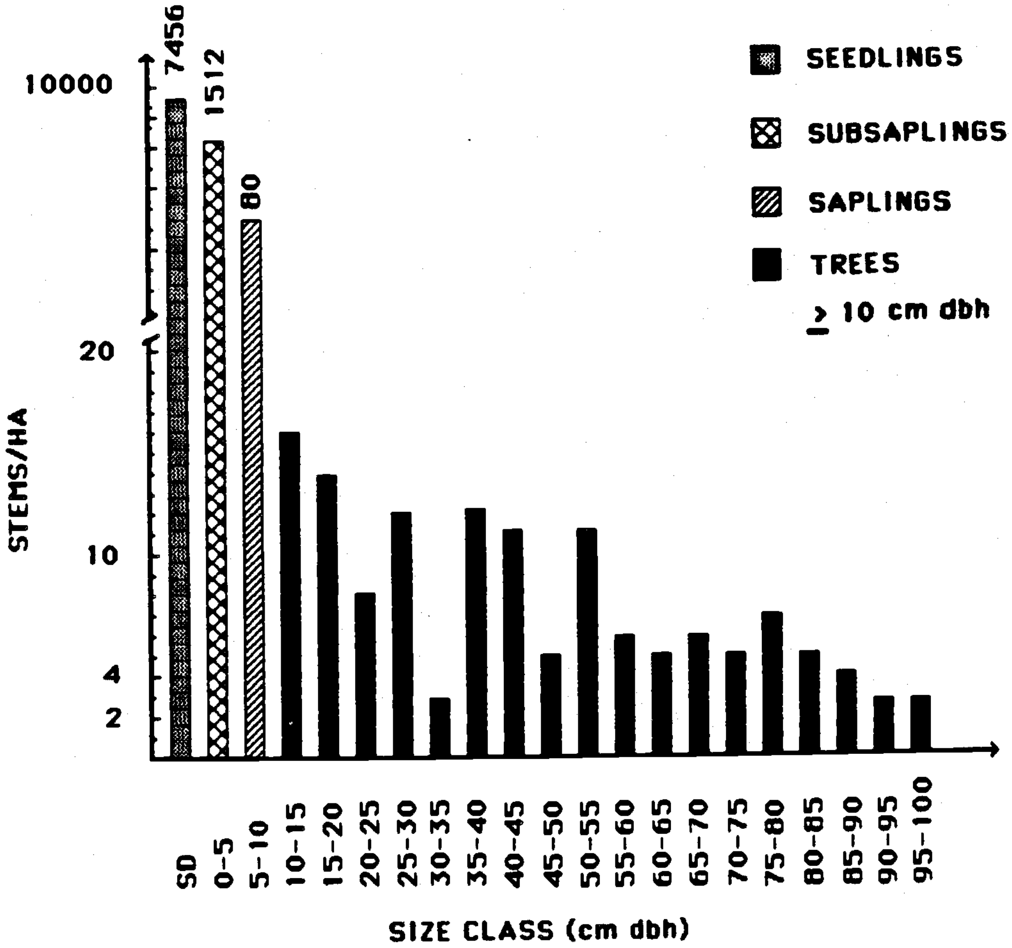

Figure 3. Size-class distribution of Pinus ponderosa in Reference Stand 29. Seedlings (SD) < 144 cm tall, subsaplings ≥ 144 cm tall and ≤ 5.5 cm dbh, saplings > 5.5 cm dbh but < 10 cm dbh.

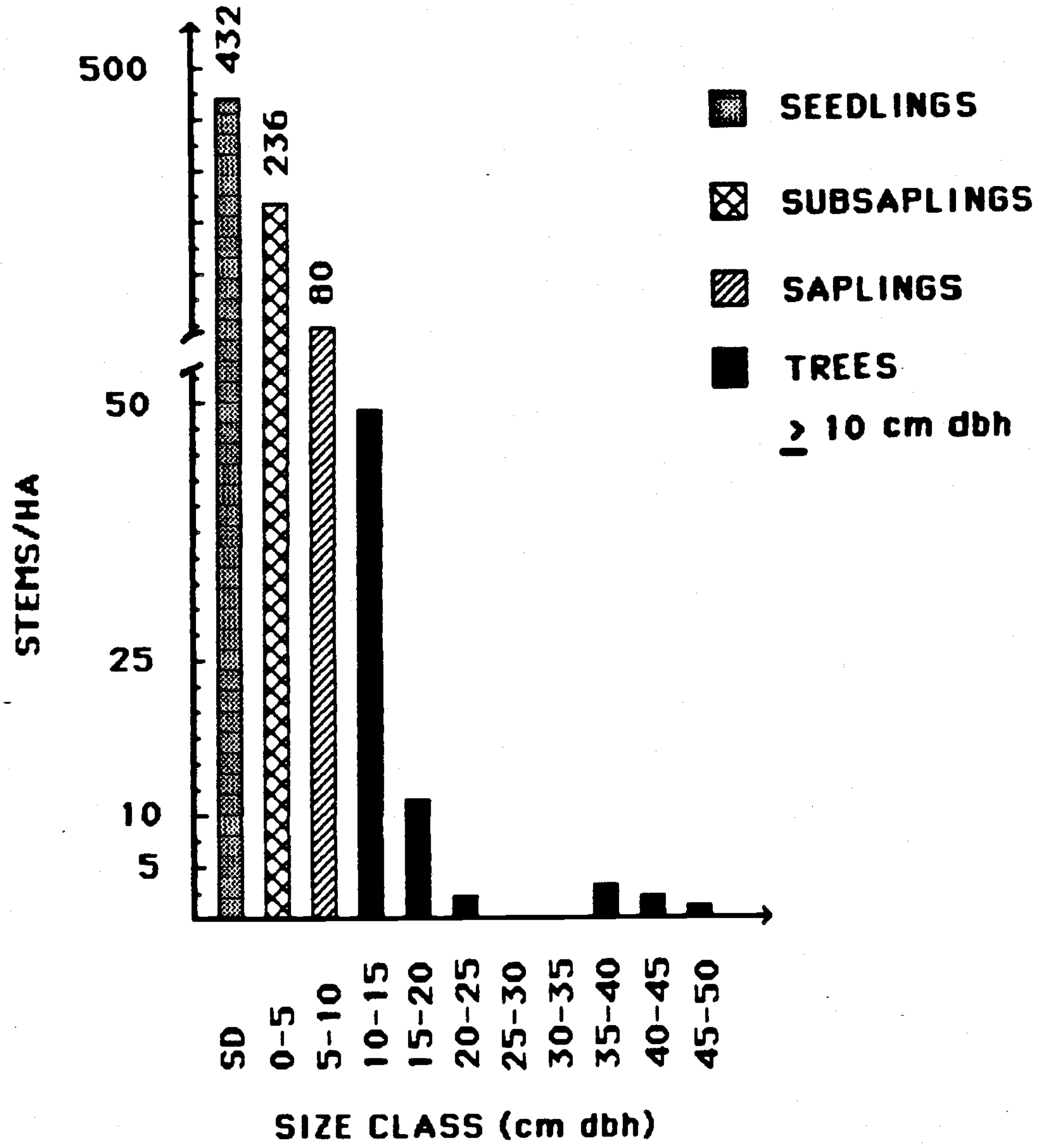

Figure 4. Size-class distribution of Pinus contorta in Reference Stand 28. Seedlings (SD) < 144 cm tall, subsaplings ≥ 144 cm tall and ≤ 5.5 cm dbh, saplings > 5.5 cm dbh but < 10 cm dbh.

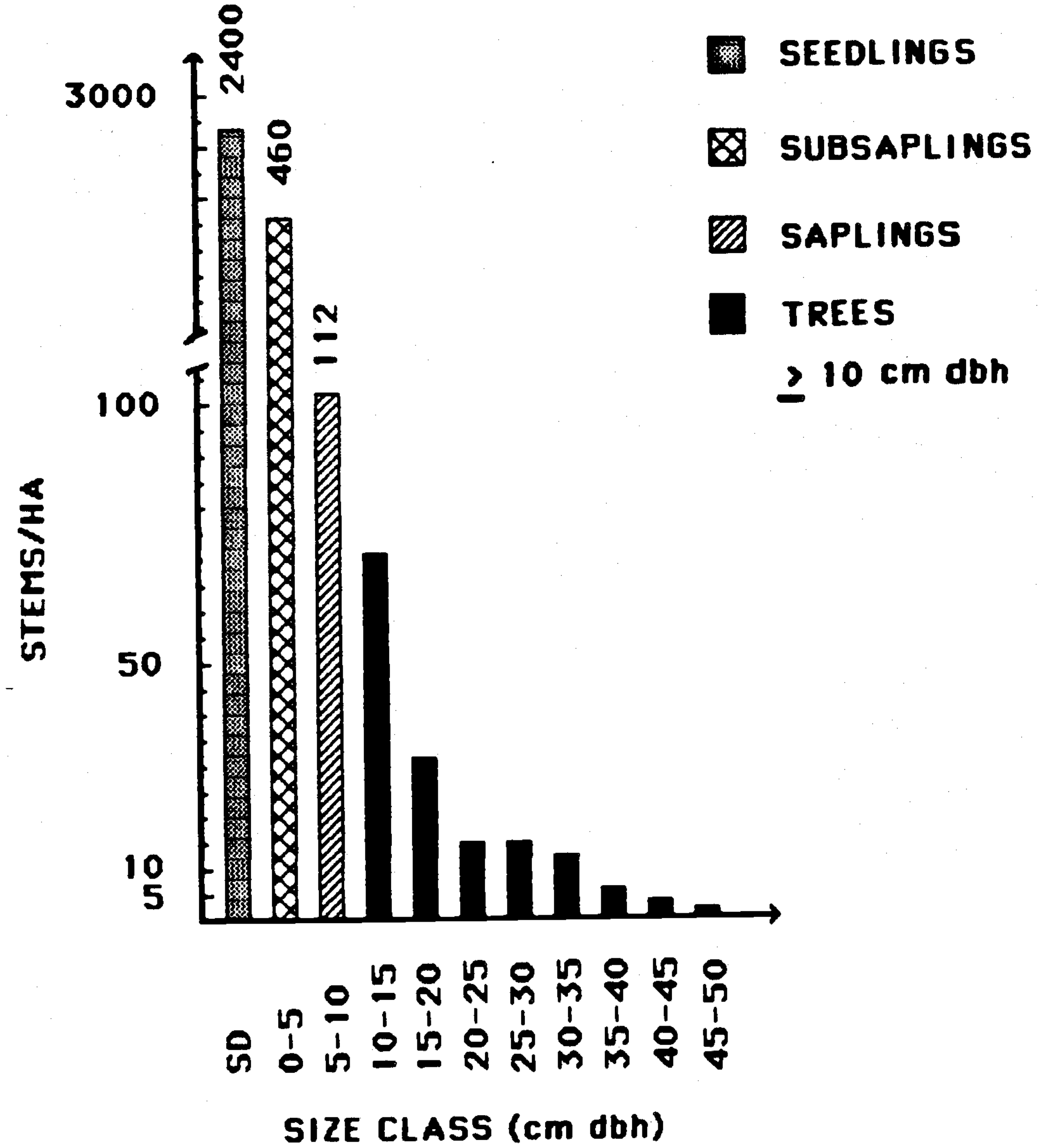

Figure 5. Size-class distribution of *Pinus contorta* in Reference Stand 29. Seedlings (SD) < 144 cm tall, subsaplings ≥ 144 cm tall and ≤ 5.5 cm dbh, saplings > 5.5 cm dbh but <10 cm dbh.

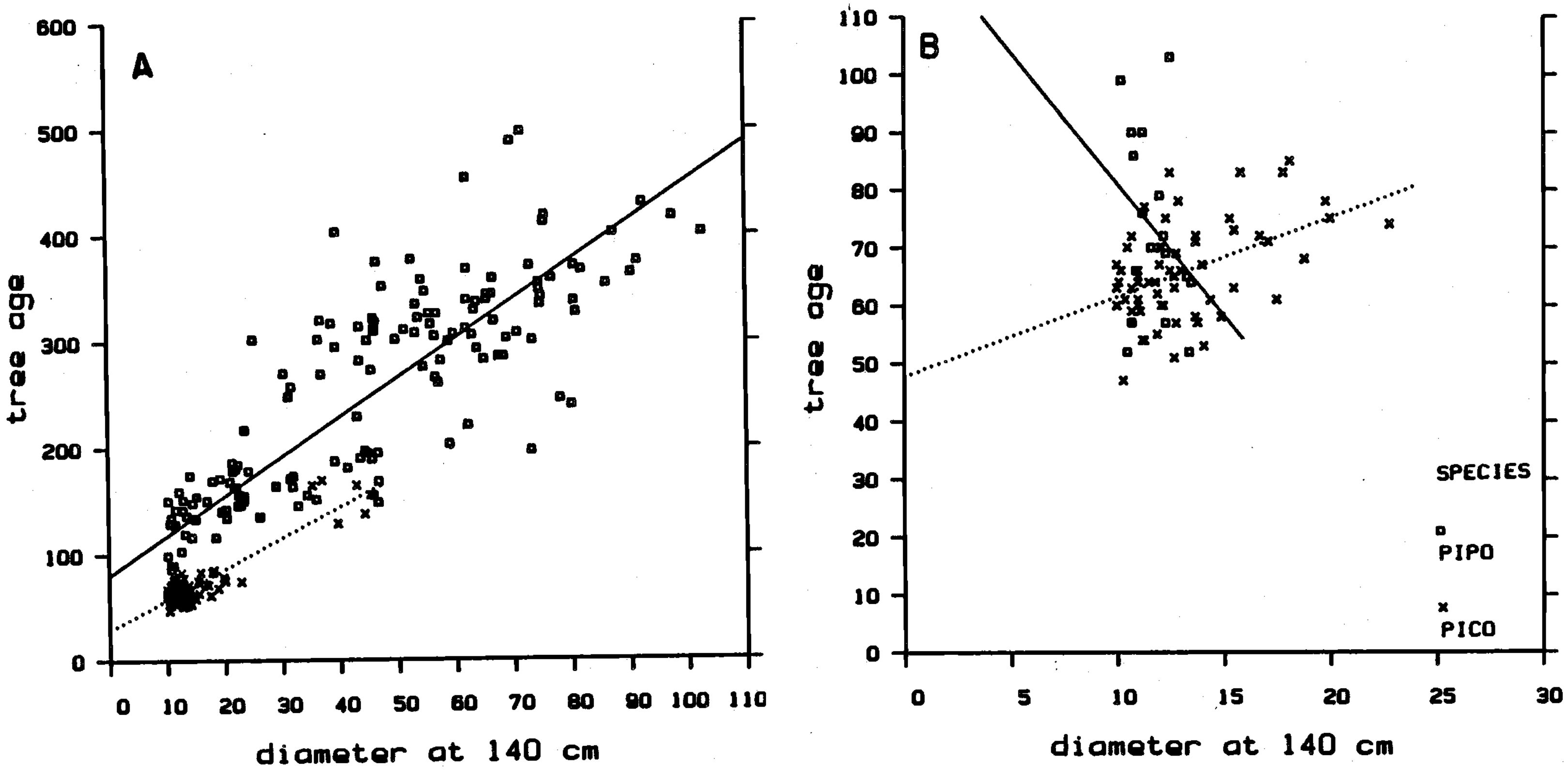

Figure 6. Age/diameter relationship of Pinus ponderosa (solid lines) and Pinus contorta (dotted lines) (≥10 cm dbh) in Reference Stand 28. (A) All trees in the reference stand. (B) Trees <110 years old. The equations were fit by a least squares linear regression. Pinus ponderosa of all ages: $y=3.71X+80.21$, $r^2=.7270$, Pinus contorta of all ages: $y=2.889X+28.45$, $r^2=.8413$, Pinus ponderosa <110 years old: $y=-4.55X+126.7$, $r^2=.094$, Pinus contorta <110 years old: $y=1.36X+47.84$, $r^2=.218$.

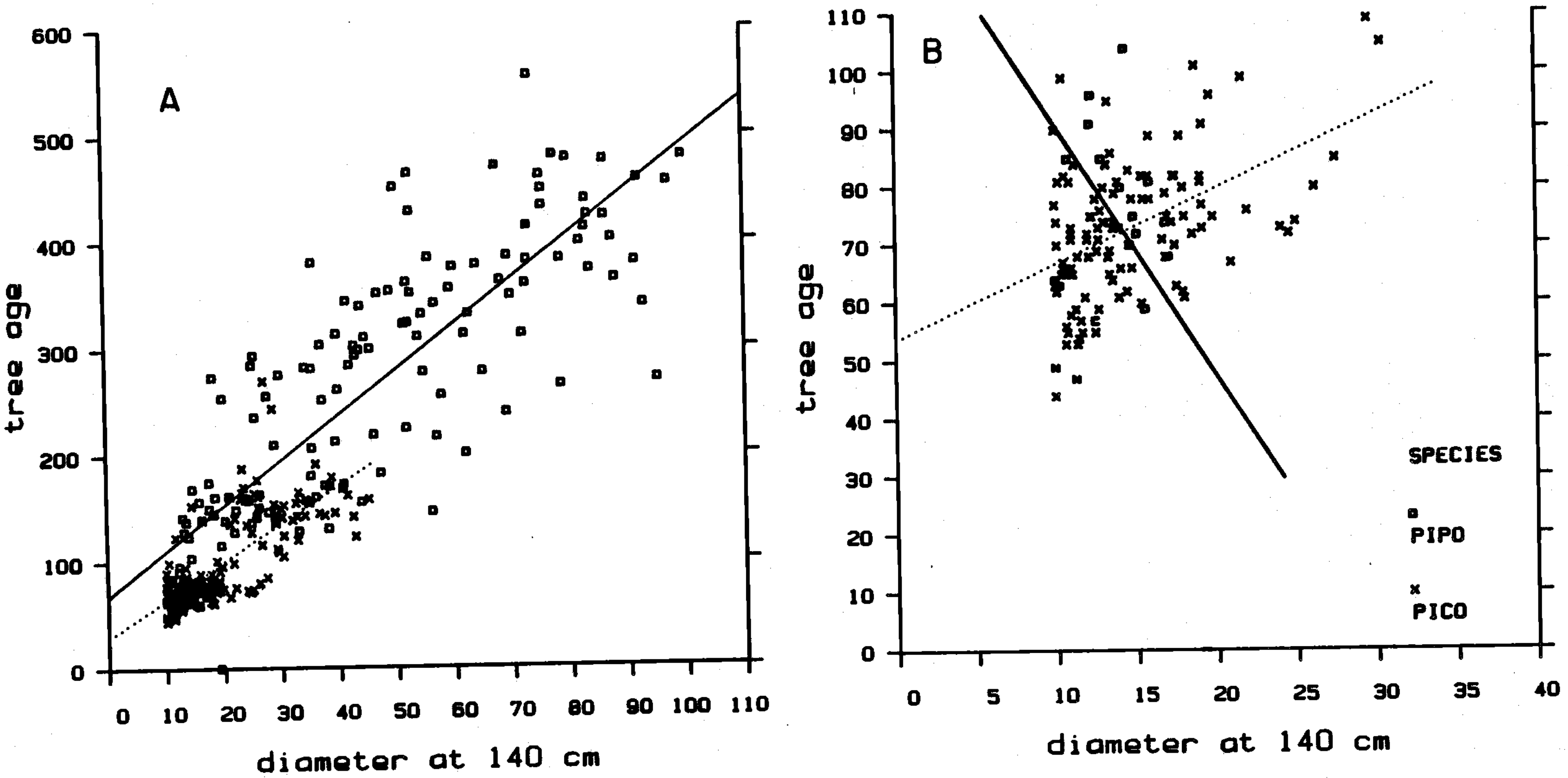

Figure 7. Age/diameter relationship of <u>Pinus</u> <u>ponderosa</u> (solid lines) and <u>Pinus</u> <u>contorta</u> (dotted lines) (≥10 cm dbh) in Reference Stand 29. (A) All trees in the reference stand. (B) Trees <110 years old. The equations were fit by a least squares linear regression. <u>Pinus</u> <u>ponderosa</u> of all ages: $y=4.24X+67.63$, $r^2=.695$, <u>Pinus</u> <u>contorta</u> of all ages: $y=3.55X+29.44$, $r^2=.552$, <u>Pinus</u> <u>ponderosa</u> <110 years old: $y=-4.32X+134.01$, $r^2=.238$, <u>Pinus</u> <u>contorta</u> <110 years old: $y=1.29X+53.88$, $r^2=.239$.

positive relationship for lodgepole pine and a weaker negative relationship for ponderosa pine. This suggested a lack of vigor for both species and stagnation occurring within the youngest age cohort.

## Age Distribution

### _Pinus_ _ponderosa_

Age-class distributions reveal patterns not obvious in the corresponding diameter distributions of ponderosa pine (Figs. 8-9). Ages of tree-size ponderosa pine within RS28 range from 54-489 years old and are represented in all 20-year age classes except the 380-400 and 460-480 year classes (Fig. 8). Within RS29, ages range from 47-556 years and are found in all age classes except 500-540 years (Fig. 9). Three distinct age cohorts, composed of several age classes, are observable on both study stands and are delimited by lower frequencies of tree ages on both stand histograms. The similarity in shape of the two histograms, although displaying differences in numbers of stems within certain age classes, suggests that the age distributions in individual stands are not unique. The age distributions reflect similar responses, though of varying degree, in natality and mortality to what appears to have been more than the characteristic low-intensity burns. Rather, the age distributions depict a response to the cumulative effect of several small

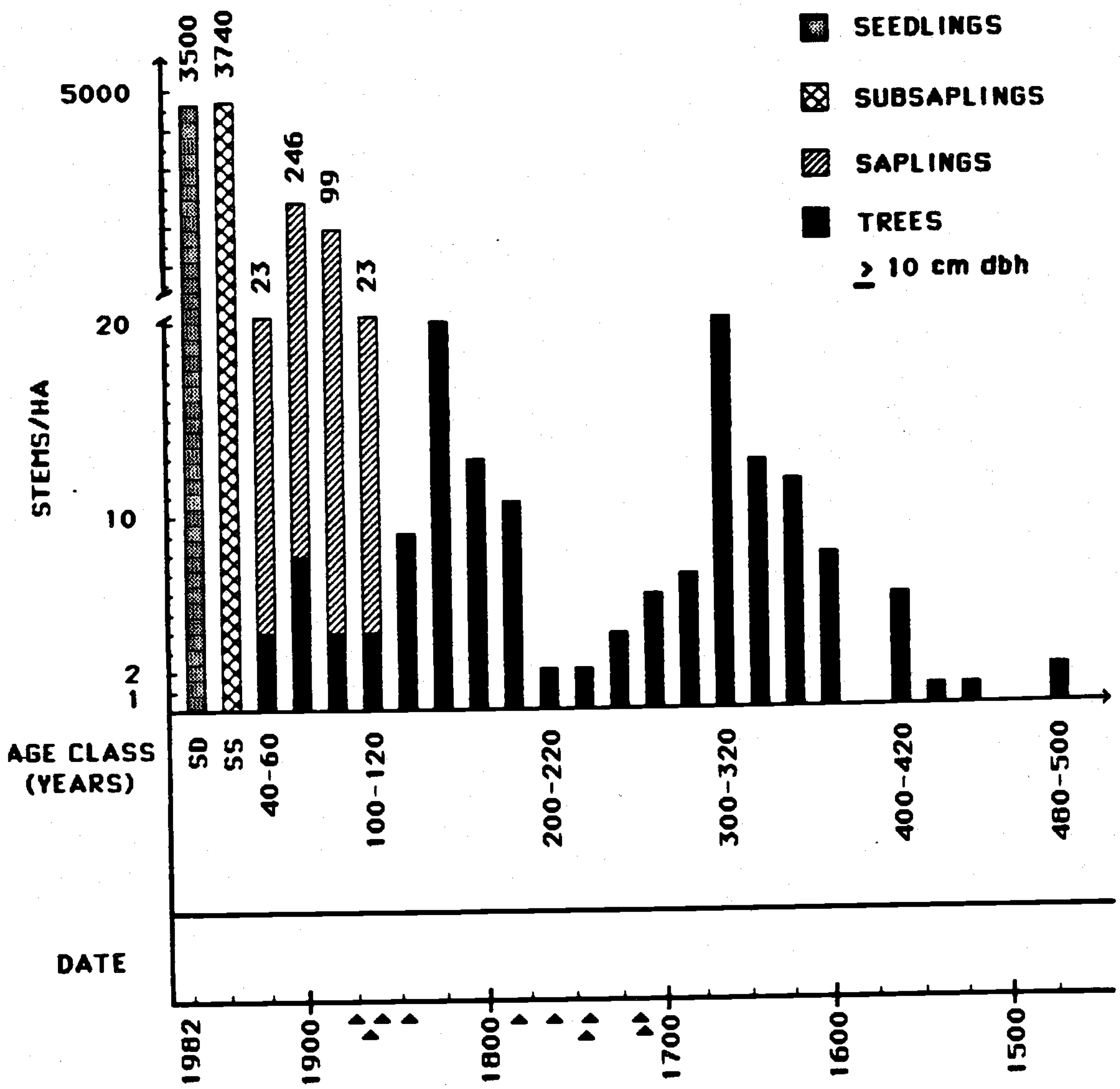

Figure 8. Age-class distribution of Pinus ponderosa in Reference Stand 28. X-axis also depicts probable fires (▲) identified by Bork (1985). Seedlings (SD) < 144 cm tall, subsaplings (SS) ≥ 144 cm tall and ≤ 5.5 cm dbh, saplings >5.5 cm dbh but < 10 cm dbh. Estimated number of seedlings, subsaplings, and saplings per hectare are calculated from the 0.25 ha reproduction subplot density. Frequencies listed above age class bars are the number of saplings in specific age classes.

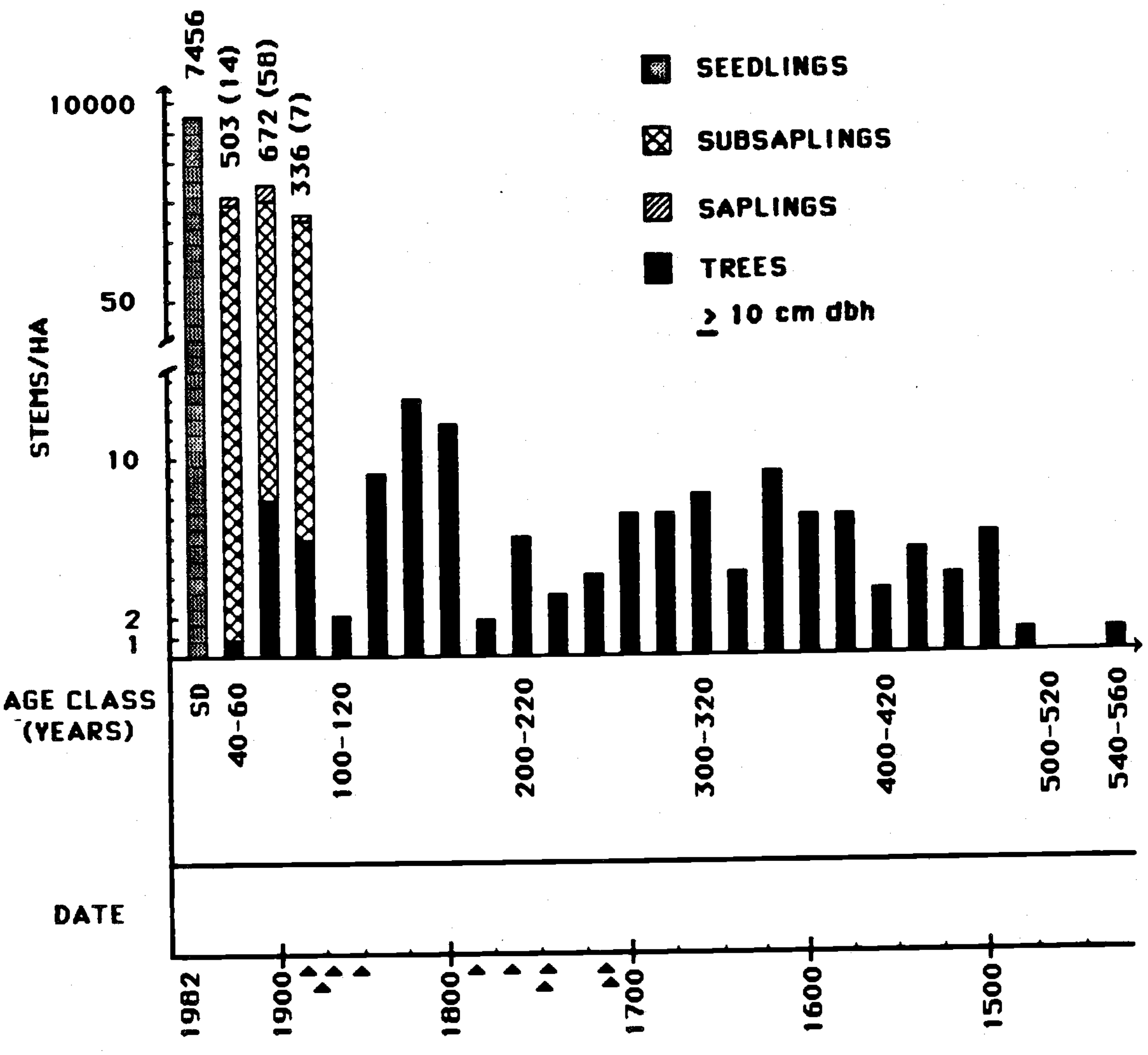

Figure 9. Age-class distribution of Pinus ponderosa in Reference Stand 29. X-axis also depicts probable fires (▲) identified by Bork (1985). Seedlings (SD) < 144 cm tall, subsaplings (SS) ≥ 144 cm tall and ≤ 5.5 cm dbh, saplings > 5.5 cm dbh but < 10 cm dbh. Estimated number of seedlings, subsaplings, and saplings per hectare are calculated from the 0.25 ha reproduction subplot density. Frequencies listed above age class bars are the number of subsaplings and (saplings) in specific age classes.

disturbances and to the variance in recruitment over a period of one or more decades. Age distributions prepared by Mastrogiuseppe (1982) for old-growth ponderosa pine in south-central Oregon also revealed three distinguishable age cohorts. The overall pattern of Mastrogiuseppe's histograms are quite similar to Figures 8-9, particularly during periods of decreased establishment, although the age ranges of some cohorts do not match exactly with the Pringle Falls data.

Within the age cohorts, corresponding age-class peaks occur on both Pringle Falls reference stands. The oldest cohort, or what may be a number of indistinguishable cohorts, established between 480 and 240 years ago within RS28 and between 560 and 240 years ago within RS29. This cohort includes the majority of the larger dominants on both stands and comprises 48 and 41 percent of the stems $\geq$10 cm dbh, RS28 and RS29, respectively. Within RS28 there is an increase in the number of stems that established between 300-320 years ago. Greater than one-quarter of the oldest cohort established during this single 20-year period. This establishment event is not as pronounced within RS29, where slightly increased frequencies beginning 380 years ago peak within the 340-360 year age class. The age distribution of RS29 suggests an older all-aged stand exhibiting changes in both mortality and natality and a gradual decrease in total stem density with age.

An intermediate cohort within RS28, established between 200 and 100 years ago, includes 36 percent of all stems $\geq$10 cm dbh. A maximum frequency occurs within the 140-160 year age class.

Within RS29 the intermediate cohort represents 25 percent of all stems ≥10 cm dbh, yet only spans 60 years, 120-180 years of age. In both study plots, the 140-160 year age class has the greatest number of trees, 38 percent of the cohort total.

Both plots have a younger cohort represented by trees ranging from 40-100 years of age, and with a peak at 60-80 years of age. RS28 has more than four times the number of saplings (5-10 cm dbh) than does RS29 (392 vs. 80), based on the reproductive subplot data. The majority of saplings in RS28 are older than 60 years, with 88 percent 60-80 years, and 27 saplings between 100 and 120 years old. Conversely, within RS29 the majority of the stems filling the youngest cohort age classes is subsaplings, showing a wide range in age (40-100 years) and indicates rather slow growth. No saplings or subsaplings in RS29 were found to be older than 100 years of age. The paucity of stems in the 100-120 year age class is common to much of the pumice zone of central Oregon and remains unexplained (Volland and Frewing, 1984 personal communication).

## Pinus contorta

Lodgepole pine, unlike ponderosa pine, has an age-distribution corresponding to its size distribution (Figs. 10 and 11). Within RS28, ages of tree-size lodgepole pine ranged from 37-164 years old, while within RS29, a limited number of older stems extend the age range from 35-244 years of age

(Fig. 10). Essentially all of the lodgepole pine found on RS28 originated since 1902, the majority of which are seedlings and subsaplings. An observable peak within this single cohort is formed by age classes 40-60 and 60-80 years. Of the stems ≥10 cm dbh within RS28, greater than 65 percent established between 80-60 years ago. Consideration of aged saplings increases the number of stems in this age-class peak but also shows a significant number of stems within the combined 40-60 year age class, indicating an establishment period lasting approximately 40 years.

Similar trends are observable within RS29 (Fig. 11); however, the greatest frequency peak occurs within the combined 40-60 year age class when the number of saplings and subsaplings are included. Since no dated subsaplings predate 1922 in RS29, it was assumed that the majority of those subsaplings in RS28 were 20-60 years old, although none were bored. Both stands show a marked decrease in saplings and subsaplings in the 20-40 year age class followed by a large number of undated seedlings. RS29 has greater than 5 times the number of seedlings per hectare than does RS28 (2398 vs. 431). More data is needed, especially the age distribution of the seedlings, to fully understand the response of this species in old-growth ponderosa pine forests free from fire for the last 60-70 years.

A second age cohort of 120-180 years occurs in both stands, although it is weakly represented in RS28. While RS28 has only 9 percent of stems ≥10 cm dbh older than 80 years, RS29 has

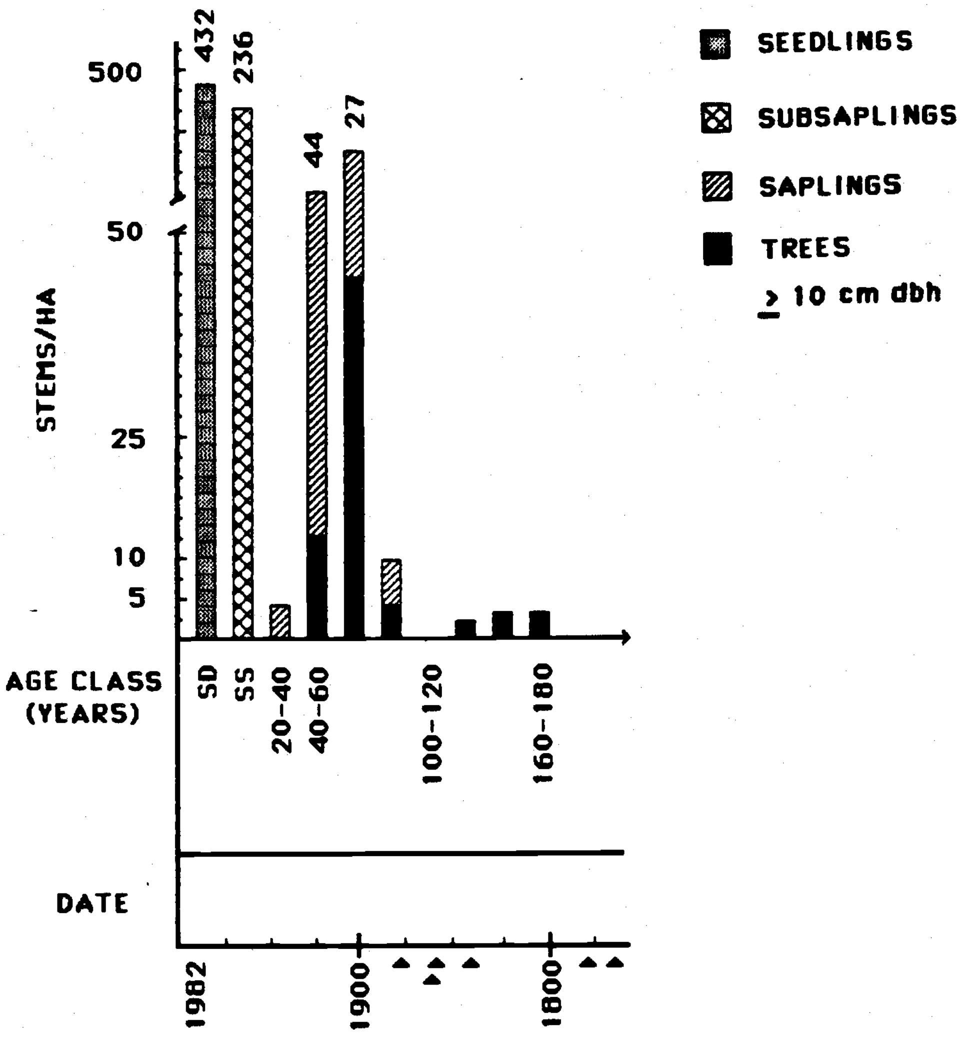

Figure 10. Age-class distribution of *Pinus contorta* in Reference Stand 28. X-axis also depicts probable fires (▲) identified by Bork (1985). Seedlings (SD) <144 cm tall, subsaplings (SS) ≥144 cm tall and ≤ 5.5 cm dbh, saplings >5.5 cm dbh but <10 cm dbh. Estimated number of seedlings, subsaplings, and saplings per hectare are calculated from the 0.25 ha reproduction subplot density. Frequencies listed above age class bars are the number of saplings in specific age classes.

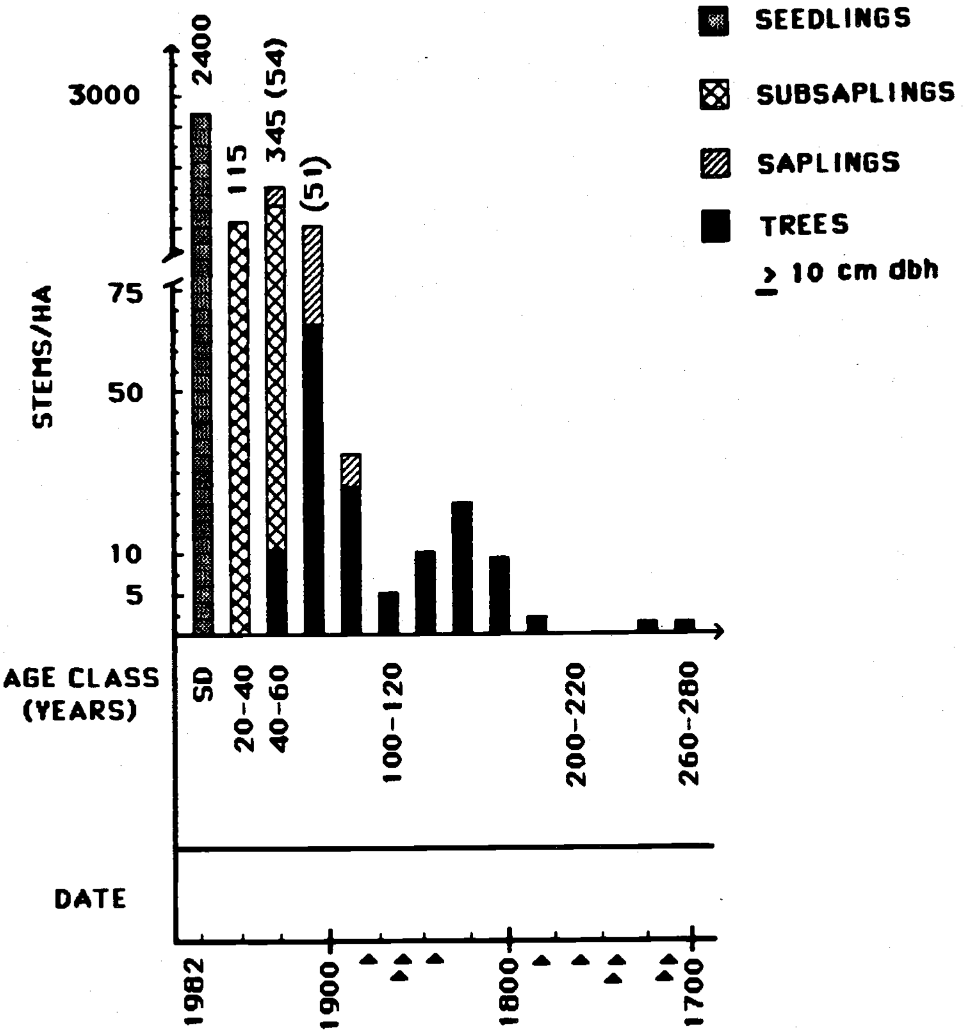

Figure 11. Age-class distribution of *Pinus contorta* in Reference Stand 29. X-axis also depicts probable fires (▲) identified by Bork (1985). Seedlings (SD) < 144 cm tall, subsaplings ≥144 cm tall and ≤5.5 cm dbh, saplings >5.5 cm dbh but <10 cm dbh. Estimated number of seedlings, subsaplings, and saplings per hectare are calculated from the 0.25 ha reproduction subplot density. Frequencies listed above age class bars are the number of saplings (in parentheses) and subsaplings in specific age classes.

50 percent of these stems in older age classes. Within the intermediate age cohort in RS29, 53 percent established in the 20-year period between 140-160 years ago. This intermediate lodgepole pine age cohort coincides with a similar ponderosa pine cohort common to both reference stands.

## Influence of Fire

It has long been recognized that fire plays a significant ecological role in the development and character of ponderosa pine forests throughout the species' range. Frequent low-intensity burns are an integral part of the natural fire regime (Weaver 1943, 1959, Barrett 1979, Laven et al. 1980, Agee 1981, Martin 1982, Warner 1980). Such fires controlled understory growth and prevented the accumulation of heavy fuel loads. Since the initiation of national fire suppression efforts ca. 1915, dense understories have developed in many ponderosa pine forests creating abnormally high fuel loads and often decreasing growth rates and vigor of understory pines (Weaver 1959).

Fire-history studies have been conducted throughout the range of ponderosa pine with the fire-return intervals exhibiting a wide range in years depending on site characteristics. Along the east side of the Oregon Cascades there are substantial ranges in fire-return intervals. Within the Warm Springs Indian Reservation of north-central Oregon, Weaver (1959) calculated mean fire-return intervals (MFRI) to be between 11 and 47 years, and

Soeriaatmadja (1966) identified fire-return intervals from 3-36 years. McNeil and Zobel (1980), examining fire-scarred ponderosa pine within the panhandle of Crater Lake National Park, measured intervals between 9 and 42 years. Bork's (1985) research in the Pringle Falls Experimental Forest indicated a MFRI of 7-20 years.

Arno and Peterson (1983) point out that as study areas become larger and the number of fire-scarred trees increases, the MFRI shortens. MFRI may be very different when averaged over large areas rather than calculated as the mean fire return at any one point on the ground (Bork 1985). Bork's data suggest that for the entire Pringle Butte site, fire burned some part of the forest an average of once every 4 years. The return of fire to the same 40-acre plot within the site averaged 11 years. Bork's MFRI of 7-20 years represents the range for six 40-acre plots within the site.

Ideally, cumulative fire-scar data and tree-age data should be collected simultaneously from the same study plots to insure accuracy of dating and in locating exact disturbance events. However, destructive sampling of fire-scarred trees is not allowed within the RNA. Nevertheless, several reasons suggest a MFRI (plot) of approximately 11 years is reasonable for interpretation of the calculated age distributions for RS28 and RS29. Bork's study plots were located in the same community type as RS28 and RS29. Based on Martin's (1982) u-shaped model describing the relationship between fuel, environment, and MFRI, basal area calculated for RS28 and RS29 support a MFRI of approximately 11 years. Bork (1985) satisfactorily tested the model using her calculated fire-return intervals and data collected from several ponderosa pine forests located on the east side of the Oregon Cascades.

Arno and Peterson (1983) point out that calculated MFRI may differ for sites and for plots within a site. All fires do not scar all trees within a plot and trees once scarred are more susceptible. Light surface fires may not scar any trees at all. Based on these variable characteristics, most investigators feel that the MFRI for particular sites is probably conservative (Bork 1985).

Figures 8-11 not only indicate age distributions for ponderosa and lodgepole pine but also illustrate periods of major fire activity within the Pringle Falls area. During the 19th century, fires occurred in 1842, 1865, 1866, and again in 1885. Based on the number of plots burned and the number of trees within a plot with dated scars, Bork hypothesized that these were most likely "smaller" fires, the largest fire being about 40 acres.

The 18th century appears to have been a period of high fire activity, with fires occurring in 1705, 1711, 1748, 1749, 1762, and 1788. This increased fire activity is evidenced by a greater number of stands burned and an increased number of trees within the stands having similarly dated scars. Within the 17th century, the fire chronology revealed limited numbers of trees scarred by fire, and this century is hypothesized to be a period of low fire activity, at least within the Pringle Falls area. Due to limited numbers of individuals within the >400-year age classes, and the difficulty of accurately dating scars of these older trees, many of which have heart rot, dating major fire years older than 400 years B.P. becomes less accurate (Bork 1985).

Examination of the age histograms (Figs. 8-11) that reveals specific age cohorts suggests that survivorship, especially influenced by increased mortality during periods of higher fire frequency and natality including periods of normal and poor recruitment, have shaped these curves. For approximately 100 years following 1550, both stands, especially RS28, experienced a period over which there was increased survivorship. Within RS28, periodic fires about every 7-20 years (Bork 1985) prepared seedbeds allowing for successful regeneration in sufficient numbers to insure an all-aged stand (Harper 1977). Within Bork's plots closest to RS28 and the RNA, ten fire-scarred trees became established between 1550-1560. Similarly, Mastrogiuseppe (1982), working in several old-growth ponderosa pine plots within Crater Lake National Park of south-central Oregon, identified "seedling recruitment periods" beginning in 1525 and lasting through 1625. However, it may be difficult to relate the Crater Lake study, 100 km south, to that of Pringle Falls except by similar regional climatic regimes.

The relationship between fire history and age distribution is the same in RS29 as in RS28, although not as pronounced. Both stands exhibit a maximum number of surviving stems occurring between 300-360 years ago.

The fire history of the area does not suggest that the latter half of the 17th century was a period of increased fire activity. However, chronologies by Bork (1985) and Keen (1937) for Pringle Falls indicate that this period may have been drier than normal.

Following a peak in establishment occurring between 300-320 years ago within RS28, a marked decrease in establishment took place. This decrease lasted roughly 150 years, from 1650-1790, and produced the trough separating the intermediate and old age cohorts (Figs. 8-9). Mastrogiuseppe (1982) indicated that following an age-class peak within the 1650-1700 period, establishment decreased steadily for the next 100 years.

This trough is the result of mortality within specific age classes and/or poor regeneration during this period. Generally, following fire, regeneration will increase as seed sources are available, suitable mineral seedbeds are present, and competition for moisture is minimal. Dahms and Barrett (1975) found that ponderosa pine within RS28 had only five good seed crops for a 22-year period between 1953-1974. Similarly, Cochran (1970) and Hermann (1970) suggest that in the Pacific Northwest successful age cohorts occur only if a good seed crop occurring in the late summer and early fall precedes a moist, mild spring followed by a wet, cool summer.

Laven et al. (1980), working with ponderosa pine forests of the central Rocky Mountains, found that successful seedling establishment was not strongly tied to the exposure of mineral seedbed attributable to fire. The high number of seedlings and subsaplings that have established on both Pringle Falls plots in the absence of fire and prepared seedbed supports this premise.

Although good seed crops occur only every 4-5 years for ponderosa pine within the Pringle Falls area, such a periodicity would insure adequate natality for the 20-year age classes of this study. The shape of the age distribution is due primarily to mortality of small trees that are preferentially killed by fire. The periods of increased fire activity coincide with the establishment troughs. Similarly, periods of increased establishment coincide with decreased fire activity.

If in the late 1600's, poor seed years and/or poor climatic conditions did not favor regeneration, and the greater fire activity during the 1700's increased mortality among seedlings and subsaplings, establishment during this period would be decreased. Cooper (1960) noted similar processes for ponderosa pine forests of Arizona, suggesting that the age and diameter structure of those forests were governed by the periodicity of seed production in combination with favorable weather conditions. Waves of reproduction coming at irregular and unpredictable intervals would result in a forest structure characterized by low frequencies within specific age classes.

Between 1790 and 1850, both stands show an increase in establishment, peaking between 140-160 years ago (Figs. 8-9). The increases were much more dramatic for RS28 than for RS29 and suggest that the more mesic environment of RS29 helps to ameliorate episodic events such as combinations of climate, fire, and seed production. Both stands, however, show a decline in the number of surviving stems during the increased fire activity of the late 1800's.

Following this fire activity, RS28 had a rapid increase in the number of stems within the 60-100 year age class. These are represented as saplings and poles <10 cm dbh. Normally, such a flush of regeneration would have been thinned by the recurring low-intensity fires; however, effective fire suppression beginning ca. 1915 allowed these dense thickets to develop. This created the situation that Weaver (1943), working in similar ponderosa pine forests of central Oregon, described as overstocked reproduction thickets resulting in stand stagnation.

The majority of the regeneration seen within RS29 occurs as seedlings and subsaplings. These subsaplings show a wide range in ages, 40-100 years, suggesting that many of these stems are very slow growing and do not show the more sensitive response that characterized regeneration in RS28. Certainly specific research is needed to examine the different growth rates exhibited by the two stands and the factors associated with such differences. Only when future studies examine ponderosa pine regeneration with respect to present stand structure (in the absence of repeated fire) can a full picture of the many processes that shape these stands be better understood.

The age distribution for lodgepole pine within RS28 (Fig. 10) indicates that very few of these stems predate the period of increased fire activity during the later half of the last century. Lodgepole pine is considered to be a prolific seeder (Minore 1979, Lotan and Perry 1983) with good seed years recorded in 9 of 16 years within RS28 (Dahms and Barrett 1975). The limited number of stems older than 100-120 years provided the seed source for the increase in lodgepole pine between 40-80 years of age. The dense regeneration by the more abundant ponderosa pine and a heavy shrub component has limited the present regeneration of lodgepole pine to relatively small numbers of seedlings and subsaplings localized in thickets.

Cooler soils, increased soil moisture, and northerly aspect have contributed to the higher density of lodgepole pine in RS29 (Fig. 11). This fire-sensitive species (Lotan and Perry 1983) exhibits two age cohorts in RS29. The oldest cohort, stems >110 years of age, shows a peak in establishment 160 years ago. As indicated by ponderosa pine age structure on both stands, the fires of the late 1800's greatly truncated lodgepole pine in this age cohort. No doubt, low-intensity fires killed a majority of any regenerating lodgepole pine during this period. Since active fire suppression, the species has shown a marked increase, primarily as 40-60 year old subsaplings. Dense seedling thickets of lodgepole pine can also be found within RS29.

## Other Disturbances

Periodic outbreaks of the mountain pine beetle (Dendroctonus ponderosae) are common to ponderosa and lodgepole pine forests of central Oregon, with outbreaks in 1920-1925, 1900-1905, and perhaps 1860 (Mitchell et al. 1983). Larsson et al. (1983) and Eaton (1941) describe the relationship between stocking levels, tree vigor, and stand susceptibility to beetle attack. Geiszler et al. (1980) put together a conceptual model on the interaction between fire, fungus, and the mountain pine beetle in lodgepole forests of south-central Oregon. The model implies a relationship in which beetle-killed trees increase normal fuel loads. Therefore, normal low-intensity fires become fires that not only kill reproduction thickets but also impact poles and overstory trees. These fire-weakened trees are prone to fungal infection and the stage is set for repeated beetle outbreaks occurring every 80-100 years.

There is only limited evidence within both stands of the characteristic scarring described by Mitchell et al. (1983) attributable to D. ponderosae. However, with the exclusion of fire, both stands may be approaching stocking rates in which tree vigor would begin to decline, increasing beetle attack susceptibility (Barrett 1979). The episodic occurrence and pattern of 100-year outbreaks described by Geiszler et al. (1980) fit the age distribution for both species, particularly lodgepole pine within RS29. More studies examining historical outbreaks within this region are needed to substantiate such a relationship. Still, such outbreaks resulting in increased fuel loading within these stands could have led to the increased mortality of not only the youngest age classes but older age classes as well. This could explain the rapid decrease in age-class survivorship seen between 280-300 and 120-140 years ago within RS28 for ponderosa pine and 120-140 years ago within RS29 for lodgepole pine (Figs. 8-9).

## Spatial Pattern

Law (1981), writing about the dynamics of a colonizing population of *Poa annua*, stated that "as a population is developing through time, it is simultaneously unfolding a pattern through space." Spatial pattern is an essential component of plant demography. Such patterns influence the temporal dynamics that are conditioned by reproductive characteristics, seed production, and survival rates of various aged stems responding to periodic disturbances. These temporal dynamics, in turn, mold spatial pattern (Law 1981). Because ponderosa pine forests are "shaped" demographically by repeated fires of variable intensity, knowledge of the spatial variability that results from and, in turn, influences the species' population and structural dynamics is essential.

Computer-generated stem maps, gridded with the smallest cell size used in Morisita's Index (5x5 m) are shown in Figures i and ii (Appendix). Downed wood $\geq$10 cm dbh is also shown. Trees of all species $\geq$10 cm dbh are drawn according to diameter class. From the digitized point locations of stems of known ages, maps of identified age cohorts for both ponderosa and lodgepole pine were drawn. (1:200 stem maps are on file at the U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon.)

Maps of the three age cohorts found in RS28 and RS29 show aggregations of similarly aged stems of both species throughout the stands (Figs. 12 and 14). Within RS28, distinct aggregations of lodgepole pine $\leq$110 years of age can be seen in the southwest 25x25 m grid cell (Fig. 12). Similarly, a concentration of young ponderosa and lodgepole pine occurs near the center of the stand. The center half of the stand (horizontal 50x100 m) is characterized by various sized aggregations of intermediate aged ponderosa pine and all the intermediate cohort lodgepole pine. Concentrations of dominant ponderosa pine within the oldest cohort, stems >240 years old, are visible around the perimeter of the reference stand (Fig. 12).

Use of Morisita's (1959) analysis of distributional patterns supports the observed clumping within RS28. Ponderosa pine $\geq$10 cm dbh and $\leq$110 years of age are contagiously distributed at quadrat sizes up to 2000 $m^2$ (Fig. 13A). The $I_\sigma$/quadrat size curve is shaped by small clusters of 4-5 trees. These clusters, found in the center and southwest corner of the plot, are in turn associated with the remaining number of young ponderosa pine and

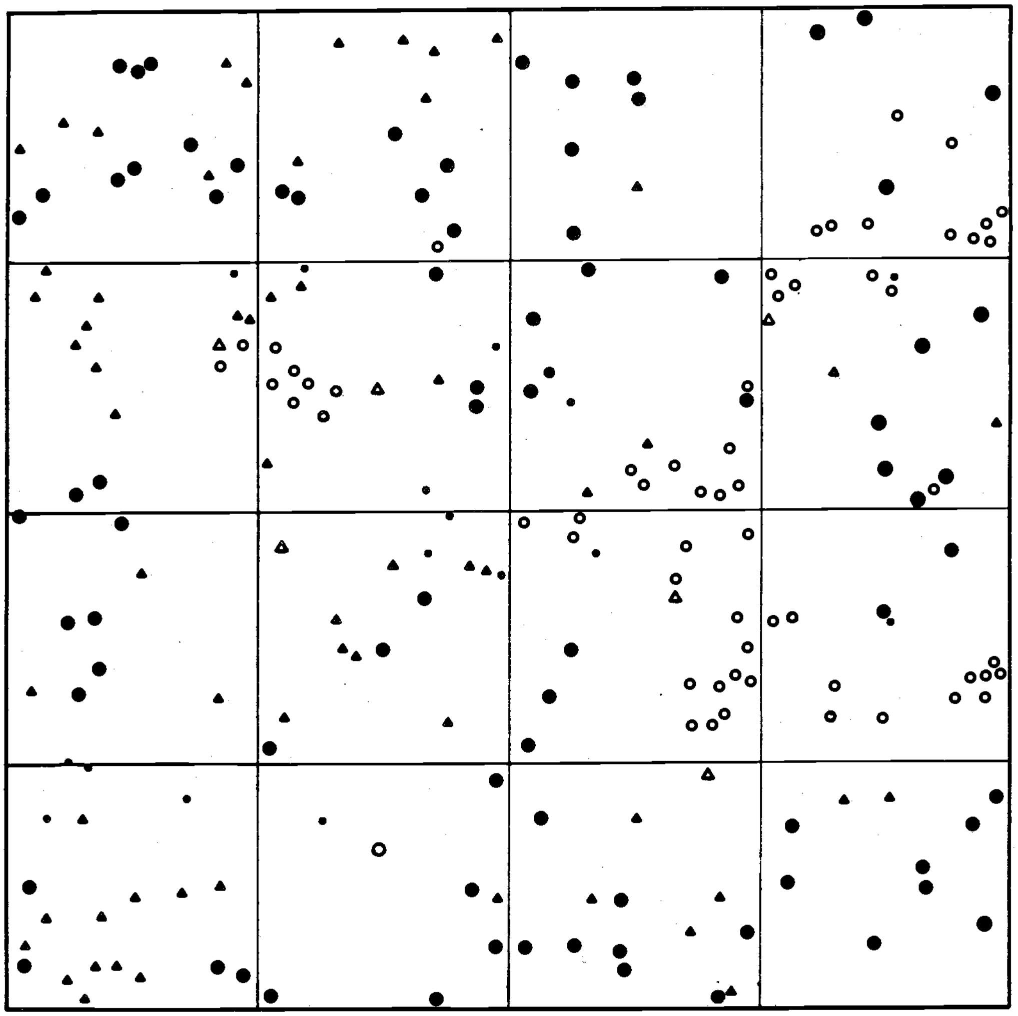

Figure 12. Stem map of the 1.0-ha Reference Stand 28. Shown are the locations of Pinus ponderosa and Pinus contorta falling into three age cohorts; oldest age cohort: >230 years old, intermediate age cohort:230-110 years old, and youngest age cohort:<110 years old. The age cohorts were identified in an age distribution analysis. The spatial distribution of the three age cohorts was tested by Morisita's Index.
(●) Pinus ponderosa >230 years old, (○) Pinus ponderosa 230-110 years old, (•) Pinus ponderosa <110 years old, (△) Pinus contorta 230-110 years old, (▲) Pinus contorta <110 years old.

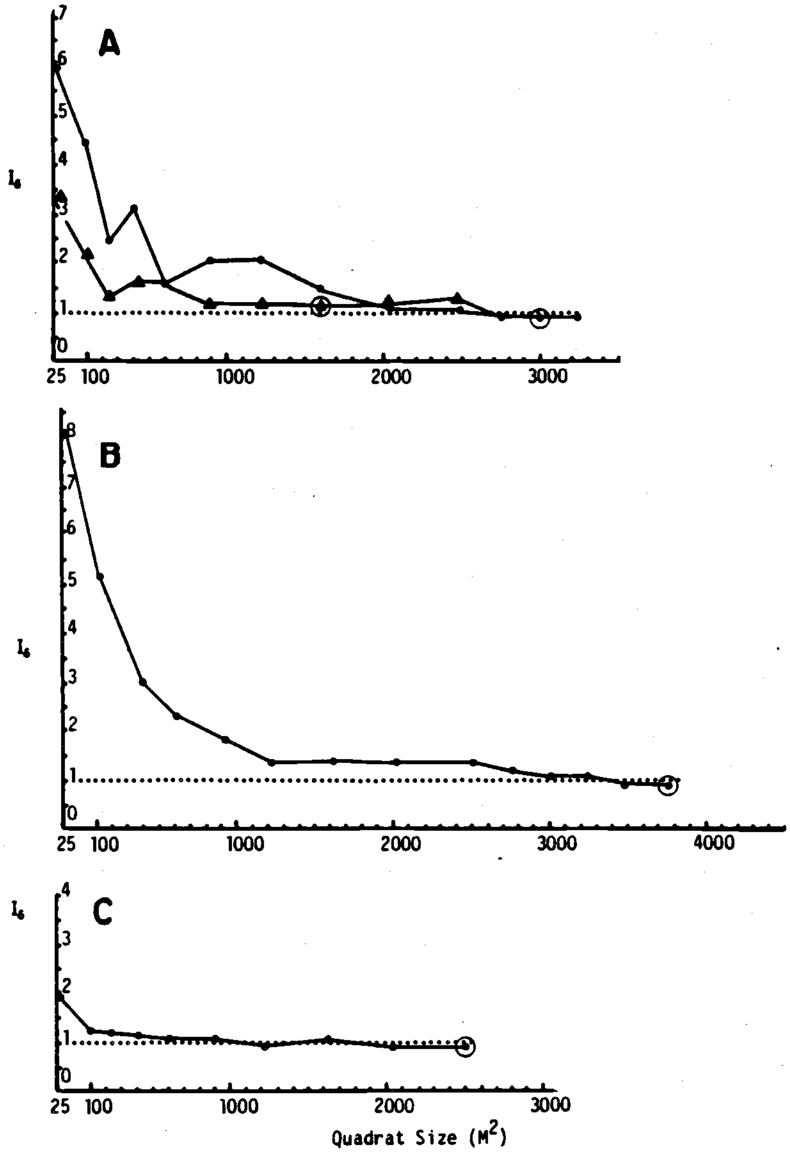

Figure 13. Values of Morisita's Index, $I_\delta$ , at different quadrat sizes for <u>Pinus ponderosa</u> (•) and <u>Pinus contorta</u> (▲) of three age cohorts within Reference Stand 28; $<110$ years old (A), 110-230 years old (B), and $>230$ years old (C). $I_\delta = 1.0$ represents a random distribution. $I_\delta$ values to the left of the encircled points are significantly greater than 1.0 ($\underline{P} < .05$) according to an F test of Morisita (1959).

together form two aggregations between 900-2000 $m^2$. Lodgepole pine shows a similar pattern for $I_\sigma$/quadrat size relationships. $I_\sigma$ values indicate contagion occurring up to 900 $m^2$ (Fig. 13A). The youngest age cohort lodgepole pine are essentially concentrated in the western half of the stand and can be found in small clusters of a few stems. These clusters form secondary aggregations between 900-325 $m^2$.

Intermediate aged cohort ponderosa pine exhibit contagion at the smallest quadrat size ($I_\sigma = 8.09$), with a steady decreasing value for quadrats up to and including 1225 $m^2$ (Fig. 13B). Concentrations of trees within this age cohort can be identified on the stem map and range from pairs of trees in a 25-$m^2$ quadrat to clusters covering 0.2 ha. Although statistically significant ($p > .05$), $I_\sigma$ values were obtained for larger quadrat sizes (1225 $m^2$-2500 $m^2$), a near random distribution is suggested at these larger quadrat sizes.

Contagious distribution is weaker ($I_\sigma = 1.85$) within the oldest age cohort and only occurs in the smallest quadrat sizes (Fig. 13C). Within this cohort, the oldest aggregations have decomposed into small clumps of trees or pairs of trees, randomly dispersed over the area. Although a limited number of old-growth pairs are located throughout the stand, distribution rapidly approaches random at quadrat sizes greater than 100 $m^2$.

Examination of the stem map drawn for the three age cohorts within RS29 (Fig. 14) reveals similar patterns. Ponderosa pine within the youngest age cohort can be seen concentrated in the

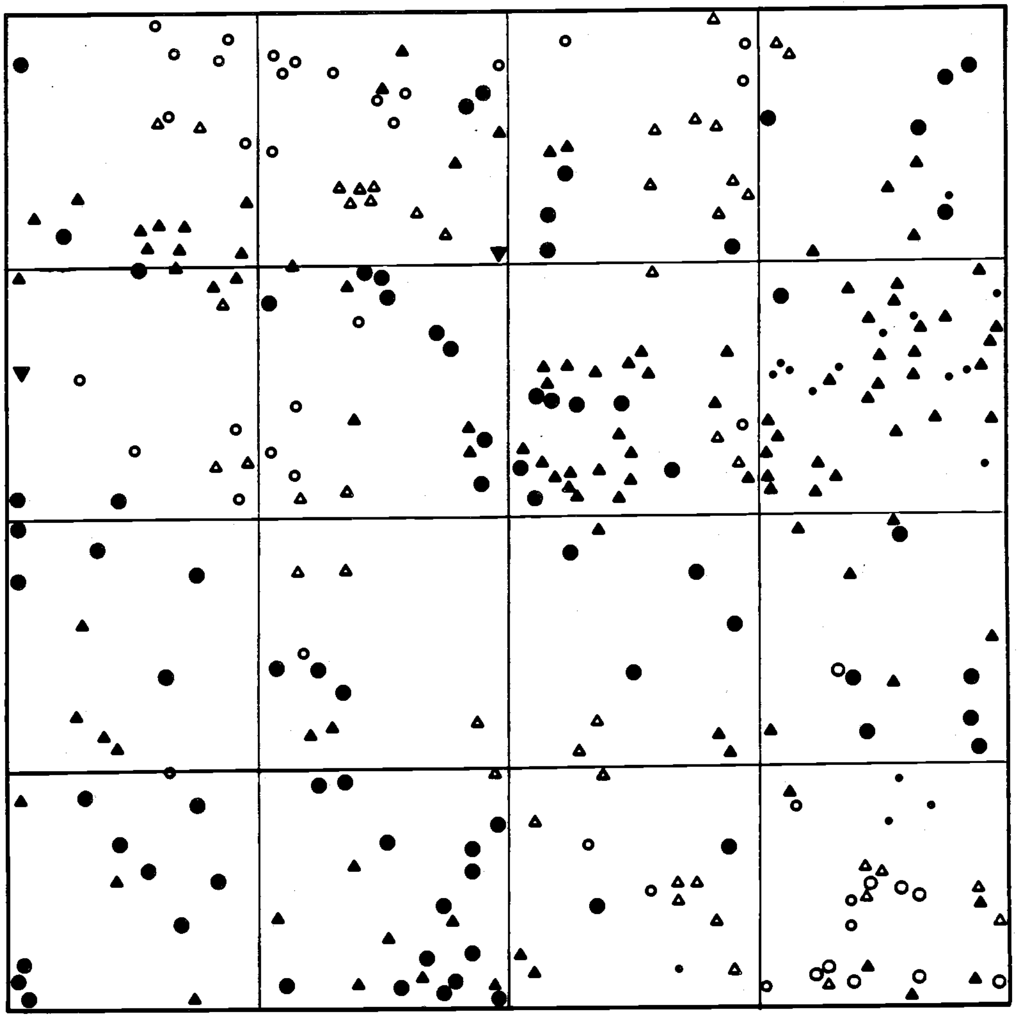

Figure 14. Stem map of the 1.0-ha Reference Stand 29. Shown are the locations of Pinus ponderosa and Pinus contorta falling into three age cohorts; oldest age cohort: >230 years old, intermediate age cohort: 230-110 years old, and youngest age cohort: <110 years old. The age cohorts were identified in an age distribution analysis. The spatial distribution of the three age cohorts was tested by Morisita's Index. (●) Pinus ponderosa >230 years old, (○) Pinus ponderosa 230-110 years old, (•) Pinus ponderosa <110 years old, (△) Pinus contorta 230-110 years old, (▲) Pinus contorta <110 years old.

northeast portion of the stand. Associated with these young ponderosa pine are aggregations of young cohort lodgepole pine that are primarily located in the upper 0.5 ha. Small clumps of young lodgepole pine can be found in the lower southwest quadrant as well.

Intermediate age ponderosa pine are concentrated with lodgepole pine of corresponding age classes in the northwest and southeast corners of the stand. Small clusters of trees within the oldest age cohort are scattered throughout the reference stand.

Similar $I_\sigma$/quadrat size relationships for RS29 as were found on RS28 indicate comparable spatial patterns for both stands. The youngest ponderosa pine ($\geq$10 cm dbh, $\leq$110 years) are strongly contagious ($I_\sigma = 13.3$) up to quadrat sizes of 1225 $m^2$ (Fig. 15A). Clumping of this age cohort occurs again at larger quadrat sizes between 1600 $m^2$–2500 $m^2$; however, these values reflect a rather small sample size (16), all but four of which are located in the upper 0.5 ha. The $I_\sigma$ values less than 1.0, indicating uniform distribution, are not statistically significant (F values, $p < .05$) and are the result of limited numbers of stems occurring in rectangular block sizes >2500 $m^2$ (see Pielou 1977, Bonnicksen and Stone 1981).

$I_\sigma$ values obtained for the youngest cohort lodgepole pine ($I_\sigma = 2.36$) indicate characteristics similar to those for ponderosa pine (Fig. 15A). Clumping of the youngest cohort is found through quadrat size 1225 $m^2$. Random distribution occurs

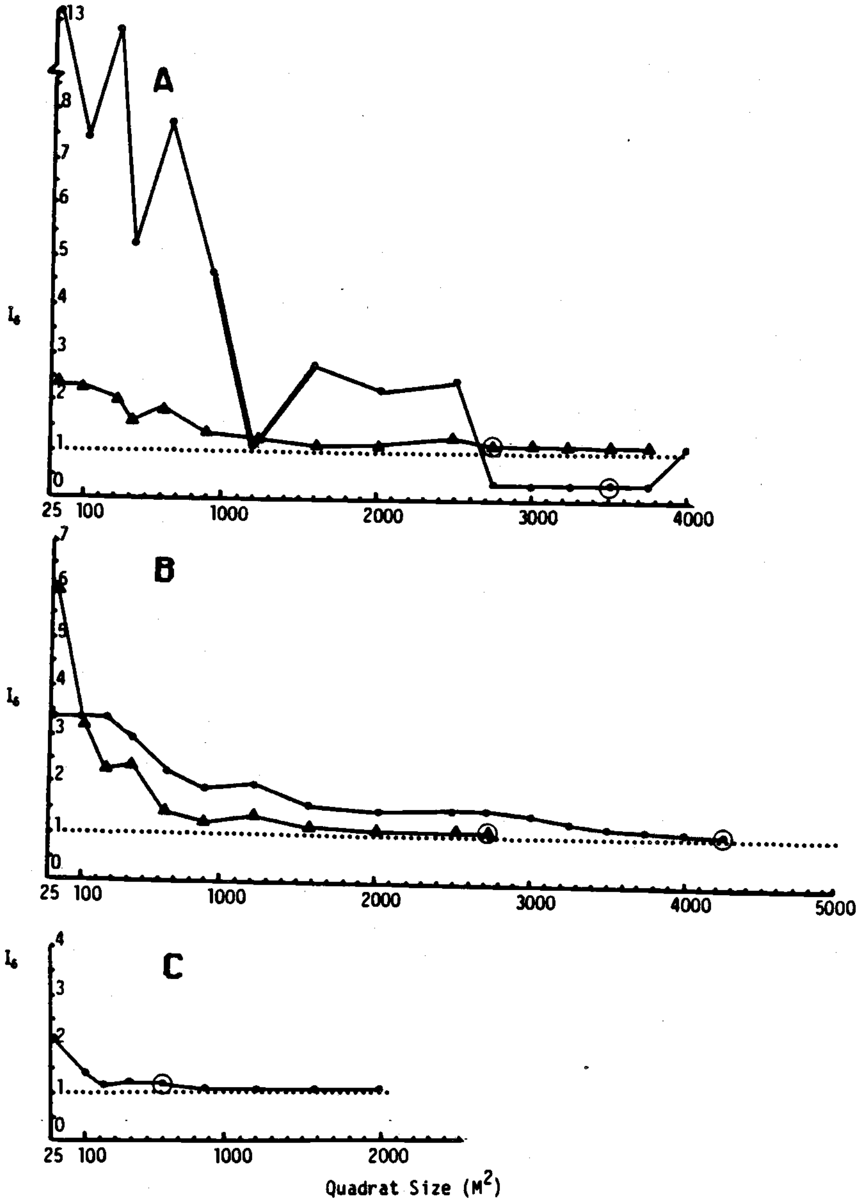

Figure 15. Values of Morisita's Index, $I_\sigma$ , at different quadrat sizes for *Pinus ponderosa* (•) and *Pinus contorta* (▲) of three age cohorts within Reference Stand 29; <110 years old (A), 110-230 years old (B), and >230 years old (C). $I_\sigma = 1.0$ represents a random distribution. $I_\sigma$ values to the left of the encircled points are significantly greater than 1.0 ($P < .05$) according to an F test of Morisita (1959).

at larger quadrat sizes. Intermediate cohort lodgepole pine have a greater $I_\sigma$ value (6.06) than do ponderosa pine ($I_\sigma$ = 3.38) of comparable ages and are strongly contagious up to quadrat size 800 $m^2$ (Fig. 15B). Small clusters of 2-3 trees combining with other clusters to form aggregations as large as 625 $m^2$ can be seen on the map, primarily in the upper 0.5 ha or lower righthand quadrant.

Intermediate aged ponderosa pine are clumped up to quadrat sizes approaching 1600 $m^2$ (Fig. 15B). At larger quadrat sizes slight aggregation is seen to approximately 3500 $m^2$. As was observed on RS28, small clusters of old-growth ponderosa pine (>230 years) are aggregated at quadrat sizes less than 100 $m^2$ (Fig. 15C). RS29 differs slightly from RS28 in that statistically significant $I_\sigma$ values were obtained for ponderosa pine in a 625-$m^2$ quadrat. This secondary aggregation can be seen on the map near the center of the stand and in the southwest quadrant (Fig. 14). Distribution of these oldest trees is random at larger quadrat sizes. Pielou (1974) stated that with random mortality, a population's patchiness will remain constant. If mortality is density dependent, however, and mortality is not random, contagion will exhibit a declining trend as time passes and the population decreases. Yeaton (1978), examining competition and spacing within white pine (<u>Pinus strobus</u>) communities, reported similar results. Intraspecific root competition resulted in aggregations of understory pines and a random distribution of canopy trees.

Both Cooper (1960, 1961) and West (1969) identified distinct scales of pattern that contribute to the complex spatial structure of ponderosa pine forest. The largest observable scale of pattern, that which results from vegetational response to physiographic variations, was not examined in this study.

On relatively uniform sites, ponderosa pine forests exhibit a second scale of pattern: the contagious distribution of trees of similar age. Cooper (1960, 1961) calculated the size of even-aged patches to be 647-1290 $m^2$. Reproduction thickets averaged 800 $m^2$ for old-growth pine stands. West's (1969) results identified a similar pattern but at a different scale; even-aged reproduction thickets averaged 2672 $m^2$ in size. Larger stems (>12 cm dbh) were distributed in patches 647-2600 $m^2$. West noted, however, that the reproduction thickets composed of relatively even-aged saplings formed the most conspicuous pattern and so dominated the data set that virtually no other pattern was visible. The size of the reproduction thickets corresponded to the size of a calculated elipse, the principal axis of which could be determined from the height of dominant overstory trees. West (1969) hypothesized that prevailing winds caused fire-killed or insect-killed trees to fall in an east-west direction. Once consumed by fire, an open, eliptical patch, 0.26 ha, could be created. Reproduction thickets were not measured within RS28 or RS29. However, no thickets of this size or shape were observed within the 0.25-ha reproduction subplots in which three size classes (seedlings, subsaplings, saplings) were mapped.

The finest scale of pattern deals with the distribution of individual trees within an age cohort aggregation. This intraclump distribution within RS28 tends toward contagious dispersion for all age cohorts and both species up to quadrats of 2750 $m^2$ (Fig. 13). Small clumps occur within larger clumps. Steadily decreasing $I_\sigma$ values result from loss of detection of smaller clumps at larger quadrat sizes. Within RS29, only the youngest age cohort of lodgepole pine and intermediate age cohort of ponderosa pine differ from the contagious intraclump distribution. Stems within these cohorts tend toward a random intraclump distribution up to quadrat sizes of 2750 $m^2$ (Fig. 15).

These results are contrary to those found by White (1985) in his study of pattern in southwestern ponderosa pine forests. Although trees $\geq$106 years were aggregated within stands, White found no evidence to indicate that groups were composed of smaller aggregations having a more homogeneous age structure. Spatial distribution within a group tended toward a random pattern. West (1969) and Cooper (1960, 1961) reported random intraclump dispersion, but suggested that as cohort aggregations matured, increased competition for available soil moisture and mineral elements resulted in a slight tendency toward a more uniform spacing within the aggregations.

## Temporal Spatial Pattern

Watt (1947) in his description of plant community development identified a dynamic mosaic of aggregation shifting through space and time. The aggregations of different aged individuals of the climax vegetation form a vast patchwork of distinct phases dynamically related to one another (Cooper 1960). The pattern in ponderosa pine is the result of a cyclical process of community development shaped by the reproductive biology of the species and fire (Cooper 1960, Kershaw 1963).

Figures 16 and 17 provide a pictorial model of the space-time mosaic created by the chronological sequence of stem establishment within each 20-year age class. Each block represents the 1.0 ha reference stand. The establishment location of all the stems of known ages ($\geq$10 cm dbh) are shown for 20-year periods beginning 500 years B.P.

There is a clear relationship between the three age cohorts and establishment location in RS28 (Fig. 16). Survivorship peaks delineated in the age histograms that occurred between 360-300 years ago are composed of stems that concentrated in both the upper and lower third of the stand. Regeneration within the center of the stand was prevented from reaching sizes able to withstand repeated fires or were destroyed by the fires early in the 1700's. As was suggested by Bork (1985), the 17th century may have been a period of drought, in which case intraspecific root competition from neighboring overstory trees would also exclude

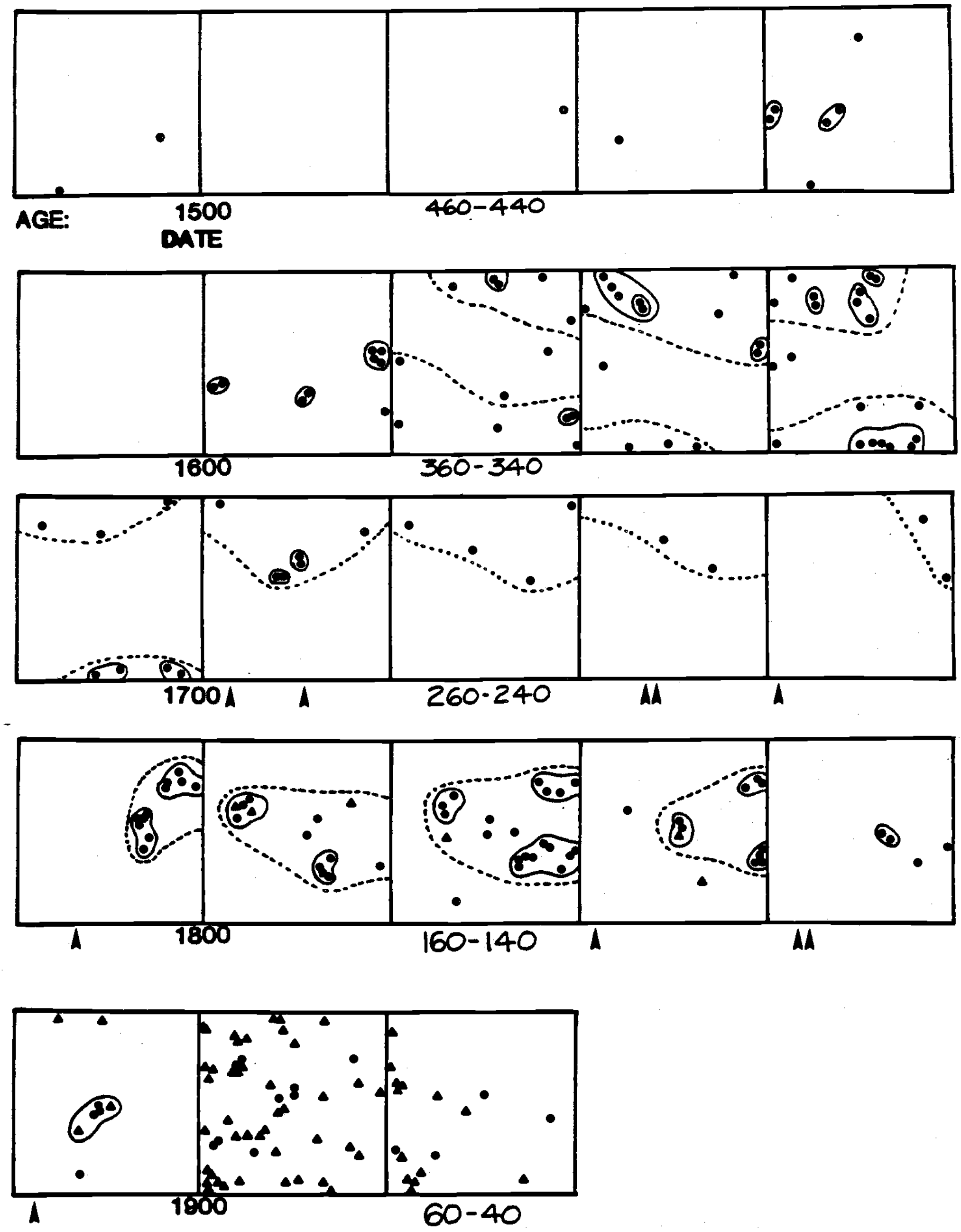

Figure 16. Chronological sequence of the initiation of surviving stems within 20-year age classes beginning 500 years B.P. Each block represents the 1.0-ha Reference Stand 28. The location of Pinus ponderosa (●) and Pinus contorta (▲) are shown as well as the occurrence of probable fires (⏶) identified by Bork (1985). Both small scale clusters of stems ⦿ and large scale aggregations ⦿ ⦿ are shown.

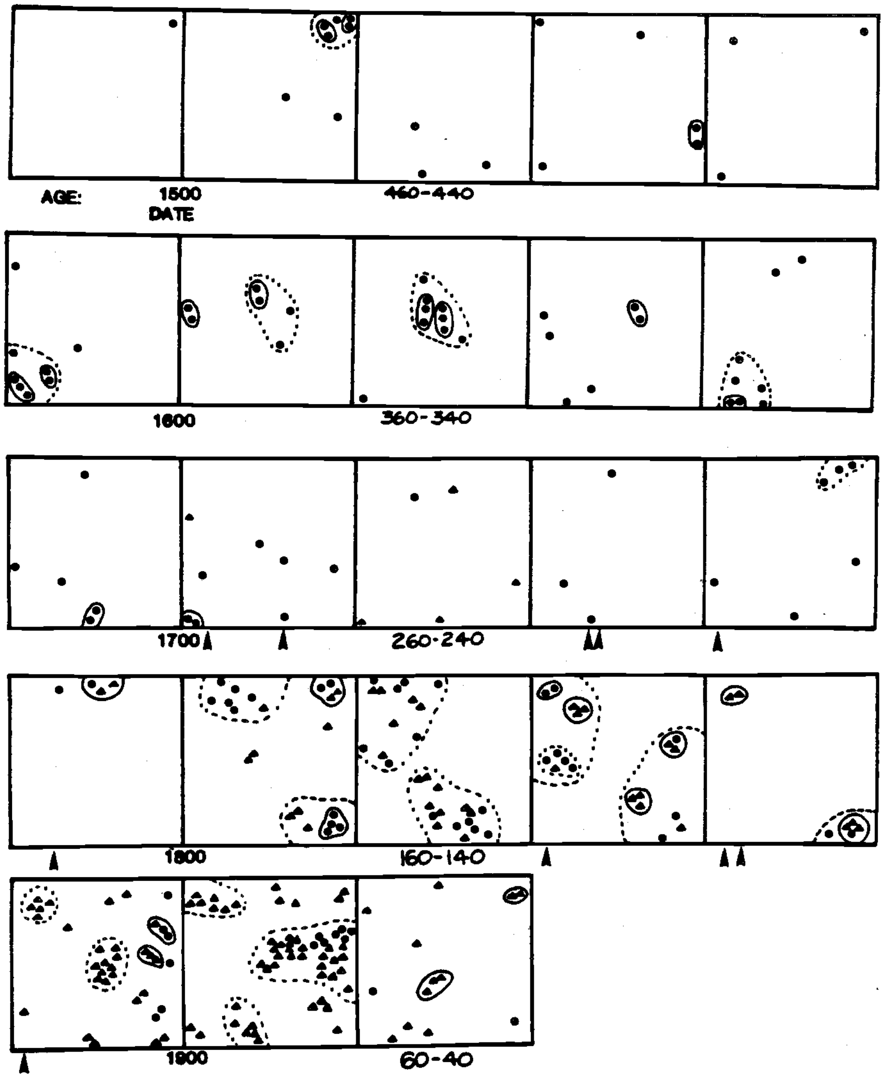

Figure 17. Chronological sequence of the initiation of surviving stems within 20-year age classes beginning 500 years B.P. Each block represents the 1.0-ha Reference Stand 29. The location of Pinus ponderosa (●) and Pinus contorta (▲) are shown as well as the occurrence of probable fires (▲) identified by Bork (1985). Both small scale clusters of stems ◉ and large scale aggregations ◎ are shown.

young seedlings from that portion of the stand (Cooper 1960). Small clusters of what were once larger even-aged patches can be seen along the northern and southern edges of the stand.

Between 280-200 years ago successful establishment was limited to the upper half of the stand. This was a period of increased fire activity during which time increased mortality greatly reduced the number of trees establishing anywhere within the stand. Similarly, hotter, drier climatic conditions would not have favored seedling establishment. Successful regeneration was still excluded from the center portion of the stand, either through competition by dominants or by fires burning through and killing regeneration thickets as well as stems as old as 80 years. This center portion of the stand may have been dominated by many old overstory trees. If this were the case and these stems were beginning to deteriorate as a cohort, increased fuel loads consumed by the fires of the 1700's could also have killed both overstory and understory trees, creating the paucity of surviving stems in this portion of the stand.

As an old-age stand degenerates, patches within the stand are formed by the death of a group of old trees or by natural events creating openings suitable for seedling establishment. These openings are filled by young trees forming an even-aged group. These groups are maintained by the relative inability of seedlings to establish under overstory trees and periodic fire that eliminates stems that do become established in those areas with heavier fuel concentrations. The even-aged group matures as a distinct unit under a natural fire regime that repeatedly thins the aggregation through the degenerative phase. Such a cycle results in a mosaic of phases at different density levels and different ages (Weaver 1943, Kershaw 1963, Cooper 1960, 1961, Bonnicksen and Stone 1981).

If successful regeneration within the center of the reference stand did take place during the first half of the 1700's, the increased fire activity in the later half of that century could have removed stems that would have been 20-60 years old and still susceptible to fire, particularly if the overstory within that portion of the stand was entering a degenerative phase.

Between 200-140 years ago a developing young aggregation began to form a patch within the 1.0 ha mosaic of RS28. It is possible that an age cohort that had maintained its integrity for more than 200 years no longer dominated the center portion of the stand. Trees that had established between 360-300 years ago along the stand's northern and southern edges were now 200-year-old dominants excluding seedling establishment in those areas. Fires of the late 1700's and 1800's destroyed most of the young trees throughout the stand except in the center of the stand. Beginning 200 years ago, 60 years of survivorship within the center of the stand created the vast majority of stems that comprise the intermediate age cohort. This large aggregation, forming a triangle with its base along the eastern edge of the stand, covers between 0.25-0.50 ha.

Morisita's Index does not detect the large 3000-5000 $m^2$ aggregation composed of intermediate aged ponderosa pine drawn in Figure 16. Bonnicksen and Stone (1981) point out that quadrat analysis may not always provide sufficient information on pattern size if large patches do not fall entirely within blocks. At quadrat sizes greater than 2500 $m^2$ rectangular blocks are used to measure aggregation. Blocks that measure 50x55 m, 50x60 m, or 50x65 m would bisect the intermediate age aggregation and essentially prevent the detection of the full size of that aggregate occupying the center of the stand. Survivorship peaks corresponding to the 200-140 year age classes could very well have been even-aged patches similar in size to those identified by West (1969).

Regeneration that has taken place since the turn of the century in the absence of fire has resulted in the gradual deterioration of the aggregation mosaic. Although the intermediate-aged cohort has begun to reach the canopy and fuel accumulation beneath these trees has increased, lack of fire has allowed successful establishment within these areas of the stand. Dense regeneration thickets dominate the understory of RS28, creating a situation in which a return to the original open forest condition may be extremely expensive in terms of silvicultural manipulations such as thinning and pre-burn treatment. Heavy fuel accumulations may have created a situation in which any fire would be catastrophic.

The space-time mosaic of RS29 does not exhibit the same locational integrity in which trees in the same age cohort are located in specific areas within the stand as was seen in RS28 (Fig. 17). Between 380-340 years ago even-aged groups established near the center of the stand; however, for the next 180 years successful establishment appears to have been located throughout the stand at random. Establishment location and subsequent age-class mosaics do not appear to be as strongly tied to fire-related understory mortality as was seen in RS28. $I_\sigma$ values for the intermediate aged ponderosa pine within RS29, which are less than half of those corresponding to similar aged stems in RS28, support this hypothesis.

The largest aggregations seen in RS29 occur as clusters (~0.125-0.25 ha) of both ponderosa and lodgepole pine, an association not common to RS28. Similar to RS28, however, is the pulse of establishment occurring 180-140 years ago. Following fire suppression, limited establishment of ponderosa pine and substantial establishment of lodgepole pine have taken place randomly throughout the stand.

Table 4 indicates patterns of association within both reference stands derived from chi-square association tests. For both ponderosa and lodgepole pine within RS29, the young and intermediate aged cohorts are positively associated. In contrast, young cohort lodgepole pine and intermediate ponderosa pine are negatively associated in RS28. Similarly, young ponderosa and young lodgepole pine, when combined, are negatively associated

Table 4. Chi-square tests for association of selected age cohorts for reference stands 28 and 29. Yates correction applied to $x^2$ tests (Greig-Smith 1957).

| | RS28 associations | | | | RS29 associations | | | |
|---|---|---|---|---|---|---|---|---|
| | Block sizes ($m^2$) | | | | Block sizes ($m^2$) | | | |
| Age cohort and species1/ | 25 | 100 | 225 | 400 | 25 | 100 | 225 | 400 |
| Pipo 1 and Pipo 2 | | | + | + | | | | |
| Pipo 1 and Pipo 3 | | | | | – | | – | |
| Pipo 2 and Pipo 3 | – | –** | –** | – | – | –**** | –** | |
| Pipo 1 and Pico 1 | | | | | +*** | | * | |
| Pico 1 and Pico 2 | | | | | – | – | –** | |
| Pipo 2 and Pico 1 | – | –*2/ | –**** | | – | | | |
| Pipo 2 and Pico 2 | | | | | +* | +**** | +** | |
| Pipo 3 and Pico 1 | – | | – | | | | + | |
| Pipo 3 and Pico 2 | | | | | – | –**** | –*** | – |
| (Pipo 1 plus Pico 1) and Pipo 2 | – | – | –** | | | | | |
| (Pipo 1 plus Pico 1) and Pipo 3 | – | | – | | | | | |

1/Pico = *Pinus contorta*; Pipo = *Pinus ponderosa*
Age cohort 1: ≥10 cm dbh, ≤110 years
Age cohort 2: ≥10 cm dbh, 110-230 years
Age cohort 3: ≥10 cm dbh, >230 years

2/Significant probability: * p < .05, ** p < .025, *** p < .01, **** p < .005. Minus sign indicates a negative association; plus sign indicates a positive association. Lack of a sign indicates no association at any block size.

with intermediate aged ponderosa pine within RS28. Intermediate aged and old aged ponderosa pine are negatively associated on both stands. Intermediate aged lodgepole pine and old aged ponderosa pine are negatively associated in RS29. The lack of significant negative association between young and old cohorts of either species suggests recent regeneration is not affected by trees in the oldest cohort. This is attributable to the lack of fire within these stands. The last major fire within the stands, ca. 1895, allowed for successful establishment of stems that would normally have been thinned in subsequent fires. Negative associations between intermediate and old cohorts bears this out.

# CONCLUSION

Two scales of pattern are observable within both stands. Long-term temporal and coarse-grained spatial patterns have been shaped by the periodic increase in fire activity that has occurred in the last 400 years. Periods of greater fire activity (Bork 1985) created broad-age cohorts that often occur in aggregations of surviving stems 2500-5000 $m^2$ and larger. These broad-aged patches cover more area than those described by White (1985), reflecting differences in fire regime, especially fire intensity.

Smaller aggregations of limited numbers of even-aged trees are apparently caused by the patchy nature of successful regeneration. Cooper (1960, 1961) identified similar aggregations while West (1969) identified even-aged aggregations much larger than were seen in the Pringle Falls area. Although White (1985) detected aggregation of stems within a broad-aged cohort, he did not identify a second scale of spatial and temporal pattern.

Both reference stands are composed of mosaics of varying size and age. Conclusions drawn from the association data suggest that the large-scale temporal and spatial patterns have remained in tact throughout the stands for the past 250 years. However, pulses of regeneration that occur following fire protection may, through time, erode the temporal and spatial pattern. Boundaries of aggregations may become less distinct. With time, these stands will most certainly become all-aged forests, characterized by the classic reverse-J shaped curve. If managers wish to perpetuate forest conditions that predate the manipulations by European settlers (primeval), reintroduction of uniformly low intensity fires will not be sufficient. A fire regime must include rare intense fires in order to perpetuate the large-scale temporal and spatial patterns of the primeval forest.

Volland and Dell (1981) and Weaver (1957, 1961) provide descriptions of southern and central Oregon pine forests by settlers in the region during the later half of the 1800's. Historical accounts of open, park-like ponderosa pine forests were made during periods of low stocking following the increased fire activity between 1840-1885. These forests were much more open during periods of increased fire activity that apparently killed smaller trees and shrubs than during periods of less fire activity and high survivorship. It is clear that the density and structure of the prehistoric stands were not constant. The historic accounts provide a short glimpse of the changing primeval forest. Such accounts can be an important source of information of the structure of the primeval forest for managers seeking to reintroduce fire, but they must be viewed in context.

Tremendous potential exists in the RNA for examination of the processes that have shaped these stands. Eighty years of fire exclusion has had a significant impact on fuel accumulation and to some degree forest succession within these stands. Prescribed fire is essential in returning these stands to conditions in which a natural fire regime is again shaping structure in this forest type. Availability of reference plots with sufficient baseline data is necessary if any research program is to be initiated to compare various management strategies. Research into survivorship of pine regeneration during varying fire intensities is needed. Spatial pattern of regeneration must also be examined. Long-term successional changes within this forest type can only be accomplished in plots of known structure and pattern.

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# APPENDIX

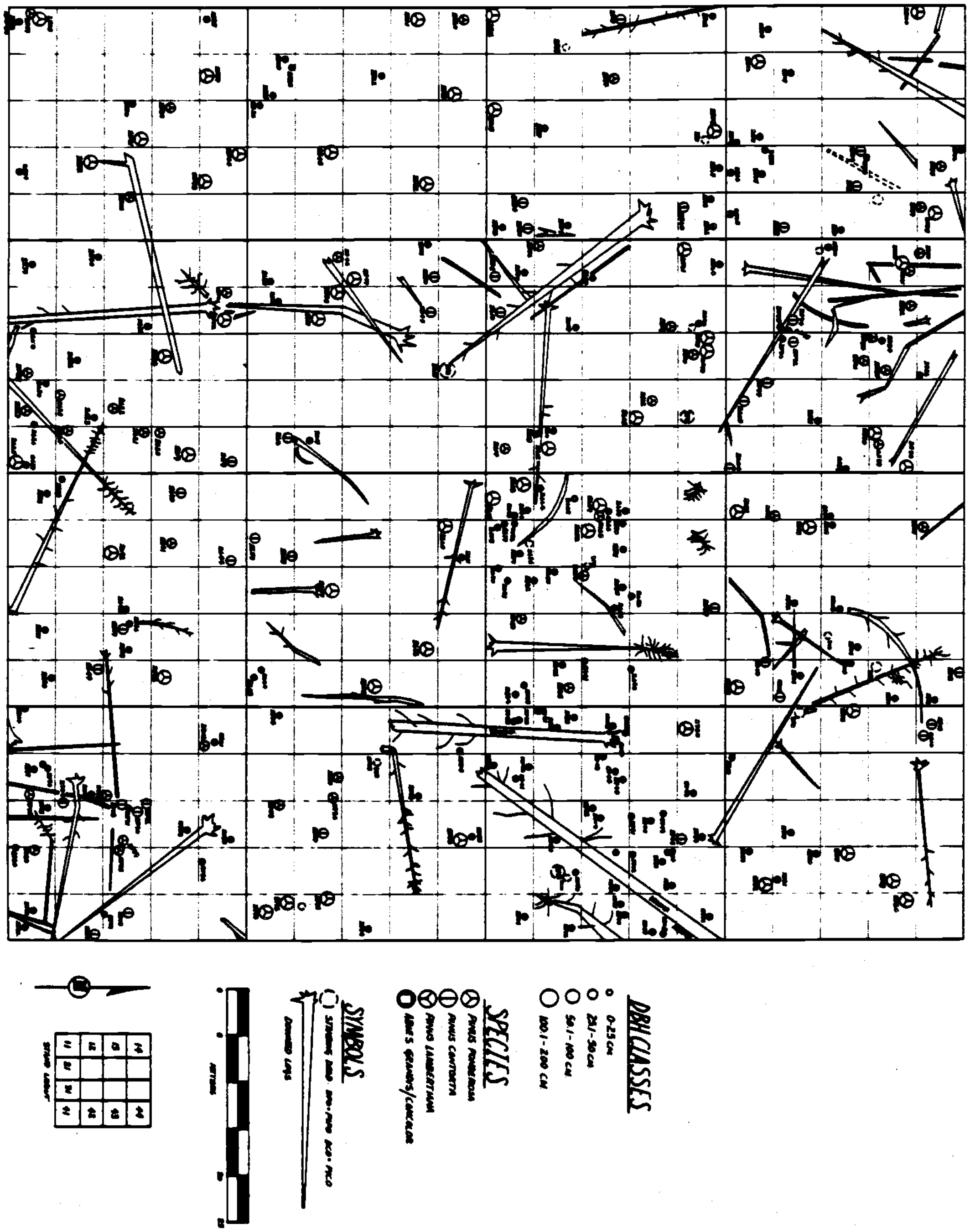

Figure i. Computer-generated stem map. Downed wood ≥10 cm dbh and tree tag numbers drawn by hand. Reference Stand 28, 1.0 ha (100x100m).

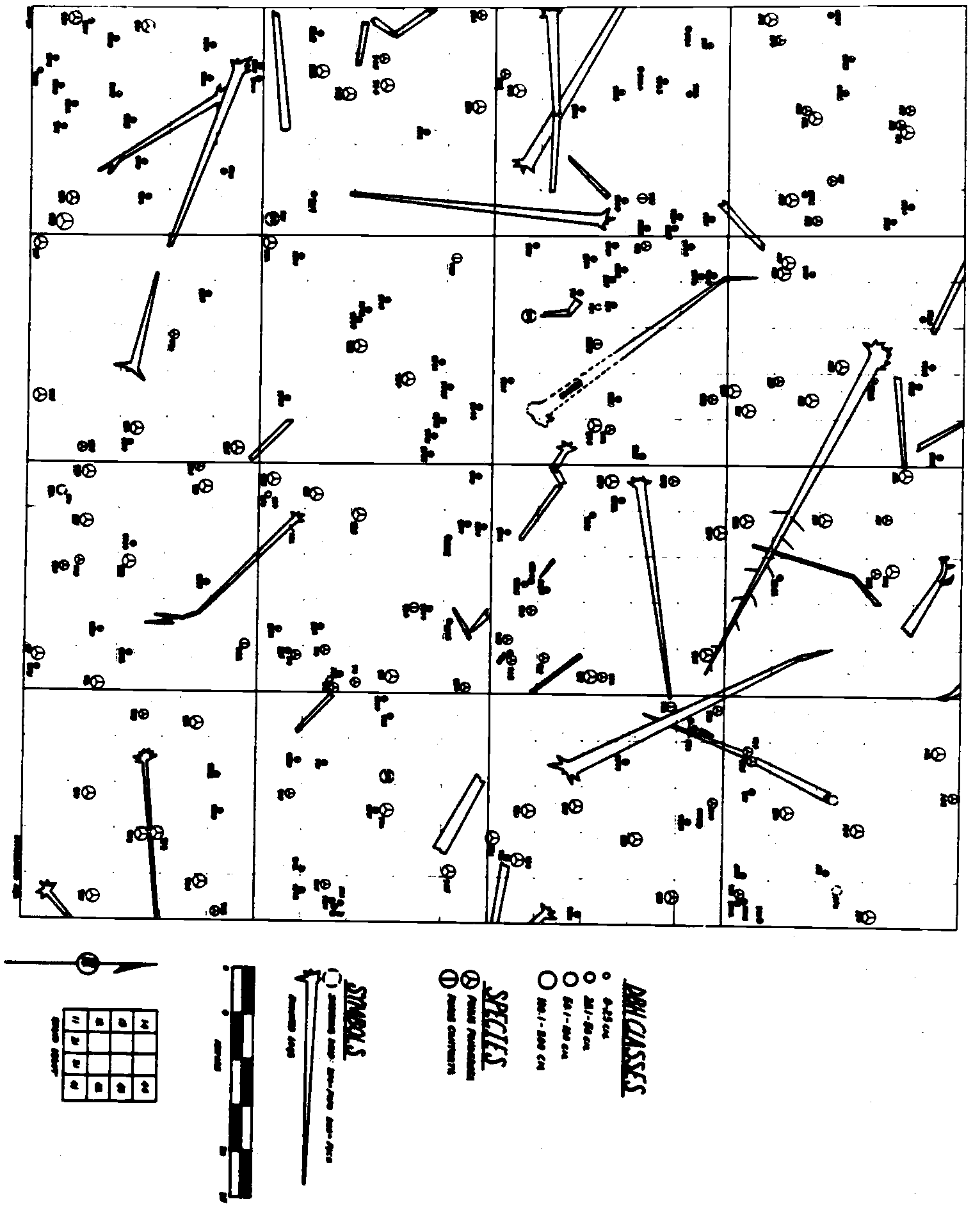

Figure ii. Computer-generated stem map. Downed wood ≥10cm dbh and tree tag numbers drawn by hand. Reference Stand 29, 1.0 ha (100x100m).