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Glenn H. Stewart for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on June 22, 1984.

Title: Forest Structure and Regeneration in the *Tsuga heterophylla* - *Abies amabilis* transition zone, central Western Cascades, Oregon

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Abstract approved: ______________________

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The dynamics of stands in the mid-elevation old-growth Douglas-fir (*Pseudotsuga menziesii*) forests of the central western Oregon Cascade Range were investigated using stand structure analysis. Trees with different growth rates were commonly present in the same stand, which resulted often in a weak correlation between tree diameter and age. Thus, age data and information on spatial dispersion and disturbance history were collected to aid in interpreting stand development.

The population structures described were influenced by periodic fires of variable intensity and extent that resulted in a mosaic of relatively even-aged patches of different conifer species. The overall pattern depends on stochastic factors, species' life history attributes, and the nature of the fire events. The species that first dominates a site following a disturbance profoundly affects subsequent stand composition and development. If *Pseudotsuga menziesii* or noble fir (*Abies procera*) dominate early, then tree regeneration of western hemlock (*Tsuga heterophylla*) and often Pacific silver fir (*Abies amabilis*) will rapidly occur. Conversely, if *Tsuga heterophylla* establishes first, regeneration will be absent

or minimal until canopy openings are formed. Several factors that influence regeneration depend on the main canopy composition. Canopy density determines how much light reaches the understory which in turn influences the abundance of tree seedlings and herbaceous species. Secondly, windfalls of old trees, branches, and snags often create canopy openings that are colonized by new seedlings or filled by previously established individuals. Lastly, decaying logs and stumps provide important substrates for tree seedling establishment, especially for *Tsuga heterophylla*. In stands without fire for at least several centuries, canopy openings are critical for the successful regeneration of the shade tolerant species *Tsuga* and *Abies amabilis*. The amount of direct beam radiation during the growing season is correlated with numbers and height growth of seedlings and saplings in larger openings.

These interactions demonstrate the need for successional schemes to include the effects of different canopy species, in addition to various disturbances, as factors controlling the rate and nature of forest succession.

Forest Structure and Regeneration in the *Tsuga heterophylla* - *Abies amabilis* transition zone, central Western Cascades, Oregon

by

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I. INTRODUCTION

Studies in forest stand development or stand dynamics focus on the changes in forest stand structure with time and the study of the behaviour of the stand (or group of trees) during and after autogenic and allogenic processes. The purpose of such studies is to investigate the interactions of groups of trees within a stand and, thus, form a basis for broader scale successional studies and management manipulations. Investigations in stand dynamics require astute observations coupled with a knowledge of autecology, physiology, morphology, anatomy, and the nature and effects of environmental influences.

Over the last two decades, the study of stand dynamics has expanded, reflecting the recognition of this field of research as a separate discipline. Since many other fields of research (such as physiology or mensuration) are partly derived from the study of stand dynamics, a lack of information on it may create a lack of perspective in these fields. Study of stand dynamics is, therefore, an integral part of the scientific investigative procedure. For example, for succession studies it provides descriptions of how forests change. Similarly, information about stand development is necessary to interpret ecosystem level changes such as total and component productivity with time and with stand structural changes.

In the Pacific Northwest, considerable research has centred on ecosystem level studies. Studies in stand dynamics have only become popular over the last 10 years, as illustrated by a recent symposium (Means 1982a) and an increasing number of publications on the subject. Studies of stand development in Oregon, especially in the western Cascade Range, have been few. Yet this area is one of the major sources of timber supply for the United States and contains one of the largest concentrations of old-growth forests, undisturbed by man, in the world - providing both an irreplaceable (but declining) source of material for study, and a high potential for the use of research results in forest management. Information on this subject forms an integral part of our understanding of these forests, and studies of this nature are necessary. This rationale provided the incentive for the study reported here.

After large, holocaustic fires with a return interval of several centuries in the Cascade Range of Washington and western Cascade Range of Oregon, Douglas-fir (*Pseudotsuga menziesii*) rapidly invades the burned areas and may form dense stands (Franklin and Dyrness 1973, Franklin and Hemstrom 1981, Hemstrom and Franklin 1982, Issac 1943, Munger 1930, 1940). After a period of rapid development, the stands begin to thin and more shade tolerant species such as western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*) begin to invade. Several centuries later, in the absence of further disturbance, the shade tolerant species usually are important components of the stand, eventually becoming the dominant species. Several exceptions to this general seral development have been documented recently (see Franklin and Hemstrom 1981), but the pattern of stand development outlined above is generally accepted as the most common for central western Oregon Cascade forests.

At elevations above 1100 m in the western Oregon Cascade Range, Pacific silver fir is often an important stand component and in many areas, noble fir (*Abies procera*) forms extensive stands. Stand structures are often complex, with generally 2 or more of the species described present. This stand complexity provides further interest in studies of stand dynamics.

There are many techniques available for stand dynamics studies. Studies of chronosequences (stands of different ages) are common, although it is often difficult to select stands on similar soils with similar site characteristics and disturbance histories. Permanent plots may be re-examined, but in this area, few had been installed for very long periods of time. Inferences may be made from physiological observations and studies and by reconstructing the growth patterns of existing stands. Perhaps the most common method used, however, is study of structure of single stands, to describe vertical stratification, foliage distribution, horizontal (spatial) patterns of stand components, or age- or size-class distribution. A combination of techniques, based primarily on stand structure, is used in the present study.

The use of size-class structure analysis requires a knowledge of the age/size relationships for component tree species. Thus, age/diameter relations are the subject of a detailed stand reconstruction in Chapter 2. As a result of this work, it became apparent that: (a) size and age are often poorly correlated, especially in stands subjected to several fires; and (b) small disturbances such as partial burns and treefalls are extremely important determinants of stand structure and regeneration. To investigate further aspects of stand structure and regeneration in stands of different composition and age, similar techniques were used in plots in other localities. This study of the influence of disturbances of different size, scale and intensity on stand development is reported in Chapter 3. In some areas where fire has not returned for several centuries, the pattern of stand development may differ from in those areas repeatedly burned. To test this hypothesis, several stands greater than 450 years of age, and apparently unaffected by fire for at least 450 years, were studied. The results of this investigation are presented in Chapter 4. Finally, the most important overall conclusions about stand dynamics in these forests are listed in Chapter 5.

II. POPULATION DYNAMICS OF A MONTANE CONIFER FOREST, WESTERN CASCADE RANGE, OREGON, U.S.A.

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ABSTRACT

Population dynamics were reconstructed in two forested stands in the western Cascade Range of Oregon, U.S.A., using size and age structure data in combination with information on stand history. Trees with different growth rates and size-age relationships occurred in the same stand, and, thus, diameter of 939 trees of 4 species was often weakly related to age. For these reasons, inferring stand dynamics from tree size distributions was not possible for some species; both age data and study of spatial dispersion added critical information which could not be gained from size alone. Such data are best gathered by detailed study of individual stands. The population structures and regeneration patterns described are strongly influenced by natural disturbances and species life history characteristics. Periodic fires of variable intensity and extent initiated a mosaic of relatively even-aged patches of different conifer species, each a result of stochastic factors, life history attributes and the specific fire event. The early establishment and dominance of a species on a site affected by a disturbance is an important determinant of subsequent forest regeneration. If _Pseudotsuga menziesii_ dominates early, then tree regeneration of _Tsuga heterophylla_ and often _Abies amabilis_ will rapidly occur; if, however, _Tsuga heterophylla_ establishes first, regeneration will be absent or minimal until canopy openings are formed.

INTRODUCTION

The life table approach to studies of population dynamics has been used successfully in plant population biology, especially for perennial and annual herbs (Harper 1977). However, its usefulness in studies of forest demography has been limited by the large size and great longevity of many forest trees; completing a periodic census would take longer than the lifespan of most research workers. Consequently detailed studies using a 'dynamic life table' approach have usually been restricted to seedlings and saplings (Hett & Loucks 1968). A more convenient method of collecting information on tree population dynamics is to use the size of trees in a population, for example, their diameter at breast height, to estimate tree age. If tree size is a reflection of age, then it is easy to approximate the age structure of the forest and construct a 'static life table'. Unfortunately, in many instances, tree size and age are poorly correlated, and often in even-aged stands the frequency distribution of tree diameters becomes exponential. Even so, size frequency distributions of forest trees have useful predictive value, since size may reflect fecundity and population growth in plants more reliably than age (Harper 1977). This predictive value is also useful in determining forest successional trends, which is an especially important consideration in forest management (Leak 1964, Meyer 1952).

A third method used in studies of forest tree populations is to infer past population dynamics from an analysis of the age structure of the present population, which is influenced by many factors that affect natality and mortality, and is therefore a reflection of a species' life history (Hibbs 1979). From age data, one can produce a survivorship curve or other form to identify age-specific events that change mortality. Thus, if there is constant natality and a stable age distribution, then the present age structure of the population (a static life table) can be treated exactly as a dynamic life table and survivorship can be predicted (Silvertown 1982). Deevey (1947) described three types of survivorship curves, of which

Types II and III are usually associated with tree species. The Type II or inverse-J curve has been described by the negative exponential model, which implies that mortality rate is constant with age, and the Type III more recently by the power function model, in which mortality rate decreases with age (Hett 1971, Hett & Loucks 1976, Leak 1975). Age structures which imply Type III survivorship have been identified in many forest tree populations including striped maple (Hibbs 1979), balsam fir, and eastern hemlock (Hett & Loucks 1976) in North American forests; Araucaria in New Guinea (Gray 1975); and several angiosperm tree species in South America (Veblen et al. 1981).

Many factors influence the shape of a population's age or size distributions. Foresters often distinguish between species they call 'shade tolerant', which show a capacity for regeneration beneath the forest canopy and an inverse-J age structure, and species called 'light demanding' or 'shade intolerant' which have no individuals in the understorey (Spurr & Barnes 1980). Gaps in the forest canopy appear to be important for the regeneration of many species, for example, pin cherry (Prunus pensylvanica L.), which produces new seedlings from dormant seeds in the soils where trees are toppled (Marks 1974). Fire, hurricanes, windthrow, and many other physical and biological disturbances also cause changes in the population structures of tree species. The shape of their population age and size distributions are therefore strongly influenced not only by the life history characteristics of the species themselves but also by the local environment.

Many studies have used size-class distribution analysis; if a relationship between size and age can be established this is a useful method for assessing population dynamics (e.g. Harcombe & Marks 1978, Lorimer 1980). Few studies, however, emphasize detailed age structure; furthermore, age information has generally been gathered from large tracts of forest (Hibbs 1979, Knowles & Grant 1983, Ross, Sharik & Smith 1982). Over these large areas the variability in growth rates due to differences in stand structure and environment makes an interpretation of the age distribution difficult. A composite age structure is often derived from widely different stands and does not provide an understanding of the spatial arrangement of age-classes in any particular spot (cf. Stewart & Veblen 1982).

The primary objective of this study is to use size- and age-class analysis and related information to assess tree species population dynamics for a small area of forest. An investigation of a given area should provide some general principles that can be used to interpret tree species population dynamics over a wider area and perhaps in other localities.

THE STUDY AREA

The two forest stands selected for study are located west of Soapgrass Mountain at Hyatt Soapgrass in the Willamette National Forest, Linn County, Oregon (latitude 44° 25'N, longitude 122° 20'W; 1200 m altitude). Stands were selected on the basis of differences in structure and disturbance history and were located in areas to be logged in 1982; no logging had occurred in the stands prior to this study.

Forests of the Pacific Northwest (Washington, Idaho and Oregon) are dominated almost exclusively by evergreen conifers. These forests are unrivalled both in the longevity and size of individual trees and in the biomass accumulations of individual stands (Waring & Franklin 1979). In the western portion of the Oregon Cascade Range, the true fir-hemlock forests at mid-elevations (_c_. 1000 - 1300 m) are composed of Douglas-fir (_Pseudotsuga menziesii_)*, western hemlock (_Tsuga heterophylla_), Pacific silver fir (_Abies amabilis_), noble fir (_Abies procera_) and locally abundant western redcedar (_Thuja plicata_) (Franklin & Dyrness 1973). Generally stands are dominated by _Pseudotsuga menziesii_ with a lower, multilayered canopy composed primarily of _Tsuga heterophylla_ and _Abies amabilis_; at elevations above 1200 m _Abies procera_ may be

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* Nomenclature follows Hitchcock & Cronquist (1973).

an important component of the main canopy (Franklin 1964a, 1964b). A general successional sequence following holocaustic fire for this lower montane zone involves initial colonization by *Pseudotsuga* or *Abies procera*, gradual replacement by *Tsuga heterophylla* and/or *Abies amabilis* and eventual dominance by *Abies amabilis* (Franklin & Hemstrom 1981). The forests studied are considered to be in a transition zone between the upper climax forests of *Abies amabilis* and the lower elevation climax *Tsuga heterophylla* forests (Franklin & Dyrness 1973).

The western Cascade Range consists of Eocene volcanic accumulations, which have been modified by erosion to form a deeply dissected, mature ridge and valley topography. Soils are generally well developed and derived from either pyroclastic parent materials or basic igneous rocks (Franklin & Dyrness 1973); surface horizons in the study area are dark-brown gravelly loams or sandy loams. Glacial deposits are conspicuous in the vicinity, although the extent of past glacial action is difficult to determine since many moraines have been obliterated by subsequent erosion. The climate of the region is complex, primarily due to the interaction of Pacific air masses with these mountain ranges. Movement of moisture-laden air off the Pacific Ocean results in high precipitation, 2000 to *c*. 4000 mm annually in this area, and a relatively mild climate, although summers are relatively dry (Waring et al. 1978, Zobel et al. 1976).

Fire is the major natural disturbance in the Pacific Northwest, with infrequent catastrophic fires (as opposed to frequent light burns) forming the general pattern, with an interval between fires of several centuries (Franklin & Hemstrom 1981, Hemstrom & Franklin 1982). Major windstorms occasionally occur and several have been recorded in recent times that must have strongly influenced forest structure. The most notable was the Columbus Day storm in 1962, which felled 11 billion board feet of timber in Oregon and Washington (Lynott & Cramer 1966). Several insects and diseases cause significant mortality in these forests, the most notable being *Phellinus weirii* (Murr.) Gilbertson root rot, especially in

Douglas-fir stands, and Douglas-fir beetle infestations following fire and windthrow (Childs 1970, Fowells 1965). Landslides and other mass movements can occur but are uncommon in the study area.

METHODS

Two stands were selected for detailed investigation; in these stands sample plots of 0.80 ha (100 x 80 m) and 0.36 ha (60 x 60 m), hereafter referred to as HY-1 and HY-2, were established and all sampling was confined to these. For this study, 'trees' are defined as ≥ 1.4 m tall and ≥ 5 cm diameter at breast height (dbh); tree 'saplings' as ≥ 1.4 m tall and < 5 cm dbh; and tree 'seedlings' as < 1.4 m tall and ≥ 10 cm tall.

Size structure

The dbh of all trees ≥ 5 cm dbh on the sample plots was measured, and all seedlings and saplings tallied by species. If a seedling, sapling or tree showed obvious signs of having established on an elevated surface such as a log, stump, trunk buttress, or upturned root plate, this was recorded. Stumps, dead standing trees and dead saplings were also measured and, if possible, identified. To describe the vertical component of stand structure, trees ≥ 1.4 m tall were assigned to the following relative canopy-height categories: emergent, upper main canopy, lower main canopy, below main canopy (intermediate), and overtopped (submerged). To represent vertical structure further, vegetation profiles of 80 x 3 m and 50 x 3 m were drawn for plots HY-1 and HY-2, respectively.

Size structure diagrams were used to depict the frequency in size classes of seedlings, saplings and of tree stems in 10 cm size-classes beginning at 5 cm.

Age structure

For HY-1 all seedlings, saplings and trees < 10 cm dbh were cut and discs removed at ground level. Trees 11 - 25 cm dbh were increment cored at a height of 30 cm above ground level and trees > 25 cm dbh were labelled at the base with numbered metal tags. Discs and cores were sanded with successively finer grades of sandpaper until annual rings could be easily distinguished and age determined under a binocular microscope. After logging of the area in October - December 1982, tagged trees were relocated and ages determined by counting annual rings on the cut stump. For Tsuga heterophylla only individuals on the northern half of the plot (n = 514) were aged, since a similar size-class distribution for this species also existed on the southern portion of the plot (n = 712).

For HY-2 all stems of Pseudotsuga menziesii ≤ 25 cm dbh were increment cored at 30 cm above ground level and all trees of this species, Tsuga heterophylla, Abies amabilis and Abies procera > 25 cm dbh were tagged, relocated after logging and aged by stump counting. An additional 20 Abies amabilis ≤ 25 cm dbh were aged from increment cores and 7 Tsuga heterophylla ≤ 25 cm dbh were aged by stump counting.

It was not possible to relocate all tagged trees following logging and a few trees were left standing. However, in HY-1, 88% of Pseudotsuga menziesii, 97% of Tsuga heterophylla, 96% of Abies amabilis, and 81% of Abies procera were aged; 99% of Tsuga heterophylla and 99% of Abies amabilis seedlings were aged. In HY-2 the percentages of individuals aged (excluding seedlings) were Pseudotsuga menziesii, 93%; Tsuga heterophylla, 17%; Abies amabilis, 28%; and Abies procera, 44%.

To determine the number of years taken to reach core or stump height, 30 - 35 saplings of each of the four main canopy tree species were aged at 30 cm above ground level in an adjacent clearcut. This location was selected since saplings here are growing in a relatively open situation similar to that which would have prevailed in plots HY-1 and HY-2 following fire. The use of growth rates for seedlings or saplings within the two plots was inappropriate, since many established and grew under closed forest conditions. Although most stumps were approximately 30 cm tall, large *Pseudotsuga menziesii* in plot HY-1 [30 stumps > 50 cm dbh (±S.E.)] averaged 54.7 ± 1.7 cm. Therefore, *Pseudotsuga menziesii* saplings on the adjacent clearcut were aged at 55 cm as well as 30 cm above ground level. The following corrections for sampling height were added to age determined from increment cores and stumps: *Pseudotsuga menziesii*, 5 years (at 30 cm) and 7 years (at 55 cm); *Tsuga heterophylla*, 6 years; *Abies amabilis*, 5 years; and *Abies procera*, 5 years. Undoubtedly some trees established under a more closed canopy, but this should be appropriate for most, which arose after a recent fire (see RESULTS AND INTERPRETATION).

Age structure diagrams were used to depict the frequency of individuals in 10 year age-classes.

Spatial pattern

Spatial distributions of species populations were assessed by mapping all individuals ≥ 10 cm tall in 5 x 5 m (HY-1) and 3 x 3 m (HY-2) contiguous quadrats, providing 320 and 400 quadrats in the two plots, respectively (also see appendix 1). A variation of the nested-quadrat technique (Greig-Smith 1964, Kershaw 1973) was used to detect scales of pattern. Morisita's (1959) index was used to determine the departure from a random distribution (see Veblen & Stewart 1982). Morisita's index is given by:

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

where q = number of quadrats, n_i = number of individuals of the species in the *i*th quadrat and N = the total number of individuals of the species in all quadrats. The index, I_δ, equals 1.0 when the population is randomly dispersed, where randomness implies an equal probability of each individual occurring in any one quadrat.

If the individuals are aggregated, $I_\delta > 1.0$, and if evenly distributed, $I_\delta < 1.0$. The statistical significance of each I_δ value > 1.0 was evaluated according to an F-test (Morisita 1959). Where the number of individuals is small (i.e. < 20), I_δ can vary erratically; thus I_δ was computed only for the more abundant tree populations. I_δ was computed for different species and different age- and/or size-classes for quadrats of increasing size from 1 unit, where each quadrat unit was 5 x 5 m (HY-1) and 3 x 3 m (HY-2). Thus, for plot HY-1, the quadrat sizes analysed were 25 m^2, 100 m^2, 225 m^2, 400 m^2, and so on. For quadrats < 8 x 8 units (HY-1) and < 10 x 10 units (HY-2) the original unit quadrats were grouped into perfect squares, thus avoiding fluctuations in I_δ which may result from changes in the shape of the blocks of quadrats (Pielou 1977). Rectangles were used for larger blocks of quadrats.

Both age and size data were used to identify populations appropriate for spatial analyses. In plot HY-1, all Pseudotsuga menziesii > 60 cm dbh were pooled for one analysis (i.e. trees 362 - 455 years of age) since this population was different from a younger (and smaller) cohort 71 - 88 years of age in one portion of the plot. Similarly, all Abies procera were analysed as one population, since only one tree was > 90 years old, and there had been no establishment for over 30 years. For comparative purposes, analyses for Tsuga heterophylla and Abies amabilis were performed using classes defined by both age and size. There were few trees of Tsuga heterophylla > 90 years old and many less than 30 years. Hence, age groups of ≤ 30 years and 31 - 90 years were used for the spatial analyses for this species. The same age groups were used for Abies amabilis and all trees > 90 years old of both species were lumped for a further analysis. Because there was considerable variation in the relationship between size and age for both Tsuga heterophylla and Abies amabilis, large size-classes were used (seedlings, individuals ≥ 1.4 m tall but ≤ 10 cm dbh and trees > 10 cm dbh). Classes used for HY-2 were: Pseudotsuga menziesii, all trees; and for Tsuga heterophylla and Abies amabilis, seedlings, ≤ 10 cm dbh and > 10 cm dbh. Dead trees were also included in several analyses.

The tendency for different pairs of species to occur together at various quadrat sizes was investigated by a chi-square test (Mueller-Dombois & Ellenberg 1974). The test was applied only to species sufficiently abundant to provide adequate cell frequencies in 2 x 2 contingency tables, but not so abundant as to be present in all quadrats.

Stand history

To determine past fire and treefall events, increment cores and/or discs were removed from scarred trees, and scars on stumps were aged in situ. In many instances fire scars only became apparent after trees were cut, especially in HY-2.

In plot HY-1 many seedlings of _Abies_ _amabilis_ produced roots from a prostrate part of their trunk. Layering of the stem is unrecorded for this species but a similar phenomenon occurred after burial by volcanic tephra (Zobel & Antos 1982). In plot HY-1, 34 of the 155 seedlings (21.9%) of _Abies_ _amabilis_ were layered. Because this could affect the age distribution of the population, a disc was removed for aging from directly above the initial rootstock. Layered seedlings of _Tsuga_ _heterophylla_ were less frequent, only 3.2% of the total in HY-1.

Stand structure models

If individuals of a species occur both in the main canopy and in the understorey [i.e. if accordance (_sensu_ Whittaker 1974) is complete], and if size reasonably predicts age, then tree species should be all-aged with reverse-J population structures (Daubenmire 1968). Such a species could be said to be regenerating continuously, and its population structure described by a negative exponential or power function model. An implicit assumption is that the forests studied should be in a 'steady-state', having suffered little or no disturbance (Hett & Loucks 1976). Also, as previously stated, species must have constant natality and a stable age distribution to generate a reverse-J structure.

In the study area, Tsuga heterophylla and Abies amabilis produce regular, but periodic, viable seed crops and are extremely shade tolerant (Christy 1982, Minore 1979), size is related to age (Table 3), and there are trees of both species in the understorey and main canopy (Fig. 1, Table 1). Fires have partially disturbed both plots over the last 450 years but there has been no major disturbance for c. 90 years, which should have been sufficient time to allow regeneration of the shade tolerant species if both regenerate in a continuous manner. In any event, a consideration of the factors that influence the goodness of fit of the population structures of these species to the negative exponential and power function models should allow a critical assessment of the utility of the models in these and other forests. Since many tree species populations have shown better fits to the power function model than the negative exponential model (Hett & Loucks 1976, Veblen et al. 1981), only the power function was used.

The power function model was applied to Tsuga heterophylla and Abies amabilis in both stands and to Pseudotsuga menziesii in HY-2. The power function is

$$y = y_0 x^{-b}$$

where y is the number in any age- or size-class x, y_0 is the number of individuals at time zero, and b is the mortality rate. The linear transformation of the model is

$$\log_e y = \log_e y_0 - b \log_e x$$

RESULTS AND INTERPRETATION

PLOT HY-1

Large, emergent Pseudotsuga menziesii, reaching heights of 50 m despite broken tops, dominate this plot (Fig. 1a, Table 1). Abies procera forms a dominant main canopy in the central portion of the stand, but the most abundant tree is generally Tsuga heterophylla, both in the main (30 - 35 m) and lower canopy tiers (Table 1). Both Abies amabilis and Tsuga heterophylla are represented as seedlings and saplings, the latter present mostly on fallen logs and tree stumps (Table 2). The Tsuga-dominated canopy is very dense, except where treefalls have created small canopy openings. Understorey herbs and shrubs are rare or absent under Tsuga, but a few small Vaccinium alaskense occur in openings or under Abies procera. Soils are deep and largely undifferentiated and may have thick litter accumulations, especially near large Pseudotsuga trees. At the southern end of the plot there are several recent treefalls where the nearly flat topography gives way to a 5° slope.

At least four fires have significantly affected this plot during the last four and a half centuries. Presumably a fire occurred c. 455 years ago (c. 1427 A.D.) that initiated the old-growth Pseudotsuga; the next dated fire occurred c. 320 years ago (c. 1662 A.D.), as aged from scars on nine Pseudotsuga. The third fire dates from c. 120 years ago (c. 1862 A.D.), and 3 Tsuga heterophylla and 2 Pseudotsuga had scars from a fire 89 years ago (1893 A.D.). Many codominant Abies amabilis and Tsuga heterophylla appeared to have been released (i.e. have increased annual ring widths following periods of suppression) at either c. 115 - 120 years or 85 - 90 years B.P., further verifying the two most recent fires. Two scars dated at c. 212 and 250 years may indicate localised fires.

Eight large Pseudotsuga, seven at the southern end of the plot, had been recently windthrown, all falling from south to north. Treefall scars on small Tsuga heterophylla and Abies amabilis

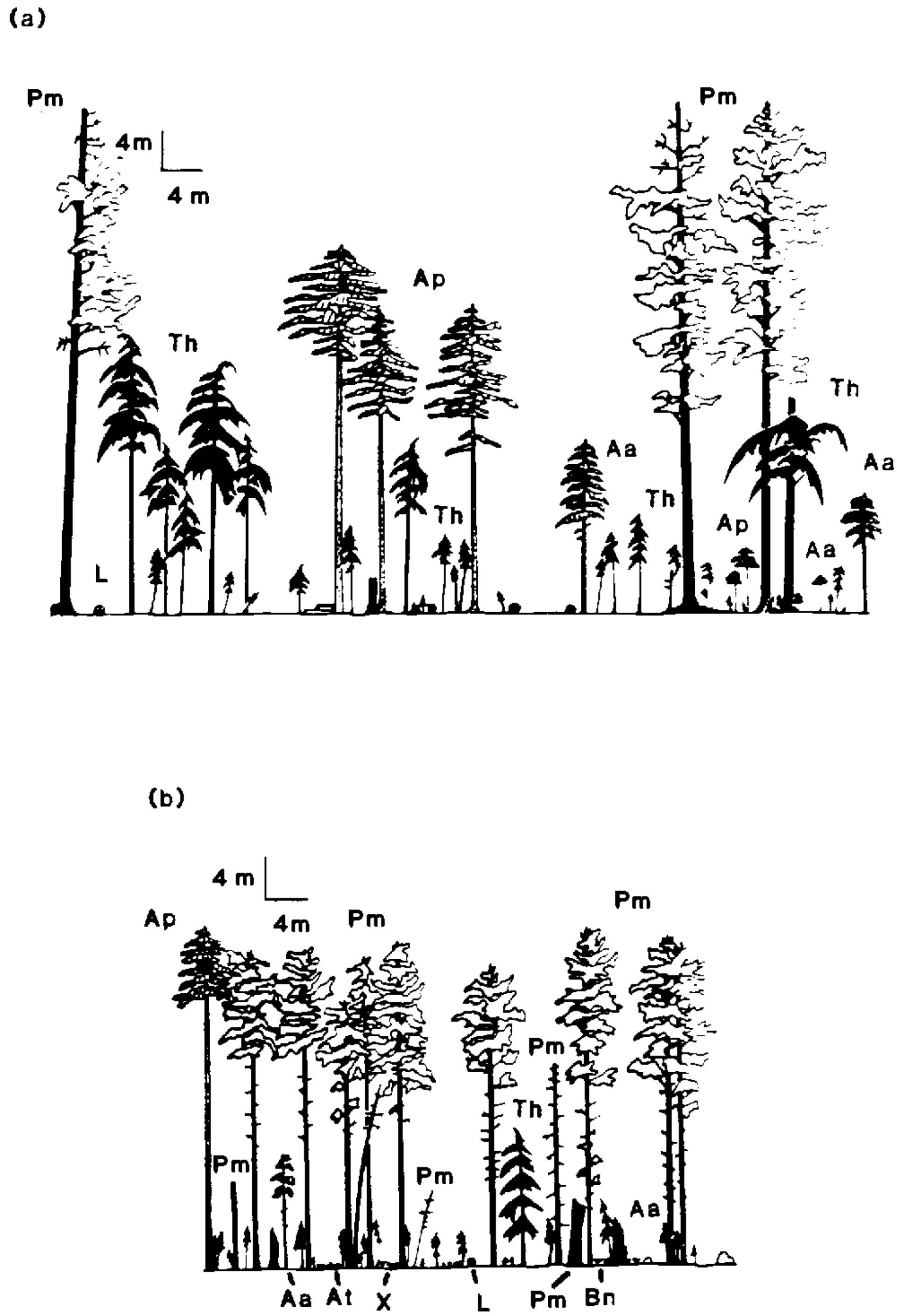

FIGURE 1: Profiles of (a) Plot HY-1 (80 x 3 m), and (b) Plot HY-2 (50 x 3 m). Aa, *Abies amabilis*; Ap, *Abies procera*; At, *Achlys triphylla*; Bn, *Berberis nervosa*; L, log; Pm, *Pseudotsuga menziesii*; Th, *Tsuga heterophylla*; X, *Xerophyllum tenax*.

TABLE 1: Number of trees $\geq$ 1.4 m tall in relative height classes in plots HY-1 and HY-2. The height classes are: I, overtopped; II, below main canopy; III, lower main canopy; IV, upper main canopy; V, emergent.

	PLOT AND HEIGHT CLASS									
	HY-1					HY-2				
SPECIES	I	II	III	IV	V	I	II	III	IV	V
Pseudotsuga menziesii	1	3	3	5	62	19	18	33	100	1
Tsuga heterophylla	725	174	85	9	1	256	28	23	38	
Abies procera	49	17	26	26	2	7	1	2	5	
Abies amabilis	112	17	45	20		95	7	7	12	
Thuja plicata						2				

TABLE 2: Number of seedlings (0.1 - 1.4 m tall) per ha and percentages of saplings and stems $\geq$ 5 cm dbh of dominant tree species established on elevated surfaces (logs, stumps, trunk buttresses, or upturned root plates) in plots HY-1 and HY-2. Numbers in parentheses refer to percentages of seedlings on elevated surfaces.

	SEEDLINGS / ha		% TREE STEMS ELEVATED	
SPECIES	HY-1	HY-2	HY-1	HY-2
Tsuga heterophylla	288	1325		
	(78.0)	(82.0)	50.3	63.5
Abies amabilis	194	1514		
	(15.0)	(29.0)	23.6	33.6
Abies procera	4	17		
	(100.0)	(33.0)	25.2	31.3
Pseudotsuga menziesii	1			
	(100.0)		0.0	45.6
Thuja plicata		11		
		(100.0)		100.0

indicate that all 8 large trees were blown over in 1962, during the Columbus Day storm.

Size structure

There are two distinct populations of Pseudotsuga menziesii (Fig. 2a); the smaller diameter population is restricted to the southeast corner of the plot. Although 67% of the larger population are 95 - 124 cm dbh, diameters range from 55 - 144 cm dbh, suggesting a long period of establishment and/or widely varying growth rates. Abies procera is represented by abundant stems in all size-classes $\geq$ 5 cm dbh, although 71% of all stems are 5 - 34 cm dbh (Fig. 2b). This size-class distribution suggests a relatively even-aged population, with some subsequent establishment following an initial pulse of regeneration, but little recent establishment. There are many stems < 15 cm dbh of Tsuga heterophylla, with declining numbers in larger size-classes and a few scattered, large individuals (Fig. 2c). There are few saplings but some seedlings, many located on logs in canopy openings (Fig. 5e). The large number of stems 5 - 14 cm dbh may reflect a past period of higher than average establishment. The size-class distribution for this species for the whole plot has many stems of 5 - 14 cm dbh (38%), indicating a slightly greater abundance of smaller Tsuga in the unaged portion of the plot. For Abies amabilis there are many individuals in the smaller size-classes, with declining numbers in successively larger size-classes, which suggests continuous replacement of older trees from a large juvenile population (Fig. 2d).

Age structure

Age-class and size-class distributions are similar in form for Pseudotsuga menziesii (Figs 2a & e). One 8 year old seedling on an upturned root plate and a few 71 - 90 year old trees constitute the younger age group. The older population spans 94 years (362 - 455 years old), with 75% of all the aged trees establishing

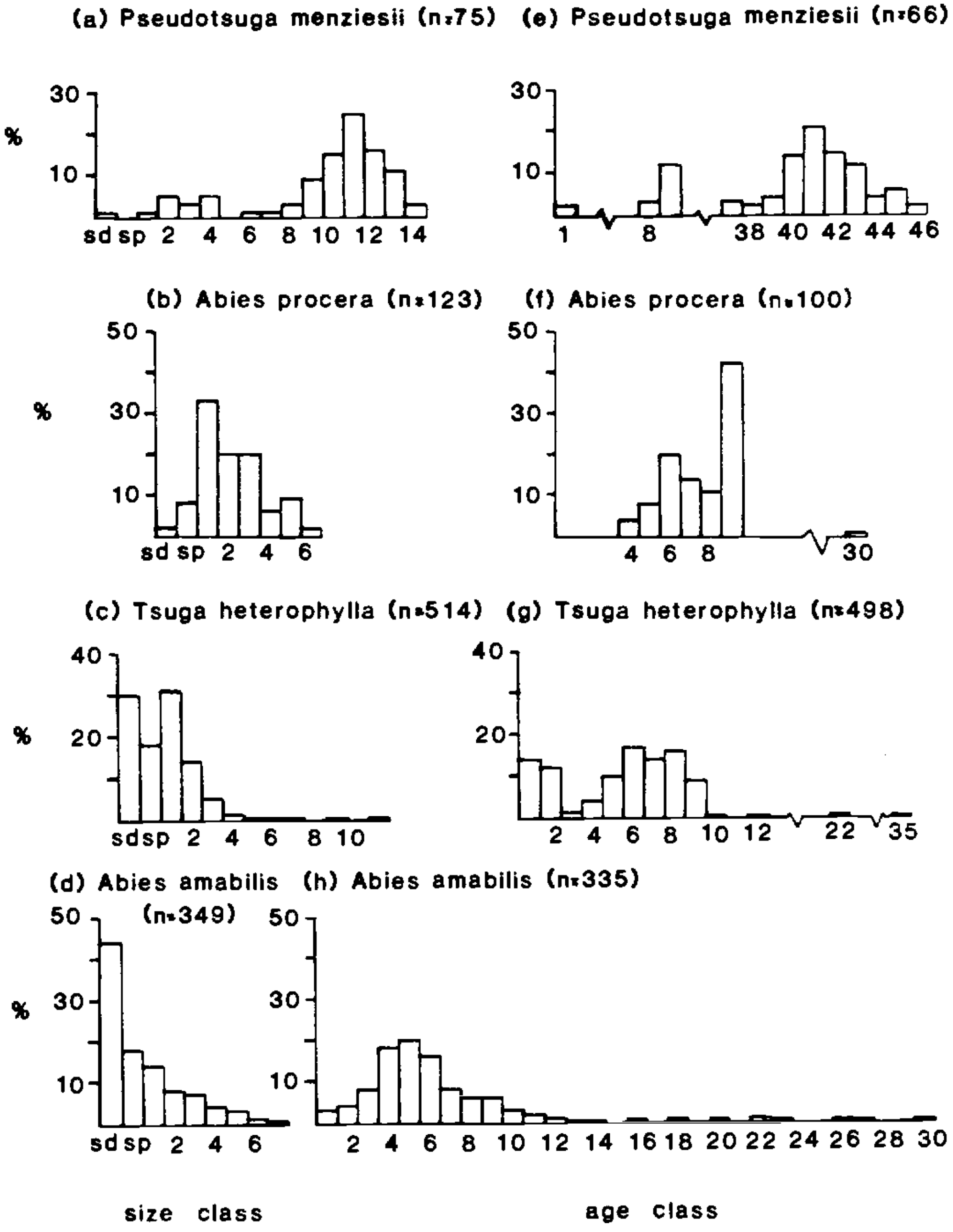

FIGURE 2: Size- and age-class frequency diagrams for main canopy tree species in plot HY-1. The size-classes are: Sd, seedlings; Sp, saplings; 1, trees of dbh 5-14 cm; 2, dbh 15-24 cm; 3, dbh 25-34 cm, etc. *n* = number of trees ≯ 0.1 m tall. The age-classes are: 1, 1-10 years; 2, 11-20 years; 3, 21-30 years, etc. *n* = number of trees aged.

from 391 - 430 years ago. This long period of establishment concurs with other published accounts of the c. 450 year old age-class common in the central western Oregon Cascades (Franklin & Hemstrom 1981, Franklin & Waring 1980, Means 1982b).

All Abies procera are less than 90 years old except one individual 299 years of age (Fig. 2f). Forty-two percent of the trees aged were established 81 - 90 years ago. Establishment dropped after this period and then rose to a second peak c. 51 - 60 years ago.

The age-class distribution for Tsuga heterophylla differs from the size-class distribution (Figs 2c & g). A few larger and older individuals are apparent in both distributions, but almost one half of the total tree population aged (47%) were established between 51 and 80 years ago. Following this establishment episode, a marked decline in establishment occurred; also, 84 dead individuals ≤ 34 cm dbh suggest high mortality in this young population. Trees younger than 20 years established on logs in several canopy openings.

Abies amabilis displays even greater differences between size- and age-class distributions than does Tsuga (Figs 2d & h). There are a few trees from 100 - 292 years old, a range in age not evident from the size-class distribution. As for Tsuga heterophylla, much of the population arose over a 30 year period; in this case, 54% were established 31 to 60 years ago, subsequent to the period of Tsuga regeneration. Of greatest significance, are the few trees including seedlings, younger than 30 years. Without age data, the regeneration pattern interpreted for Abies amabilis would have been dramatically incorrect.

Size/age relations

Least squares linear, exponential, logarithmic and power function regression models were fitted to the diameter and age data for each species and to the height and age data for Abies amabilis and Tsuga heterophylla. In almost all cases, the best fit was obtained using logarithmically transformed data in the power function regressions (Table 3). For *Abies procera*, *Abies amabilis*, and *Tsuga heterophylla* size appears to predict age reasonably well ($r = 0.71 - 0.82$, $P < 0.001$). No apparent relationship exists between size and age for the older population of *Pseudotsuga menziesii* ($n = 55$), but if the younger ten trees are added to the equation then a good relationship exists ($n = 65$, $r = 0.92$, $P < 0.001$; Table 3). From these results it would seem reasonable to use size to predict age in an analysis of age distributions for all species.

In any consideration of the relationship between two variables using regression analysis, an assessment must be made of the goodness of fit of the data to the regression curve. This can be done by examination of residuals or outliers (Sokal & Rohlf 1981), or simply gauged by a visual assessment of the data depicted as scattergrams of the two variables. An advantage of a visual assessment is that other factors such as variable growth rates, life history characteristics and disturbance effects may be considered in any interpretation. For example, due to different dates of establishment and variable growth rates, the relationship between size and age within a relatively even-aged population is often poor. This is illustrated for the older *Pseudotsuga menziesii* which, although spanning only about 100 years of age, vary from 60 - 145 cm in diameter (Fig. 3a). The younger population of this species similarly shows a wide range in diameter for a small variation in age. An excellent regression equation is obtained for age versus size for this species because two groups of points have been joined by a regression line (Fig. 3a, Table 3). This illustrates that, without first examining the raw data, any interpretation of the diameter/age relationship for a species could be misleading.

Many of the 81 - 90 year old *Abies procera* grew extremely rapidly and attained main canopy dominance, resulting in diameters 3 - 4 times that of other trees of similar age (Fig. 3b, Table 1). Trees that established subsequently under this canopy grew more slowly; thus, although size and age are correlated (Table 3), there

TABLE 3: Regression equations for estimating tree age in years (Y) from diameter at breast height in cm (X) and from seedling height in cm (Z); *n* is the number of trees sampled for age determination.

SPECIES	PLOT	*n*	REGRESSION EQUATION	RANGE IN Y	RANGE IN X, Z	*r*	*P*<
Trees and saplings							
*Pseudotsuga menziesii**	HY-1	55	$\log_e Y = 5.8643 + 0.3297 \log_e X$	93	82	0.12	NS
*Pseudotsuga menziesii***	HY-1	65	$\log_e Y = 1.5438 + 0.9487 \log_e X$	384	130	0.92	0.001
Abies procera	HY-1	97	$\log_e Y = 3.5867 + 0.2606 \log_e X$	267	67.5	0.80	0.001
Abies amabilis	HY-1	181	$\log_e Y = 3.4900 + 0.3440 \log_e X$	265	65.5	0.82	0.001
Tsuga heterophylla	HY-1	344	$\log_e Y = 3.6736 + 0.2322 \log_e X$	318	63.5	0.71	0.001
Pseudotsuga menziesii	HY-2	159	$\log_e Y = 3.6687 + 0.2262 \log_e X$	71	59	0.67	0.001
Abies amabilis	HY-2	33	$\log_e Y = 3.9439 + 0.1562 \log_e X$	65	51.5	0.77	0.001
Tsuga heterophylla	HY-2	60	$\log_e Y = 3.2363 + 0.3445 \log_e X$	73	53	0.69	0.001
Seedlings							
Tsuga heterophylla	HY-1	154	$\log_e Y = 0.1551 + 0.7257 \log_e Z$	47	116	0.81	0.001
Abies amabilis	HY-1	154	$\log_e Y = 0.8900 + 0.6557 \log_e Z$	64	128	0.82	0.001

* includes only trees 362 - 455 years old

** also includes 10 trees 71-88 years old

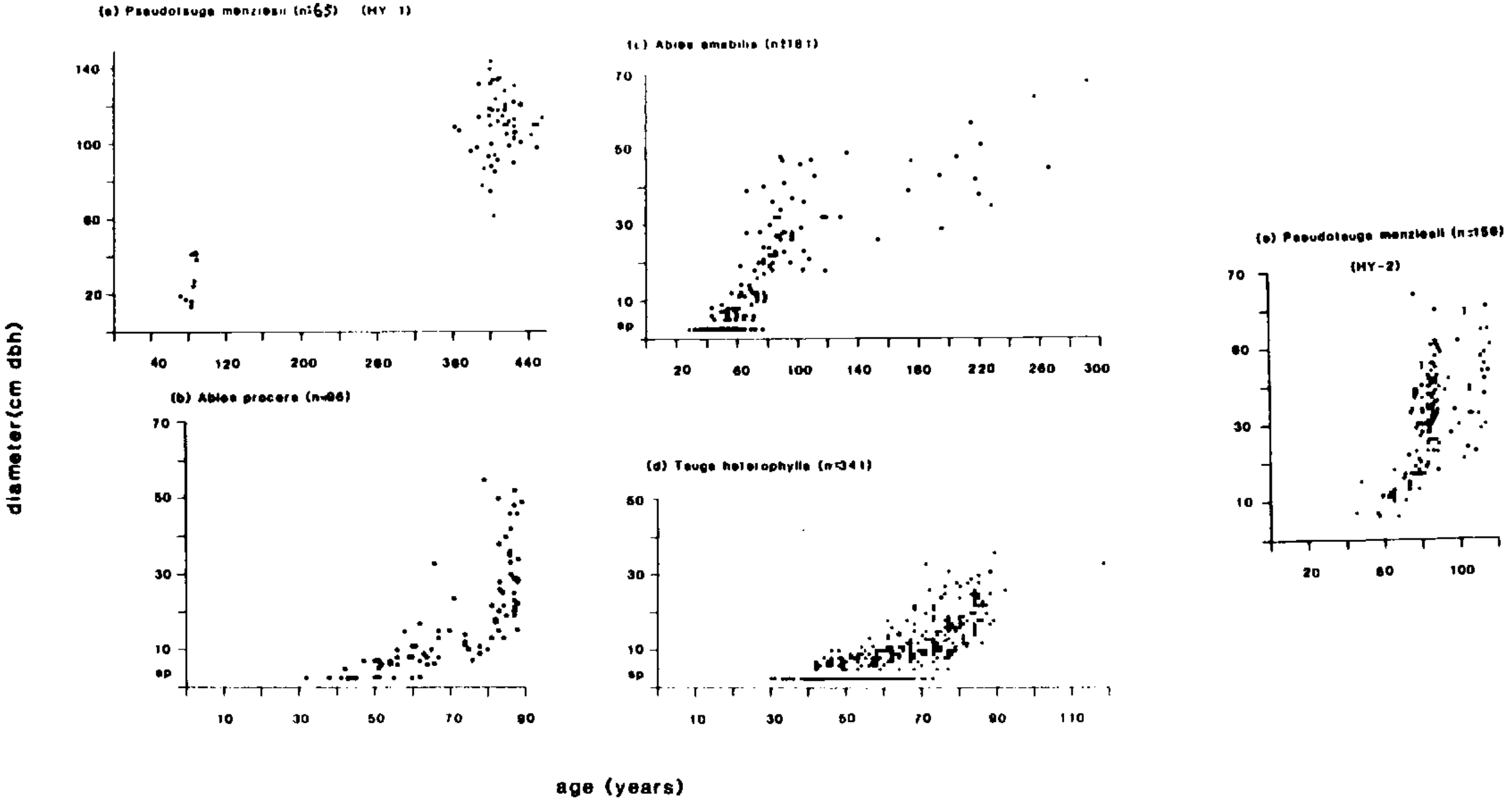

FIGURE 3: Relationship of age to breast height diameter for main canopy tree species in plot HY-1 and for Pseudotsuga menziesii in plot HY-2. One Abies procera (dbh = 56 cm, age = 299 years) and 3 Tsuga heterophylla (dbh, 25, 55, 66 cm; age = 217, 220, 348 years, respectively) are not shown. n = number of trees aged, sp = saplings.

is considerable variation in the relationship, because trees in the population have established and grown under a variable set of conditions. A variable relationship between size and age also exists for *Abies amabilis* (Fig. 3c). Thirty percent of trees > 90 years of age show periods of release from very suppressed growth (as seen in wider annual rings) either at c. 85 -90 or c. 110 - 115 years ago. These trees obviously have different size/age relationships than trees that grew rapidly to similar diameters in the last 90 years. The high degree of shade tolerance of saplings of this species is apparent, as they range in age from 27 - 77 years (Fig. 3c).

There is a considerable range in diameter for *Tsuga heterophylla* at all ages from saplings to trees of 90 years old (Fig 3d). For example, saplings range in age from 30 to 73 years and trees *c*. 10 cm dbh range from 45 to 80 years old. Only a few large, fire-scarred trees which are older than 90 years show markedly different growth rates. Compared to *Abies amabilis* there are many more *Tsuga* of intermediate height (Table 1), and these show a range in age (Fig. 3d). Perhaps *Tsuga* is more shade tolerant than *Abies amabilis* at intermediate tree heights and thus has lower mortality rates. Almost half of the *Abies amabilis* 5 - 14 cm dbh were dead (43 of 91) but only about one fifth of the *Tsuga heterophylla* of that size were dead (43 of 201). Therefore, the lack of individuals of *Abies amabilis* of intermediate height may be due to its inability to persist as a subcanopy tree. An ability to persist as seedlings (Fig. 4) or saplings and an apparent inability to survive under a dense canopy as small trees may explain why there are large differences between the size and age structures for this species. In contrast, *Tsuga heterophylla*, which may be extremely shade tolerant at all tree heights, would be less likely to have such disparate size and age structures.

Most *Tsuga* seedlings were less than 20 years old; those of *Abies amabilis* were all aged, many 30 - 60 years old (Fig. 4). Regressions of seedling height versus age for both *Tsuga heterophylla* and *Abies amabilis* indicate that the two variables are

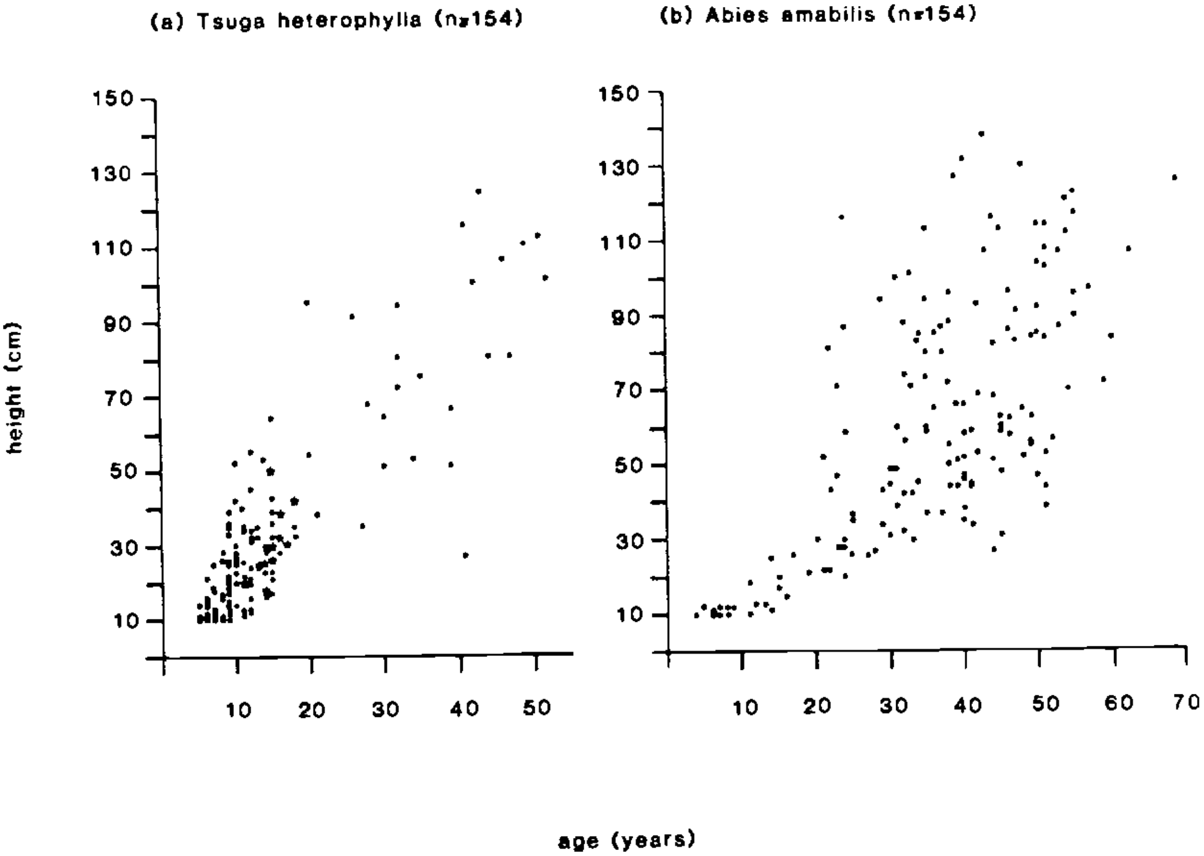

FIGURE 4: Relationship of age to height for seedlings in plot HY-1. Stars are seedlings 17-50 cm tall and 11-18 years old from one clump on a fallen log. _n_ = number of seedlings aged.

correlated (Table 3). However, seedlings generally occur in relatively even-aged groups (especially Tsuga) in which the individuals may vary markedly in height; for example, one group of Tsuga on a stump had an age range from 7 - 11 years whereas height ranged from 13 - 42 cm. The occurrence of relatively even-aged groups of seedlings of different growth rates results in extreme variability in the age/height relationship (Fig. 4). Therefore, a good fit to a regression equation of age and height does not necessarily indicate that an accurate age could be predicted from a given height.

Spatial pattern

Since the disturbance history of HY-1 varies from place to place, a knowledge of the spatial variability is essential to understand the species' population dynamics. For example, many trees of Abies amabilis that originated after the 1893 fire grew rapidly, resulting in a different relationship between size and age compared to trees that have grown under a closed canopy for over 200 years. In areas with such variation, a knowledge of the size and location of such patches of trees is necessary for accurate interpretation of the population dynamics of species in the stand.

Pseudotsuga menziesii 362 - 455 years old are widely distributed over the plot and, although uniformly distributed up to block sizes of 100 m^2, tend to be randomly distributed at all larger block sizes (Figs 5a & c). Dead Pseudotsuga $\geq$ 65 cm dbh are randomly distributed at all block sizes but analysis of live and dead stems together shows a similar pattern to that for live trees only. These patterns may reflect sporadic mortality and intense competition over a long period of time in a large, old even-aged population. Trees of Tsuga heterophylla and Abies amabilis > 90 years old are limited in distribution and clumped at all quadrat sizes up to and including 625 m^2 (Figs 5b & d). This is a direct result of survival in clumps following the 1893 fire; several of these trees bear fire scars dated to that event (Figs 5a & b).

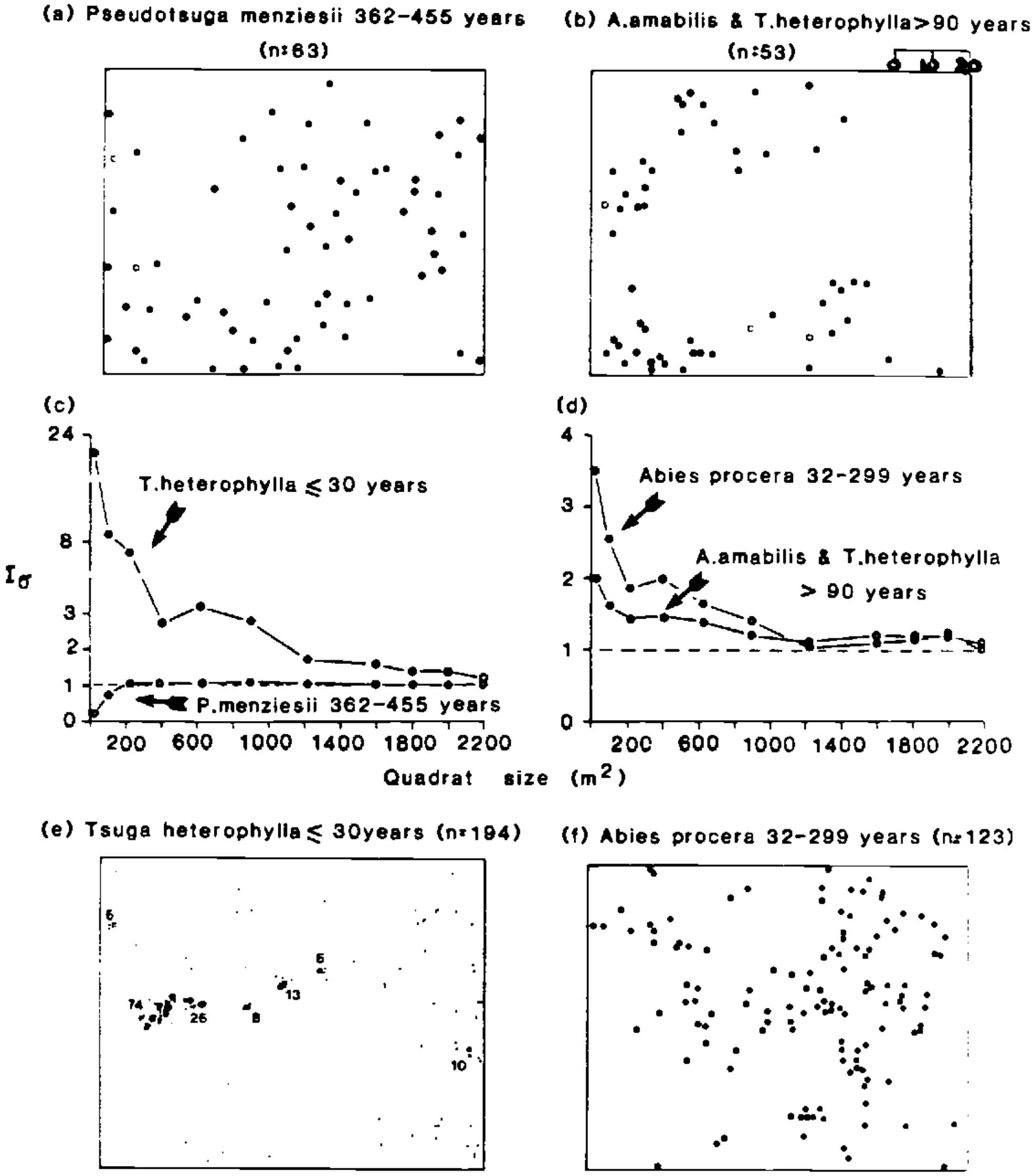

FIGURE 5: Maps of species of different age-classes in plot HY-1 ((a), (b), (e) & (f)) and their values of Morisita's index, I_σ, at different quadrat sizes ((c) & (d)). Filled symbols in (c) & (d) are I_σ values significantly $>$ 1.0 ($P < 0.05$) according to an F-test of Morisita (1959). The dashed lines at $I_\sigma = 1$ represent random patterns. Unfilled circles in (a) & (b) are trees that had fire scars from the 1893 fire.

Tsuga heterophylla $\leq$ 30 years old are extremely clumped at small block sizes, being restricted to logs in canopy openings, and are clumped up to 2000 m^2 reflecting the presence of several large patches (Figs 5c & e). Trees of this species 31-90 years old also occur in clumps up to 2000 m^2; large patch size in this instance is related to regeneration in openings following fire (I_δ = 1.32 at 25 m^2, I = 1.11 at 2000 m^2). The lower values of I_δ for older stems probably reflect heavy thinning of patches as they age, which results in a tendency towards a random distribution within each patch. Neither *Tsuga heterophylla* < 30 years old nor those 31 - 90 years old occur with *Tsuga* and *Abies amabilis* > 90 years old, as indicated by a consistently negative association (also see Figs 5b & e); *Tsuga* $\leq$ 30 years old are often associated with dead *Pseudotsuga* (Table 4).

Abies amabilis $\leq$ 30 years old and 31 - 90 years old have similar spatial patterns to *Tsuga heterophylla* of the same age-classes but I_δ values are lower. For example, trees $\leq$ 30 years old are aggregated up to and including 625 m^2 and trees 31 - 90 years old are clumped in patches up to 900 m^2. Clumped distributions of $\leq$ 30 year old *Abies amabilis* (I_δ = 11.5 at 25 m^2) and a positive association with *Tsuga heterophylla* $\leq$ 30 years old indicate similar sites of establishment (Table 4). Patches of *Abies amabilis* 31 - 90 years old formed in canopy openings created by the 1893 fire.

Abies procera also established in the openings formed by the 1893 fire. A comparison of Figs 5b & f shows the abundance of this species in areas where *Abies amabilis* and *Tsuga heterophylla* > 90 years old do not occur. *Abies procera* is clumped at quadrat sizes up to 900 m^2 and the several larger patches (1800 - 2000 m^2) that resulted from establishment into openings following the 1893 fire are evident (Figs 5d & f). *Tsuga heterophylla* 31 - 90 years old and *Abies procera* < 90 years old both occur in the area most affected by the 1893 fire, as verified by a positive association (Table 4).

Spatial analyses of size-classes for *Abies amabilis* and *Tsuga heterophylla* provided very similar results to the age-class

TABLE 4: Significant associations of live and dead trees by species and age- or size-class in plots HY-1 and HY-2, based on a X^2 test applying Yates' correction (Greig-Smith 1964). *n* is the number of quadrats assessed.

PLOT HY-1	BLOCK SIZE (m^2)	TYPE OF ASSOCIATION	X^2	*n*	*P*<
T.heterophylla ≤ 30 years : *A.amabilis* > 90 years	225	-	4.6	30	0.05
T.heterophylla ≤ 30 years : *T.heterophylla*+*A.amabilis* > 90 years	225	-	4.6	30	0.05
T.heterophylla 31-90 years : *A.amabilis* > 90 years	25	-	8.9	320	0.005
T.heterophylla 31-90 years : *T.heterophylla*+*A.amabilis* > 90 years	25	-	12.1	320	0.001
T.heterophylla ≤ 30 years : *A.amabilis* ≤ 30 years	25	+	14.8	320	0.001
	100	+	5.1	80	0.025
	225	+	5.7	30	0.025
T.heterophylla 31-90 years : *A.procera* < 90 years	25	+	4.6	320	0.05
T.heterophylla ≤ 30 years : DEAD *P.menziesii* ≥ 65 cm dbh	100	+	7.1	80	0.01
A.amabilis 31-90 years : LIVE *P.menziesii* ≥ 362 years	100	+	5.1	80	0.025
T.heterophylla seedlings : *T.heterophylla* > 10 cm dbh	25	-	5.6	320	0.025
A.amabilis seedlings : *T.heterophylla* > 10 cm dbh	25	-	5.4	320	0.025
A.amabilis > 10 cm dbh : *T.heterophylla* > 10 cm dbh	25	-	9.2	320	0.005
A.amabilis > 10 cm dbh : DEAD *P.menziesii* ≥ 65 cm dbh	100	-	5.6	80	0.025

TABLE 4: continued

T.heterophylla $\leq$ 10 cm dbh : *A.amabilis* $\leq$ 10 cm dbh	25	+	5.4	320	0.025
A.amabilis seedlings : LIVE *P.menziesii* $\geq$ 60 cm dbh	100	+	5.0	80	0.05
PLOT HY-2					
T.heterophylla seedlings : *T.heterophylla* > 10 cm dbh	9	–	8.3	400	0.005
	36	–	4.3	100	0.05
A.amabilis seedlings : *T.heterophylla* > 10 cm dbh	9	–	10.5	400	0.005
T.heterophylla seedlings : *A.amabilis* seedlings	9	+	15.3	400	0.001
	36	+	5.5	100	0.025
	81	+	8.8	36	0.005
T.heterophylla $\leq$ 10 cm dbh : *A.amabilis* $\leq$ 10 cm dbh	36	+	5.4	100	0.025
T.heterophylla $\leq$ 10 cm dbh : *T.heterophylla* > 10 cm dbh	9	+	10.1	400	0.005
T.heterophylla $\leq$ 10 cm dbh : LIVE *P.menziesii* 5-64 cm dbh	9	+	5.9	400	0.025
T.heterophylla $\leq$ 10 cm dbh : DEAD *P.menziesii* > 64 cm dbh	9	+	4.0	400	0.05
T.heterophylla $\leq$ 10 cm dbh : DEAD *P.menziesii* $\leq$ 64 cm dbh	9	+	8.7	400	0.005
	36	+	6.3	100	0.025
T.heterophylla > 10 cm dbh : DEAD *P.menziesii* $\leq$ 64 cm dbh	81	+	11.6	36	0.001
A.amabilis $\leq$ 10 cm dbh : *A.amabilis* > 10 cm dbh	9	+	9.9	400	0.005
A.amabilis $\leq$ 10 cm dbh : LIVE *P.menziesii* 5-64 cm dbh	9	+	4.2	400	0.05
LIVE *P.menziesii* 5-64 cm dbh : DEAD *P.menziesii* $\leq$ 64 cm dbh	36	+	3.9	100	0.05

analyses. For example, seedlings of *Tsuga heterophylla* show clumped distributions similar to trees ≤ 30 years old (Fig. 6). Similarly, trees ≤ 10 cm dbh and trees 31 - 90 years old for both species have similar spatial distributions to the age-classes. Generally I_δ values were lower in the size-class analyses but the patterns were the same. Therefore, it would be reasonable to use size-classes for spatial analyses provided the appropriate size-classes could be recognised.

Additional insight into regeneration patterns was obtained through chi-square analyses using the size-class information. For example, *Abies amabilis* seedlings occurred under large, live *Pseudotsuga* but tended to be negatively associated with *Tsuga heterophylla* > 10 cm dbh (Table 4). This and the fact that *Tsuga* seedlings were also negatively associated with *Tsuga* > 10 cm dbh supports the observation that *Tsuga* canopies are dense enough to limit regeneration of both *Tsuga* and *Abies amabilis*.

PLOT HY-2

Pseudotsuga menziesii, some *Tsuga heterophylla* and scattered individuals of *Abies procera* and *Abies amabilis* form a relatively even canopy at 25 - 35 m tall in plot HY-2 (Fig. 1b, Table 1). Intermediate tiers contain *Tsuga heterophylla* and suppressed *Pseudotsuga*; regeneration is *Abies amabilis* and *Tsuga heterophylla*, with a few *Abies procera* and *Thuja plicata* (Tables 1 & 2). The shrubs *Vaccinium alaskense*, *Acer circinatum* and *Rhododendron macrophyllum* occur in occasional canopy openings; low shrubs and herbaceous plants are locally abundant and include *Achlys triphylla*, *Smilacina stellata*, *Berberis nervosa*, and *Xerophyllum tenax*. Boulders are exposed on the surface in some areas on this south facing 10° slope.

A single old-growth *Pseudotsuga menziesii* (396 years old) is indicative of a fire at least 400 years ago, probably the same fire that initiated the old-growth in HY-1. Two other fires occurred,

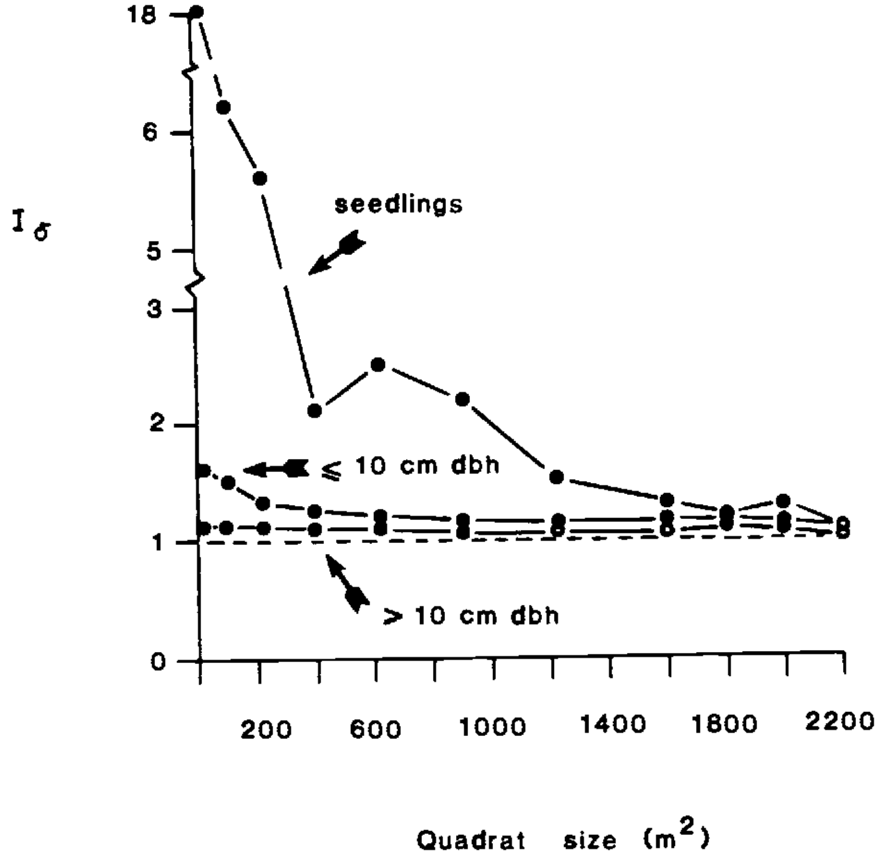

FIGURE 6: Values of Morisita's index, I_σ, at different quadrat sizes for <u>Tsuga heterophylla</u> of different size-classes in plot HY-1. Filled symbols are I_σ values significantly $>$ 1.0 ($P < 0.05$) according to an F-test of Morisita (1959). The dashed lines at $I_\sigma = 1$ represent random patterns.

one in c. 1862 and one in 1893. At the eastern end of the plot, one Abies amabilis and six Pseudotsuga > 89 years of age had internal fire scars dated to 1893; patches of Pseudotsuga and Tsuga heterophylla now 90 - 115 years old escaped the fire in this portion of the plot. Although most of the plot must have been devastated, several clumps of small Abies amabilis survived; these were recognised only after ages > 90 years were obtained for the trees.

Size structure

All trees are ≤ 64 cm dbh, apart from the one large Pseudotsuga menziesii, and 69% of these are 25 - 54 cm dbh, indicating a relatively even-sized population (Fig. 7a). There are 99 standing dead Pseudotsuga 5 - 34 cm dbh that may reflect heavy thinning due to density dependent mortality (Fig. 7b). The population previous to the 1862 fire was similar in structure to that in plot HY-1, 50 m distant, as indicated by stump diameters of 65 - 124 cm dbh. Abies procera are not abundant in this plot but occur sporadically as seedlings, saplings, and dominant trees (Fig. 7c, Table 1). Abies amabilis and Tsuga heterophylla are well represented by seedlings and small stems with declining numbers in larger size-classes (Figs 7e & f). As in HY-1 many of the seedlings and trees ≥ 5 cm dbh occur on elevated surfaces, even the Pseudotsuga menziesii (Table 2).

Age structure

In contrast to the size-class distribution, the Pseudotsuga menziesii age-class distribution is bi-modal (Fig. 7d). There is a group of trees ≥ 90 years old and a more abundant population < 90 years old, many of which established 81 - 90 years ago. The older age-class could not have been discerned from the size-class information. Similarly, trees ≥ 90 years old were found for the other species; the oldest Tsuga was 117 years old; Abies procera,

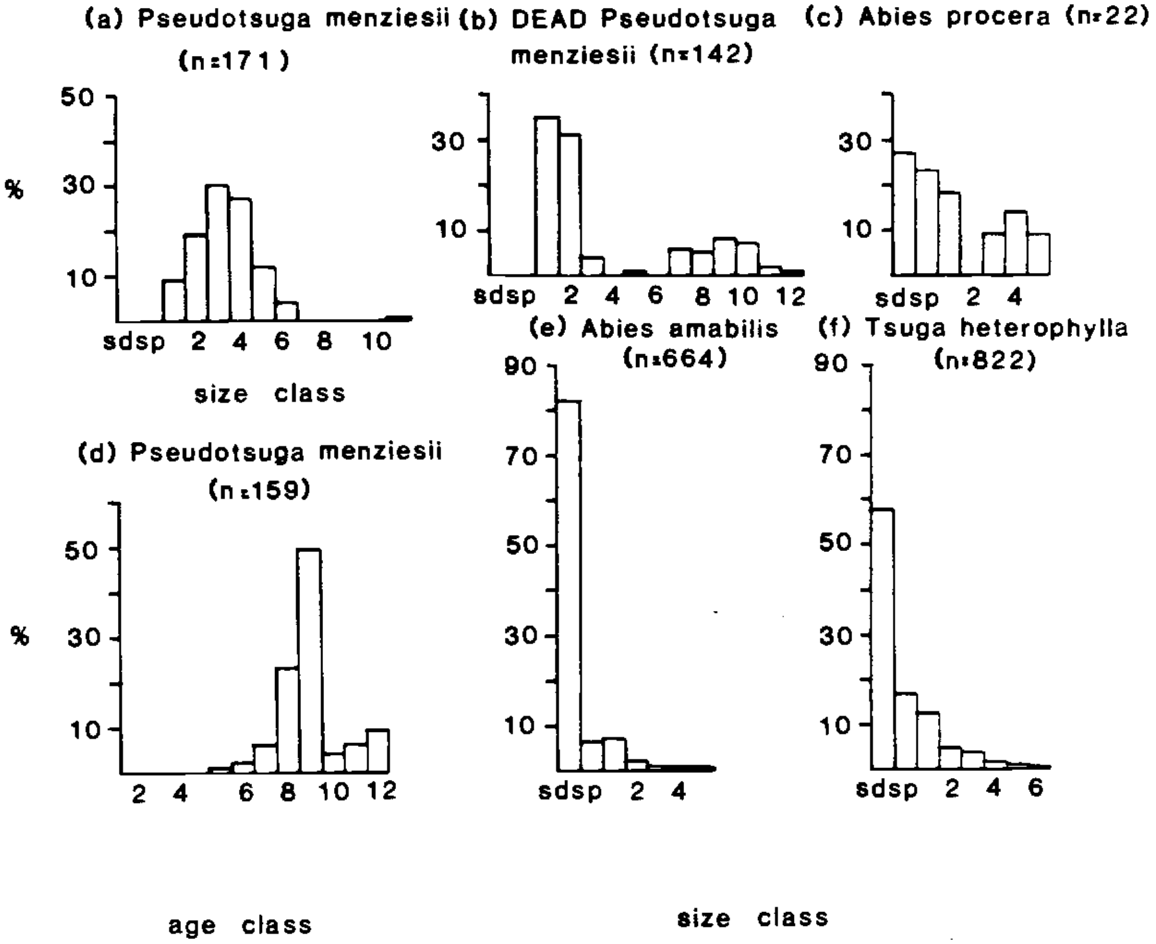

FIGURE 7: Size- and age-class frequency diagrams for main canopy tree species in plot HY-2. Size-classes, age-classes and n as in FIG. 2.

94 years old; and *Abies amabilis*, 118 years old. Although the total populations of *Abies procera*, *Tsuga heterophylla* and *Abies amabilis* were not aged, the ages obtained (for mostly main canopy trees) indicate individuals both ≥ 90 years old and < 90 years old and peaks of establishment 81 - 90 years ago.

Size/age relations

As for plot HY-1, the power function regressions best described the relation between size and age (Table 3). For *Pseudotsuga menziesii* the relationship is weak, because trees vary greatly in size at most ages (Fig. 3e). Within the population two distinct age groups (45 - 89 and 90 - 116 years old) are evident, both with a large range in diameter for a narrow range in age. Variable growth rates related to microsite conditions and competition among neighbouring trees of similar age are the most likely reasons for the poor correlation. Most of the *Tsuga heterophylla* aged were > 25 cm dbh and the relationship between size and age would probably be improved (Table 3) if the ages of smaller stems had been included, as was done for *Abies amabilis*.

Spatial pattern

Combining dead and live *Pseudotsuga menziesii* ≤ 64 cm dbh reveals that the trees in the population several decades ago were clumped up to 144 m^2 (Fig. 8a). Subsequent rapid thinning of these patches has left the clumps of live trees at 144 m^2 but with fewer trees in each patch (Fig. 8a). An approximation of the distribution of the previous *Pseudotsuga* population using stumps ≥ 65 cm dbh revealed clumps of 2 or 3 trees at quadrat sizes of up to 36 m^2; these clumps occurred in patches of 144 - 225 m^2 (Fig. 8a). This patchy distribution suggests that mortality in the original population was also influenced by fire or windthrow, resulting in the death of trees in some areas but not in others. The similarity in dispersions for live *Pseudotsuga* 5-64 cm dbh and

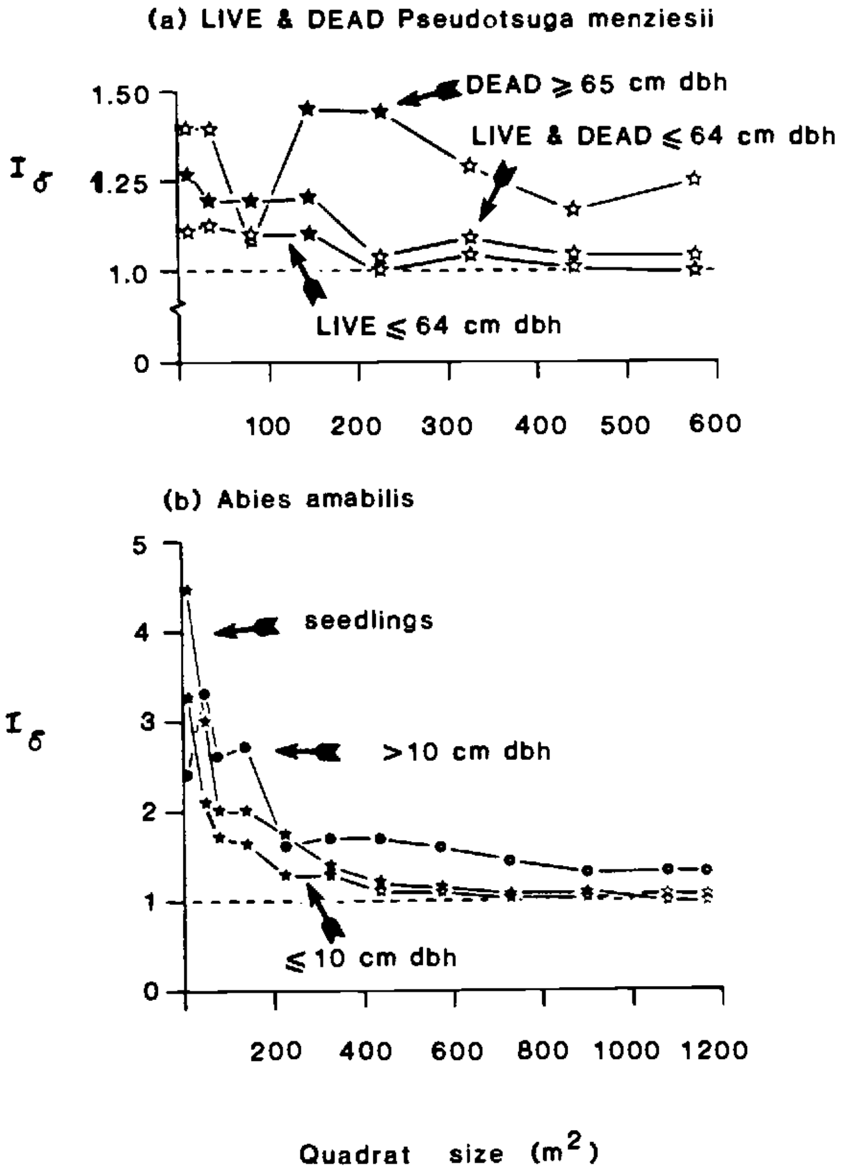

FIGURE 8: Values of Morisita's index, I_δ, at different quadrat sizes for (a) Pseudotsuga menziesii and (b) Abies amabilis of different size-classes in plot HY-2. Filled symbols are I_δ values significantly > 1.0 ($P < 0.05$) according to an F-test of Morisita (1959). The dashed lines at $I_\delta = 1$ represent random patterns.

dead trees $\geq$ 65 cm dbh also suggests that many of the current live trees could have established on the remains of the trees of the previous population.

The spatial patterns of Tsuga heterophylla and Abies amabilis are similar; therefore, only Abies is illustrated (Fig. 8b). Seedlings occur in dense clumps at small quadrat sizes and clumps occur up to 900 m^2. Stems $\leq$ 10 cm dbh and > 10 cm dbh show similar patterns to those described for plot HY-1, except that patches occur only up to 600 m^2. Reasons for the dense clumps of seedlings and trees $\leq$ 10 cm dbh include establishment in openings and on logs and stumps. As in HY-1, Tsuga heterophylla and Abies amabilis seedlings occur together and are consistently rare under Tsuga heterophylla > 10 cm dbh (Table 4). Tsuga heterophylla $\leq$ 10 cm dbh is positively associated with live and dead Pseudotsuga $\leq$ 64 cm dbh and with dead Pseudotsuga $\geq$ 65 cm dbh, indicating that this species is regenerating both under the current Pseudotsuga trees and on or near the stumps of the previous Pseudotsuga population. Abies amabilis similarly is often found under the live Pseudotsuga. Clearly, current regeneration is being strongly influenced by the species of dominant canopy tree present in both the current and previous stands.

Stand structure models

The size-class distributions for Tsuga heterophylla and Abies amabilis in plot HY-1 are well described by the power function model (r = -0.81 to -0.84; Table 5). Assuming steady state conditions, this suggests that large numbers of individuals become established, but many die, leaving fewer trees in older age-classes. However, the age-class distributions of both species are not described as well by the power function model (r = -0.61 and - 0.68), due primarily to the lack of individuals less than 50 years old for Tsuga and less than 30 years old for Abies amabilis. If there is a regular input of seedlings of both species in this stand, then mortality of the younger individuals must have been much higher

TABLE 5: Applications of the power function model to the size- and age-class distributions of several of the dominant tree species in plots HY-1 and HY-2; *n* is the number of pairs of X (midpoint of size- or age-class) and Y (number of stems in a size- or age-class) variables.

SPECIES	PLOT	*n*	REGRESSION EQUATION	*r*	*P*<
Size-class distributions					
Tsuga heterophylla (northern half of plot)	HY-1	11	$\log_e Y = 5.6817-1.1476\log_e X$	-0.84	0.01
Tsuga heterophylla (entire plot)	HY-1	13	$\log_e Y = 6.6700-1.3430\log_e X$	-0.81	0.001
Abies amabilis	HY-1	9	$\log_e Y = 5.0312-0.7902\log_e X$	-0.84	0.01
Pseudotsuga menziesii	HY-2	6	$\log_e Y = 3.8042-0.2024\log_e X$	-0.17	NS
Pseudotsuga menziesii (Dead + live stems)	HY-2	6	$\log_e Y = 7.0981-1.0553\log_e X$	-0.74	NS
Tsuga heterophylla	HY-2	8	$\log_e Y = 5.9155-0.8930\log_e X$	-0.94	0.001
Abies amabilis	HY-2	7	$\log_e Y = 4.9687-0.7199\log_e X$	-0.77	0.05
Age-class distributions					
Tsuga heterophylla (northern half of plot)	HY-1	13	$\log_e Y = 6.8706-1.0391\log_e X$	-0.61	0.05
Abies amabilis	HY-1	23	$\log_e Y = 6.2092-1.0223\log_e X$	-0.68	0.001

in the last 50 years than in the preceeding 40 years. The use of the power function model with size-class distributions, assuming size represents age, could therefore lead to an erroneous interpretation of population structure (especially mortality patterns) for these two species.

In plot HY-2, the size-class distributions of Tsuga heterophylla and Abies amabilis are well described by the power function model, again suggesting a continual replacement of stems from a large cohort of seedlings and small individuals (Table 5). The even-aged Pseudotsuga menziesii population is not well described by the model, but when all dead stems $\leq$ 64 cm dbh are included with live stems $\leq$ 64 cm dbh the relationship, although not significant, is vastly improved. This could suggest that mortality decreases over time but is difficult to assess because many of the small trees (< 5 cm dbh) have decomposed and were therefore unrecorded.

DISCUSSION

Both size- and age-class frequency distributions provided useful information for the interpretation of population dynamics in the two plots. However, due to variability in the relationship between size and age, size-class analysis alone was insufficient to interpret forest development. For the relatively shade intolerant Pseudotsuga menziesii and Abies procera, which usually regenerate in relatively even-aged stands following major disturbances, size-class analysis alone may provide some insight into population dynamics but having age information greatly improves the interpretation. However, for shade tolerant species such as Abies amabilis and Tsuga heterophylla age information is essential. These species regenerate both in even-aged patches following catastrophic events and in canopy openings created by lesser disturbances, such as small windfalls. Also, as in HY-2, both species can regenerate continuously under a Pseudotsuga menziesii canopy. These differences in regeneration result in patches of different sizes and ages within an area of forest, and, consequently, the size/age relationships for a species are dependent on how many of each of these differently aged groups are present in the sample as well as on the circumstances which originated the patches. In studies of age structure over large tracts of forest it is difficult to differentiate these age groups and hence an interpretation of the age/size relationship is difficult. Furthermore, the goodness of fit of size- or age-class distributions to either a negative exponential or power function model is dependent on the abundance of differently aged groups in the sample. For example, in HY-1 the Abies amabilis age structure is not described well by either model, but combining all stems from both plots produces a composite age structure which fits the models well.

The inclusion of dead stems further enhances the understanding of present stand structure and aids in the interpretation of forest development over time. The use of age- and size-classes for spatial analysis and in the chi-square associations further demonstrates the benefits of using a combination of age and size information. Several authors have suggested that size is more important than age in studies of tree population dynamics (Buchholz & Pickering 1978, Knowles & Grant 1983, Peet 1976). However, for the forests studied direct age determination revealed patterns not obvious from the diameter distributions. Therefore, the author concurs with Ross, Sharik & Smith (1982) and others that age is of primary importance in any reconstruction of stand history. In lieu of a large age sample, at least some age data are required, along with information on spatial distribution of tree species.

The power function model provided little additional information besides that which could be assessed visually from the age and size frequency histograms. The goodness of fit of size or age structures to either the power function or negative exponential model is a reflection of both the area considered and the number and extent of disturbances that have affected it. If a large forest area is considered or if all main canopy and understorey tree species are included in one analysis, then a good fit to either model is conceivable (Christensen 1977, Harcombe & Marks 1978, Muller 1982).

This may indicate a 'steady-state' condition over a large area but says little about population dynamics of individual species or local areas. Furthermore, if detailed age information is not collected and either model is applied to size structures, a misleading interpretation of species or whole forest tree age structures may result (e.g. Muller 1982).

The frequency and pattern of fires in these stands are different from those documented for other areas in the western Cascades. For example, fires in the study area have been more frequent and less destructive than described for Mount Rainier National Park (Franklin & Hemstrom 1981, Hemstrom & Franklin 1982). The two forest plots described have somewhat similar recent fire disturbance histories but quite different structures. Plot HY-1, with emergent, old-growth *Pseudotsuga menziesii*, is now dominated by main canopy *Tsuga heterophylla* and *Abies procera*. In contrast, plot HY-2, subjected to the same fire in 1893, is dominated by *Pseudotsuga menziesii*. Variations in fire intensity and species life history characteristics may account for much of the difference in present structure.

The four common conifers in these stands can be separated on the basis of many different life history characteristics including: seed crop size and frequency, seed size and distance of dissemination, degree of vegetative reproduction, shade tolerance, and resistance of various life stages to fire, snow, windthrow, insects, animals, disease and drought (Christy 1982, Christy & Mack 1984, Gashwiler 1970, Isaac 1930, Minore 1979, Thornburgh 1969). These life history characteristics all may potentially affect species population structures but must be considered in the context of the influence of natural disturbances; disturbance type, frequency, intensity, and scale are all important. In the study area, local windthrow has occurred but intermittent fires of variable intensity have had the major effects on forest development. Although it is impossible to reconstruct the pattern of the older fires, the approximate area and probable nature of the 1893 fire can be inferred; this disturbance has had the most important influence on present stand structure.

In stand HY-1, the 1893 fire must have been of variable intensity; in some areas all trees were killed while, in others, trees were scarred but lived. All 4 canopy species survived, providing seed during invasion of the openings created. These openings remained sheltered by a scattered *Pseudotsuga* canopy; *Tsuga heteropyhlla* and *Abies procera* were the most successful invaders into them. Chance events are especially important determinants of forest development; it is possible that these species had the best seed years shortly after the disturbance. However, certain life history characteristics may have favoured *Tsuga* and *Abies procera*; both also have rapid growth rates and can quickly attain dominance on a site (Franklin 1964a, Kotar 1972). On the other hand, *Abies amabilis* must reach a certain height or 'social position' in the canopy before it produces much seed (Long 1976). Since, at the time of the 1893 fire, most *Abies amabilis* in the area would have been suppressed individuals < 100 years old, they probably produced very little seed. The absence of *Pseudotsuga menziesii* < 90 years old over most of the plot may result from the susceptibility of small stems of this species to repeated snow breakage (Minore 1979); this would be possible if heavy snowfalls occurred in consecutive years. Recent regeneration of all species has been limited beneath the dense *Tsuga* canopy; even though *Tsuga* and *Abies amabilis* are extremely shade tolerant, they have established only in canopy openings. Furthermore, since most of the old-growth *Pseudotsuga* survived the 1893 fire, the availability of log substrates for seedling establisment is limited. As noted by Christy & Mack (1984), the age-class structures of *Tsuga heterophylla* juveniles may be related to the amount of fallen wood of an appropriate decay class on the forest floor.

Regeneration following the same fire in HY-2 followed a different pattern. The *c*. 1862 fire probably destroyed the previous old-growth *Pseudotsuga*. The 1893 fire destroyed most of the resulting young stand, creating large openings. On such open south-facing sites seedlings of shade-intolerant species with greater tolerance to summer drought, such as Pseudotsuga menziesii, would be favoured. A lesser tolerance to drought and greater distances from a seed source probably reduced early Abies establishment on this plot. The large number of more recent Abies amabilis may have resulted from highly favourable conditions under the Pseudotsuga canopy and seed input from a few trees that survived the last fire. Direct observation suggests that snowpack is shallower and its duration shorter in HY-2, affecting Pseudotsuga less adversely than in HY-1. Woody material would have decomposed sufficiently following the c. 1862 fire to provide an ideal substrate for establishment following the 1893 fire, resulting in establishment of many of the current population on it (Table 2). Seedling populations have also been been enhanced by the decomposition of trees killed by the 1893 fire. Therefore, in contrast to HY-1, abundant regeneration is currently possible due to more suitable substrates and probably to greater light penetrating the Pseudotsuga canopy.

The different stand development between HY-1 and HY-2 suggests that the initial colonizers after disturbance have important effects on subsequent tree regeneration (cf. 'initial floristic composition' of Egler (1954)). If Pseudotsuga establishes first, then regeneration of Tsuga and often Abies amabilis may occur; if, however, Tsuga dominates early after fire, regeneration may be excluded or remain at a low level until canopy openings are formed.

This detailed study of the population dynamics of two conifer stands revealed important aspects of pattern and process in the transition zone forests. As emphasized by Harper (1982), such studies may further substantiate Watt's (1947) view of the regeneration complex as the appropriate level to view community change.

III. STRUCTURE AND DYNAMICS OF OLD-GROWTH *PSEUDOTSUGA* FORESTS IN THE WESTERN CASCADES, OREGON

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ABSTRACT

The dynamics of old-growth forests dominated by *Pseudotsuga menziesii* at mid-elevations in the central western Cascade Range of Oregon are inferred from detailed stand structural analyses. In the absence of holocaustic fires, the shade intolerant *Pseudotsuga* is being replaced by the shade tolerant species, *Tsuga heterophylla* and *Abies amabilis*. Although large, destructive fires are important determinants of forest structure, more frequent, less catastrophic disturbances are also important.

Partial burns often allow regeneration of conifers other than *Pseudotsuga*, frequently resulting in a mosaic of stands of different composition and structure. The species that dominates after such a fire strongly influences subsequent regeneration. If it is *Pseudotsuga*, regeneration of other conifers is often rapid and understory plants frequently are abundant. On the other hand, if substantial *Tsuga* establishes early, subsequent regeneration may be absent and understory plants rare or held at a low level until canopy openings are formed.

Several key regeneration processes depend on the composition of the main canopy. Firstly, differences in available light occur under different canopy species that influence the abundance of tree seedlings and cover of herbaceous species. Also, windfalls of old-growth trees, large branches, and snags often create canopy openings that are colonized by new seedlings or filled by previously

suppressed individuals. A third contributor to regeneration is the abundance of decaying logs and stumps as substrates for establishment of some species, especially Tsuga heterophylla.

Due to repeated disturbance, the old-growth forests described, therefore, are not in a steady-state condition. In such a disturbed situation I suggest that the vegetation be viewed as a non-equilibrium system in which succession can be understood using the concept of patch dynamics. Patches of forest of different size and structure are the result of the interactions of species availabilities, adaptations, and a complex disturbance regime.

INTRODUCTION

In a climax or 'steady-state' forest (sensu Whittaker 1975) there must be a balance between income and loss of individuals in order to maintain a relatively constant species composition and structure over time. Two important considerations significantly affect whether one believes any forest to be in a steady state: (1) the influence of natural disturbances and (2) the scale at which it is viewed. For example, in some forests and woodlands, if disturbances are of small size and low frequency, on the scale of the single stand (one to a few hectares), these communities may appear to be in a steady-state. However, the steady-state condition may not be restricted only to areas with a low frequency of small disturbances. For example, the _Pinus ponderosa_* forests of central Oregon had a high frequency of natural fires (a fire every 6-18 years) but they were extremely stable in structure and composition (Martin 1982, Weaver 1943, Wright 1978). Also, if the time considered is great enough or the area studied small enough, then no forest community could be considered to be in a steady-state. For example, in forests that suffer massive disturbances at infrequent intervals equivalent to or shorter than the life span of the dominant trees, no stand could achieve stability in composition (Heinselman 1973, Oliver 1981). However, within such a system, landscape units of several hundred or thousand hectares could be considered stable, because stands of all ages could be included in a dynamic landscape equilibrium. Also, as a forest recovers from major catastrophe, the rate of community change decreases with succession (Whitmore 1982).

Natural disturbances frequently prevent the attainment of the steady-state condition. Our increased understanding of the influence of disturbances has led to revised concepts of forest succession (White 1979) and a decline in the use of developmental

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* Nomenclature follows Hitchcock and Cronquist (1973).

models of vegetation change (Connell and Slatyer 1977, Drury and Nisbet 1971, 1973).

In the western Cascade Range of Washington and Oregon secondary forest succession in the absence of disturbance has been well documented. Large, infrequent catastrophic fires result in relatively even-aged forest stands that are widespread over the landscape (Franklin and Hemstrom 1981, Hemstrom and Franklin 1982, Kilgore 1981). The dominant pioneer species in these stands is Douglas-fir (*Pseudotsuga menziesii*), although at higher elevations it may be noble fir (*Abies procera*). *Pseudotsuga menziesii* and *Abies procera* regenerate and grow vigorously on surfaces created by fire. Regeneration of *Pseudotsuga* is usually absent in old-growth forests in the absence of subsequent fires (except on dry sites, e.g., Means 1982b) and a shift in composition and structure to shade tolerant species such as western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*) generally occurs (Franklin and Dyrness 1973, Franklin and Hemstrom 1981, Franklin et al. 1981, Isaac 1943, Munger 1930, 1940).

However, at the individual stand or watershed level (one to several hundred hectares) these forests are often subjected to recurrent disturbances of smaller size and lesser intensity (Chapter II). In the northeastern American deciduous hardwood forests, it has been suggested that the formation of canopy openings of various sizes due to small scale disturbances favor species with different life history strategies (Brewer and Merritt 1978, Forcier 1975, Fox 1977, Runkle 1979, Woods and Whittaker 1981). The present study focuses on changes at the individual stand level and considers them relative to concepts of forest succession. The aim of this paper is to evaluate the hypothesis that regeneration of the tree species present is a function of their different life histories and the size of the gap created by the disturbance (cf. Pickett 1976, 1980, Watt 1947, Whitmore 1982).

THE WESTERN OREGON CASCADE RANGE

The Cascade Range in Oregon includes two distinct physiographic provinces (Franklin and Dyrness 1973). The High Cascades, on the east, are composed of Pliocene to recent andesite and basalt flows, cinder cones and all the major volcanic peaks in the state. The Western Cascades resulted from volcanic activity earlier in the Cenozoic and consist of volcanic flows and pyroclastic rocks which have been modified by subsequent glaciation and erosion (Wells and Peck 1961). Numerous small glaciers in the Pleistocene left steep headwalls and cirques in the upper valleys and differential erosion on the boundaries between rock types has also strongly enhanced the development of a steep, incised ridge and valley topography (Peck et al. 1964). Two major soil groups are recognized in the province: those derived from pyroclastic materials (principally tuffs and breccias) and those formed from basic igneous rocks, mainly basalt and andesite (Franklin and Dyrness 1973).

The Pacific Ocean exerts a maritime influence on the Cascade Range, which experiences a mediterranean climate of cool, wet winters and warm, relatively dry summers. An increase in elevation results in greater precipitation and snowfall, with a corresponding decrease in temperature. Rainfall, except in localised rain shadow areas, generally exceeds 1500 mm annually and may reach 3-4000 mm on west-facing slopes (Lahey 1973). Such abrupt changes in moisture and temperature over short distances in broken mountain topography act as the primary environmental controls of plant community composition and structure (Dyrness et al. 1974, Zobel et al. 1976).

There are several forest types in the western Oregon Cascade Range, most dominated by conifers; in the central portion of the range, the forests are classified into two major zones differentiated by the potential climax tree species (Franklin and Dyrness 1973). The *Tsuga heterophylla* zone lies between c. 300 and 1050 meters and the *Abies amabilis* zone begins at c. 1050 and extends to 1550 meters elevation. Within these zones, communities are usually differentiated by the importance of shrub and herb species, rather than their presence, since many are widely distributed (Dyrness et al. 1974). In the upper portions of the Tsuga and lower portions of the Abies zone (referred to as the "transition zone"; c. 1000-1300 m), both Tsuga and Abies may assume a climax role (Franklin and Dyrness 1973). This study is concerned with the forests of the transition zone in the central Western Cascade Range (Fig. 9).

Before the arrival of Europeans, Indians set many fires in these mountains, predominantly to increase the available area of berry fields (Burke 1979). Subsequently, European settlers greatly increased fire frequency in the mountains by activities such as grazing, road construction, logging and recreation. Fire, coupled with prolonged dry summers and convective easterly winds, often led to catastrophic conditions. Two common tree age-classes in the region resulted from holocaustic fires (c. 140 and c. 450 years old). Many areas, however, have also experienced frequent lighter burns, especially during the late 19th and early 20th centuries. Younger tree age-classes are often present as even-aged stands or as an understory component of old-growth forest.

METHODS

Selection of study sites

Four localities were selected (Fig. 9) for sampling which possessed: (i) a main canopy of trees at least 250 years old or with the structural characteristics that qualify the forest as 'old-growth' (sensu Franklin et al. 1981); (ii) tree species composition 'representative' of the transition zone; (iii) upland, well drained soils; and (iv) no evidence of man-related disturbance such as logging. Several plots with few trees in excess of 120 years of age (eg. plots HY-5 and SM-1) were located in a matrix of old-growth, so were sampled. Judgements about whether an area was representative were based upon extensive reconnaissance and comparison with U.S. Forest Service forest inventories.

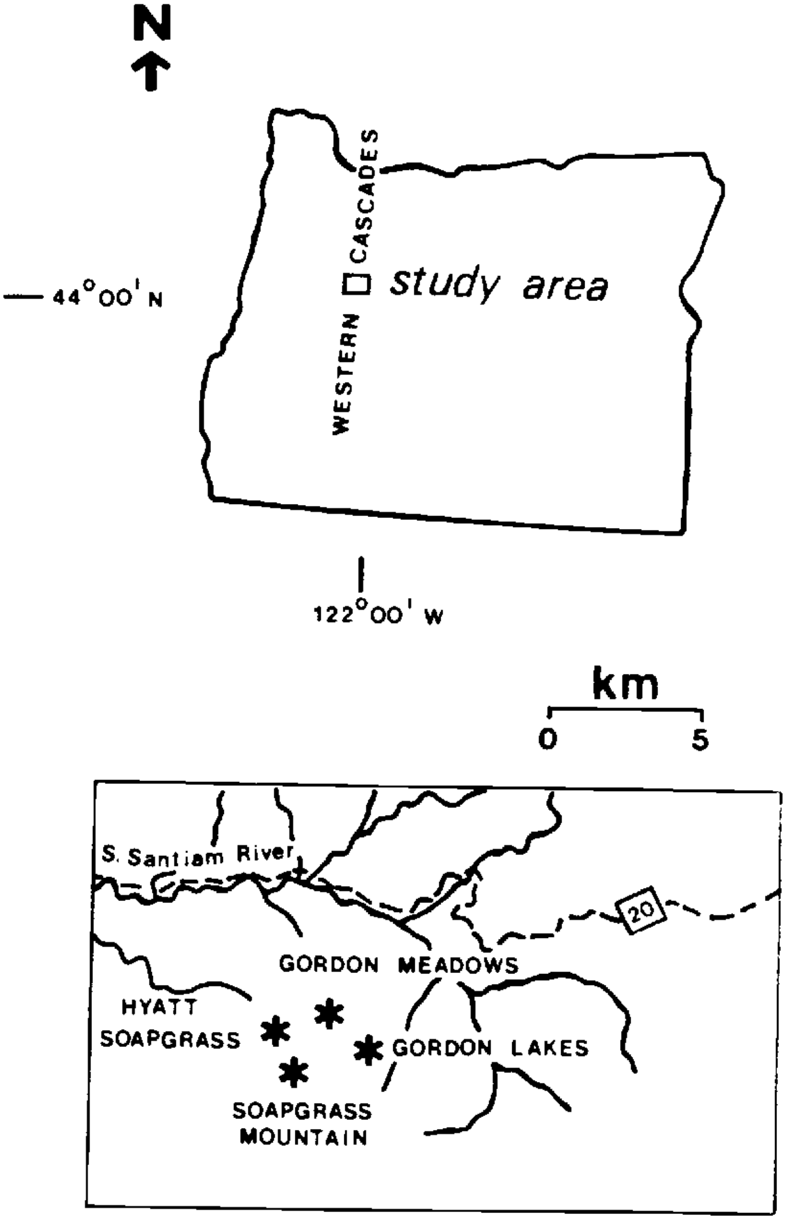


FIGURE 9: Map of Oregon showing location of study sites. Stars indicate study locations, the dashed line indicates a highway.

In each area 1 - 5 plots 0.19 - 0.80 ha were sampled (Table 6). These plots represent a range of structural types differentiated by species composition and by the time since disturbance. Because my primary objective was the interpretation of patterns of regeneration of various species in different types of habitat and forest, similar structural types in the same general habitat were not repetitively sampled.

Analysis of stand structure

Tree diameters at breast height (dbh) of all individuals $\geq$ 5 cm dbh were measured. The numbers of saplings (i.e. trees < 5 cm dbh but at least 1.4 m tall) and seedlings (stems 0.1 - 1.4 m tall) were also recorded. If an individual showed obvious signs of having established on an elevated surface such as a log, stump, trunk buttress, or upturned root plate, this was recorded. Stumps, dead standing trees and dead saplings were also measured and, if possible, identified to species.

Using tree size-class analysis to interpret stand dynamics assumes a consistently positive relationship between diameter and age. However, detailed analysis of plots HY-1 and HY-2 (see Chapter II) revealed that for all species age may be at best only approximated by diameter in stands that have been subject to recurrent fires. Several species, notably _Abies_ _amabilis_ and _Tsuga_ _heterophylla_, regenerate both under relatively closed canopies and in openings. As a result, trees of similar age can have very different growth rates in the same stand, causing a weak relationship between diameter and age. Even if the disturbance history of an area is known, it is very helpful to have information about age, spatial relationships, and the species' life history in addition to size-class analysis, to interpret stand dynamics (see Chapter II). Therefore, in each plot (except HY-1 and HY-2) from 16-66 trees were aged, the number aged being greater for the more structurally complex stands. Ages at Hyatt Soapgrass were obtained from increment cores (HY-3, HY-4) and for larger trees from stumps

TABLE 6: Study site characteristics

LOCATION AND PLOT	DOMINANTS OF THE MAIN CANOPY	ELEVATION (m)	ASPECT	SLOPE (°)	SAMPLE PLOT DIMENSIONS (m)
Hyatt Soapgrass					
HY-1	*Pseudotsuga menziesii*-*Tsuga heterophylla*-*Abies procera*-*Abies amabilis*	1220	S	0-5	100 x 80
HY-2	*Pseudotsuga menziesii*-*Tsuga heterophylla*	1180	S	10	60 x 60
HY-3	*Tsuga heterophylla*-*Pseudotsuga menziesii*	1170	SW	10	54 x 36
HY-4	*Pseudotsuga menziesii*-*Tsuga heterophylla*	1140	SW	10	54 x 54
HY-5	*Abies procera*	1200	-	Flat	54 x 36
Gordon Lakes					
GL-1	*Abies procera*-*Tsuga heterophylla*-*Abies amabilis*	1190	N	0-20	80 x 60
Gordon Meadows					
GM-1	*Tsuga heterophylla*-*Abies amabilis*	1280	-	undulating	54 x 42
GM-2	*Abies amabilis*-*Tsuga heterophylla*-*Pseudotsuga menziesii*-*Abies procera*	1250	NW	0-3	66 x 54
Soapgrass Mountain					
SM-1	*Pseudotsuga menziesii*	1140	SE	15	54 x 54
SM-2	*Tsuga heterophylla*-*Pseudotsuga menziesii*	1140	SE	15	60 x 36

left following logging (HY-3, HY-4, HY-5) and corrected for growth to aging height (see Chapter II). In all other plots increment cores were extracted at c. 30 cm above ground level; ages reported for these plots have no correction for growth to 30 cm. In some instances trees were too large to be increment cored; in a few of these cases, ages were estimated from stumps of similar-sized trees on adjacent clearcuts. The stumps of these trees indicated that the previous forest was of a similar structure to that in the plots sampled.

For each plot I prepared size-structure diagrams to depict the frequency of seedlings, saplings, and of stems in 10 cm size classes beginning at 5 cm. The age-class distributions of all species were pooled together in each stand into 10 year age classes.

To describe the vertical component of stand structure, trees $\geq$ 5 cm dbh were classified into: emergent, upper main canopy, lower main canopy, below main canopy, and overtopped. Due to the presence of species with different growth rates and varying tolerances to dense forest conditions, these categories do not necessarily indicate vigor of an individual tree nor its probability of survival to maturity. They only approximate the predominant, dominant, codominant, intermediate and suppressed categories often applied to even-aged stands. The vertical structure was also depicted by vegetation profiles drawn for forest strips 50 x 3-5 m, width depending on tree density.

To assist in the interpretation of stand structure, scars created by fire and windfall were identified for each plot and aged from increment cores. Occasionally cores were extracted from trees in the surrounding forest and often fires were dated from scars on cut stumps in adjacent clearcuts. Two pits were dug in each plot to search for gross differences in soils that could account for differences in stand structure or reflect past disturbance.

Spatial pattern

The spatial dispersion of trees was assessed in all plots by mapping all individuals ≥ 10 cm tall in 3 x 3 m or 5 x 5 m (plots GL-1 and HY-1 only) contiguous quadrats in blocks of 192 - 540 quadrats. This mapping permitted application of a variation of the nested quadrat technique (Greig-Smith 1983, Kershaw 1973); the measure selected for determining the departure from a random distribution was Morisita's (1959) index. The application of this measure has been described by Williamson (1975) and Veblen (1979). Morisita's index is given by:

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

where q is the number of quadrats, n_i is the number of individuals in the ith quadrat, and N is the total number of individuals in all quadrats. The index I_δ is 1.0 when the population is randomly dispersed, where random implies an equal probability of each individual occurring in any one quadrat. If the individuals are aggregated, I_δ is greater than 1.0, and if evenly distributed, I_δ is less than 1.0.

Morisita's index, I_δ, was computed for different species and size-classes for quadrats of increasing size, beginning with quadrats of 3 x 3 m or 5 x 5 m. Quadrat sizes for plot HY-3, for example, would therefore be 3 x 3m ($9m^2$), 6 x 6 m ($36m^2$), 9 x 9 m ($81m^2$), and so on. For quadrat sizes < 9 x 9 units (< 8 x 8 units for plots HY-1 and GL-1 and < 6 x 6 units for plot SM-2) the original quadrats were grouped into perfect squares, thus avoiding fluctuations in I_δ due to a change in the shape of the blocks of quadrats (Pielou 1977). Larger blocks of quadrats were rectangles 9 x 10, 9 x 11, 9 x 12 units, and so on (8 x 9, 8 x 10, 8 x 11, etc. for HY-1 and GL-1 and 6 x 7, 6 x 8, 6 x 9, etc. for SM-2). All quadrat sizes are reported as areas in square meters. In cases where the quadrat sizes were not evenly divisible into the total area, I_δ was computed for the largest subareas containing whole quadrats of a given size. In such instances the average index was computed from the results obtained from different subareas of the total grid of 3 x 3 m or 5 x 5 m quadrats. When the number of individuals is small, I_δ tends to vary erratically; thus I_δ was computed only for those species with at least 20 individuals in the sample.

To determine the size-classes to be used in the spatial analyses, age information and other stand structural attributes were considered. For example, in plot HY-5 all Abies procera > 25 cm dbh were analysed as one group, because there was strong evidence that the population was even-aged, and established following fire in 1893. Similarly, in plot SM-1 all Pseudotsuga menziesii were analysed as one group of relatively even-aged trees. On the other hand, for the shade tolerant Tsuga heterophylla and Abies amabilis, differently aged groups were often not as easily recognised. In instances where even-aged cohorts of these species established following fire (e.g. plot SM-2), a similar procedure to that described above for Abies procera was employed. In many cases, however, such groups were not easily recognised so large groups were used (seedlings, stems ≤ 10 cm dbh and > 10 cm dbh) to allow for considerable variation in the size-age relationship. Dead trees were included in several analyses to describe spatial dispersions at times in the past.

Tests of association

The tendency for different species to occur together at various quadrat sizes was investigated using a chi-square test (Mueller-Dombois and Ellenberg 1974). The test was applied only to species sufficiently abundant to provide adequate cell frequencies in 2 x 2 contingency tables, but not so abundant as to be present in all quadrats. The test was applied also to seedlings or stems ≤ 10 cm dbh and to canopy openings.

Understory sampling

On each unit quadrat (3 x 3 m or 5 x 5 m) in all plots, the total cover of understory species (excluding tree species) was estimated in percentage cover classes of < 1, 1-5, 6-25, 26-50, 51-75, and 76-100.

Differences in composition and cover of the understory vegetation, within stand GM-2, and between stands SM-1 and SM-2, were investigated, in relation to variation in canopy species. In and around plot GM-2, and in SM-1 and SM-2, 50-100 1 x 1 m quadrats were located in a restricted random manner, but always beneath a specified canopy condition and, except for canopy openings, within 1-3 m from the trunk. Canopy conditions in GM-2 were predominantly (1) *Tsuga heterophylla*, (2) *Pseudotsuga menziesii*/*Abies procera* and (3) canopy opening (a gap in the main canopy at least 3 m in diameter); in SM-1 the canopy tree was *Pseudotsuga menziesii* and in SM-2, *Tsuga heterophylla*.

In each 1 x 1 m quadrat, total cover of each vascular species (excluding tree species) was estimated as in the unit quadrats. Tree seedlings were counted by species, height of the tallest individual of each species measured, and the numbers rooted on fallen logs recorded.

Tree canopy density

Each unit quadrat was assessed as occurring beneath a canopy opening, closed canopy, or an intermediate canopy condition. Light conditions in each plot were assessed by the analysis of hemispherical photographs of the canopy of overstory trees (Anderson 1964). Between 5 and 24 photographs were taken (at a height of 1 m) at approximately 10 m intervals along a transect bisecting the plot longitudinally or, for plots HY-1 and HY-2, along 3 equally spaced transects. If a low branch or understory plant obstructed the view of the main canopy, the photograph was taken at a point displaced 1-2 m along the transect. The percentages of total diffuse plus direct radiation, and percentages of direct radiation, were calculated for the growing season only (May-September) (for details of the calculations from the photographs see Veblen, Veblen and Schlegel 1979).

Also, photographs were taken in plots GM-2, SM-1 and SM-2 (at 1 m above ground level) to assess radiation differences under different canopy conditions. In and around plot GM-2, 11-13 photographs were taken in randomly selected plots under each canopy condition (canopy opening, *Pseudotsuga*/*Abies* canopy and *Tsuga heterophylla* canopy). For plots SM-1 and SM-2, 8 and 11 photographs, respectively, were taken along a transect bisecting each plot longitudinally.

RESULTS

Stand structure

Hyatt Soapgrass

Plots HY-1 and HY-2

The 5 plots at Hyatt Soapgrass are highly variable in structure due to a number of disturbances over the past 450 years. At least 4 fires and one major windstorm (1962) occurred in plots HY-1 and HY-2 (see Chapter II). Plot HY-1 has large, emergent c. 362-455 year old *Pseudotsuga menziesii* and a dense main canopy of *Tsuga heterophylla* c. 60-90 years old. *Abies procera* is also locally abundant in the main canopy along with *Abies amabilis*. A few *Tsuga heterophylla* and *Abies amabilis* > 90 years old survived a fire in 1893 (Table 7). Under the *Tsuga* canopy tree regeneration is sparse or absent except where *Tsuga heterophylla* and *Abies amabilis* seedlings occur on logs and stumps in canopy openings, and where it is dense shrubs and herbs are almost entirely absent.

Plot HY-2, on the other hand, has *Pseudotsuga menziesii* of two age classes (c. 40-89 and 90-116 years old) that arose after fires in 1862 and 1893, with some *Tsuga heterophylla* and a few patches of

TABLE 7: Fire history for the plots at the four study sites

PLOT	SPECIES	NUMBER OF TREES FIRE SCARRED (1)	NUMBER OF FIRE SCARS (2)	NUMBER OF SCARS AGED (3)	APPROXIMATE FIRE DATES (4)	(5)
HY-1	*Pseudotsuga menziesii*	-	12	9	1662	1527
				1	1770	1893
				2	1893	
	Tsuga heterophylla	4	4	1	1732	1893
				3	1893	
	Abies amabilis	3	3	1	1862	1893
	Abies procera	1	1	-	-	1893
HY-2	*Pseudotsuga menziesii*	-	5	5	1893	1527
						1862
						1893
	Tsuga heterophylla	-	-	-		1862
						1893
	Abies amabilis	-	1	1	1893	1862
						1893
	Abies procera	-	-	-		1893
HY-3	*Pseudotsuga menziesii*	-	2	2	1662	1527
			1	1	1893	
	Tsuga heterophylla	1	1	1	1893	1893
HY-4	*Pseudotsuga menziesii*	-	-	-		1527
						1662
	Tsuga heterophylla	9	12	12	1893	
	Abies amabilis	1	1	1	1893	
HY-5	*Abies procera*, *Tsuga heterophylla*, *Abies amabilis* *					1893

TABLE 7: continued

GL-1	*Abies amabilis*	11	NA	4	1897	1876
	Abies procera	3	NA	1	1897	1803
						1876
	Tsuga heterophylla	5	NA	-	-	1803
						1876
	Pseudotsuga menziesii	-	NA	-		1803
GM-1	*Abies amabilis*	4	NA	1	1823	1823
				4	1913	1874
	Tsuga heterophylla	5	NA	3	1823	1874
				2	1874	
GM-2	*Abies amabilis*, *Abies procera*, *Tsuga heterophylla* *					1874
	Pseudotsuga menziesii	1	NA	1	1413	1233
				1	1543	1874
				1	1874	
SM-1	*Pseudotsuga menziesii*, *Abies procera*, *Tsuga heterophylla* *					1862
SM-2	*Tsuga heterophylla*	-	NA	-		1838
	Pseudotsuga menziesii	-	NA	-		1413

(1) Number of fire scars found on live trees during plot data collection.
(2) Number of fire scars found on cut stumps during age counts.
(3) Number of fire scars aged, and (4) corresponding dates of fires from scars aged in (3).
(5) Approximate dates of fires based on large cohorts of trees of similar age.
* = all species have similar age cohorts.
NA = stumps not aged following logging.

Abies amabilis that survived the 1893 fire. Under this less dense Pseudotsuga canopy there is abundant regeneration of Tsuga heterophylla and Abies amabilis, especially on fallen logs and stumps. Several shrubs (Vaccinium alaskense, Acer circinatum and Rhododendron macrophyllum) and many herbaceous plants (e.g. Smilicina stellata, Achlys triphylla, and Cornus canadensis) are locally abundant.

The last fire in 1893 was less intense in plot HY-1, and allowed regeneration of Tsuga heterophylla and Abies amabilis, whereas it almost destroyed the stand in plot HY-2 resulting in domination by Pseudotsuga menziesii. The other 3 plots at Hyatt Soapgrass illustrate further variations in stand structure caused by differences in fires and other disturbances.

Plot HY-3

In plot HY-3 Tsuga heterophylla almost entirely dominates the 22-25 m tall main canopy, with 11 emergent Pseudotsuga menziesii being 20-25 m taller (Fig. 10a, Table 8). The large Pseudotsuga are all 381 - 420 years old; there is one anomalous 79 year old tree (Fig. 11a, i). Many 2-5 m tall Pseudotsuga snags of similar diameters to the live trees indicate trees that died following the fire in 1893 (Table 7, Fig. 10a, 11b), which charred trunks of most live Pseudotsuga > 65 cm dbh. One Tsuga heterophylla (281 years old) survived the fire; most Tsuga established on elevated surfaces in a relatively even-sized stand after this fire (Table 9, Fig. 11c, i). Ages of 36 Tsuga (< 45 cm dbh) ranged from 44-86 years, indicating a long period of establishment. Trees of this shade tolerant species as small as 4 cm dbh were older than 40 years. Substantial mortality has occurred, however, as the 45 dead Tsuga stems 5-24 cm dbh indicate. Most Tsuga seedlings now establishing are in canopy openings, many on elevated surfaces (Table 10). Abies amabilis are rare; a few trees established following the recent fire and a small number of seedlings and saplings are present in one canopy opening (Fig. 10a, 11d). Understory plants are rare (Table 10); Berberis nervosa occasionally occurs in canopy openings.

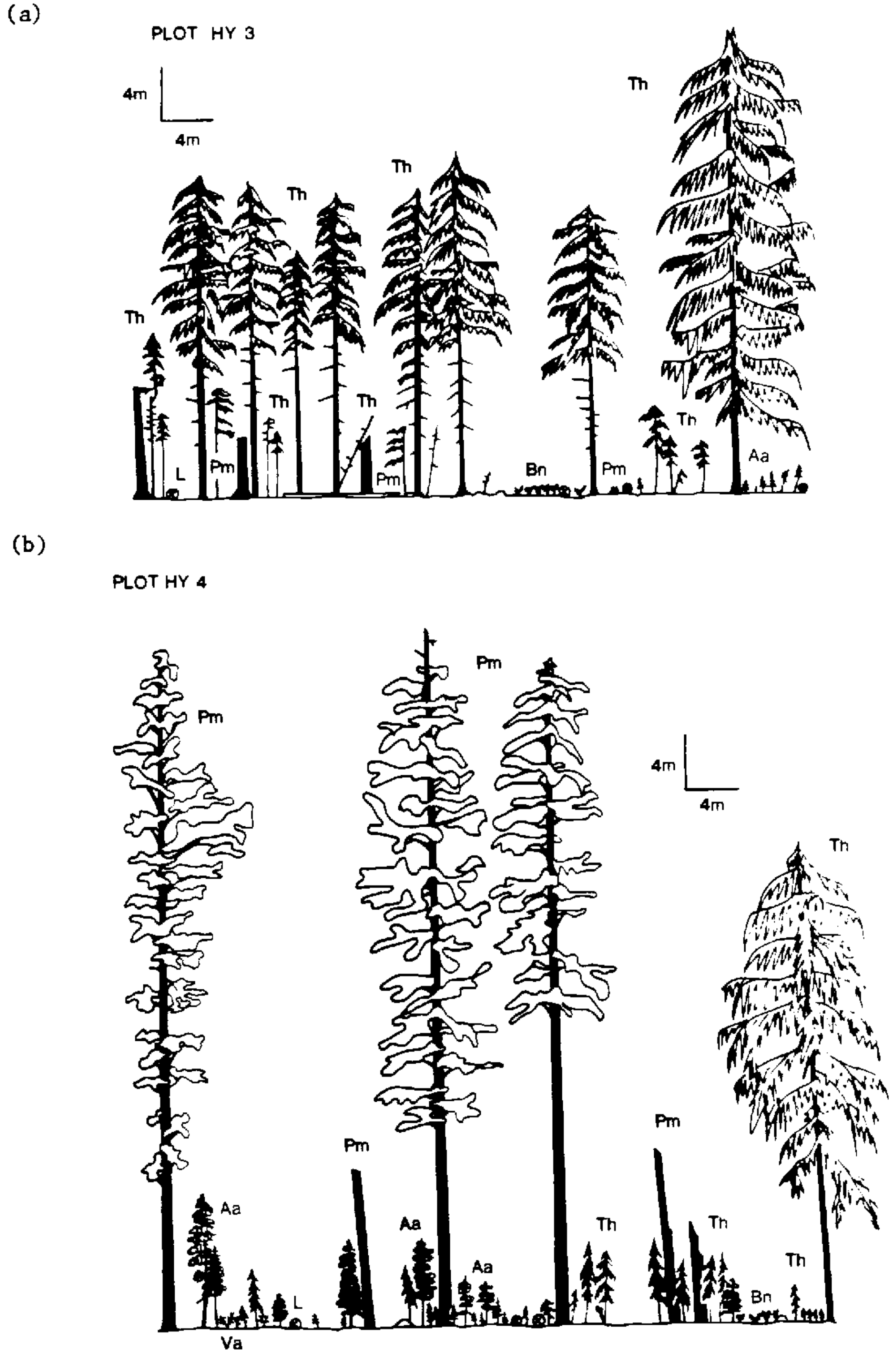
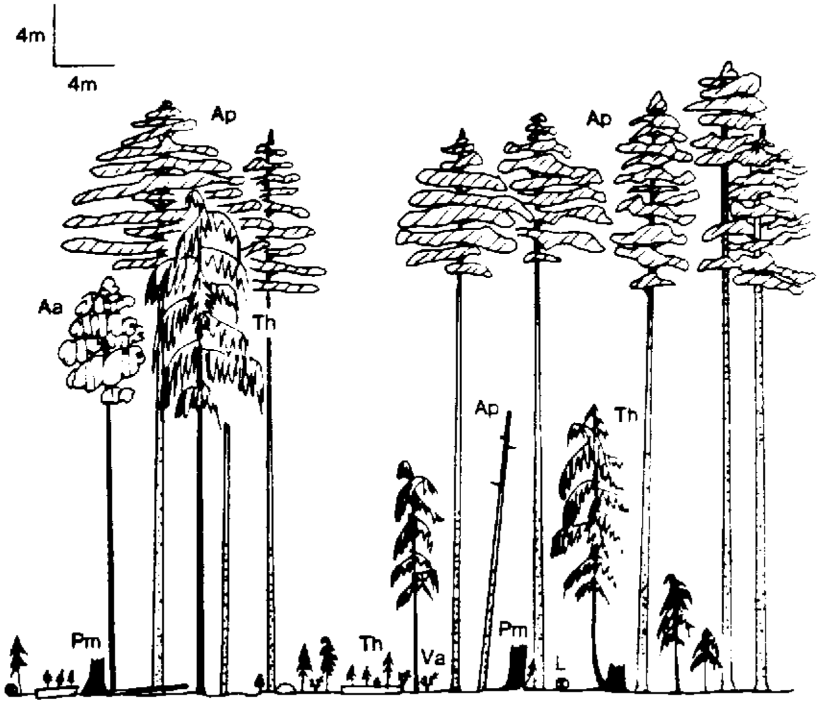


FIGURE 10: Profiles of (a) plot HY-3, (b) plot HY-4, (c) plot HY-5, and (d) plot GL-1. Pm, Pseudotsuga menziesii; Th, Tsuga heterophylla; Aa, Abies amabilis; Ap, Abies procera; Bn, Berberis nervosa; L, log; Va, Vaccinium alaskense; Oh, Oplopanax horridum; Oo, Oxalis oregana.

Figure 10: continued

(c) PLOT HY 5



(d) PLOT GL 1

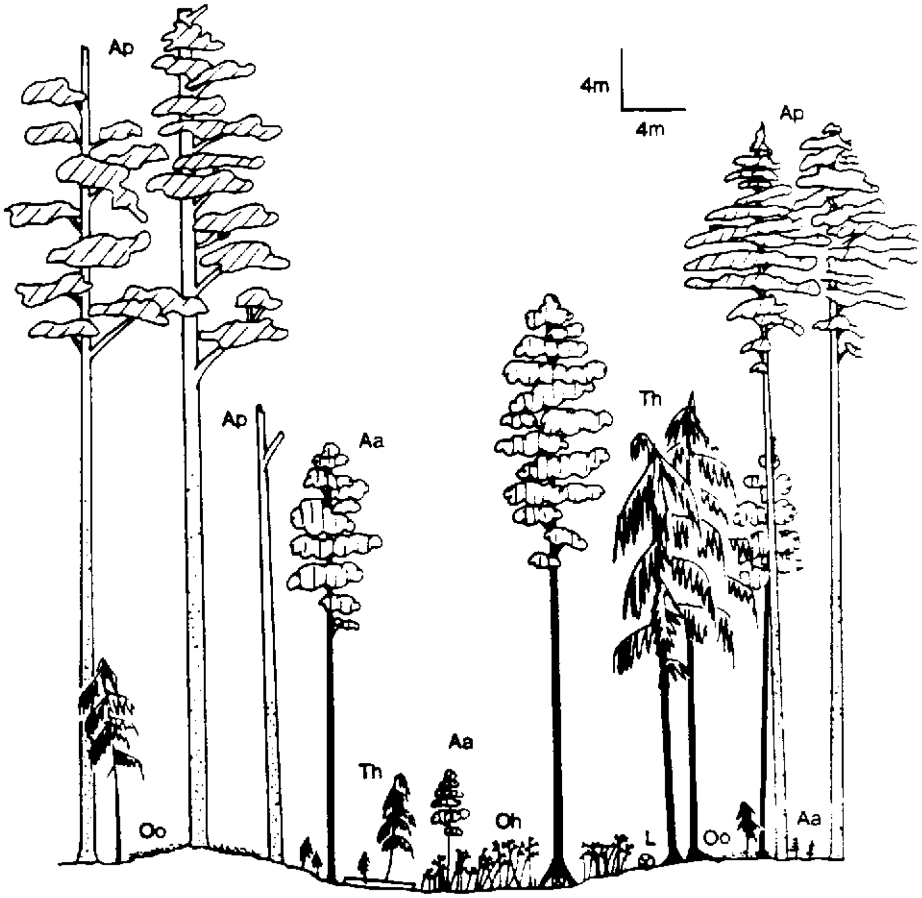
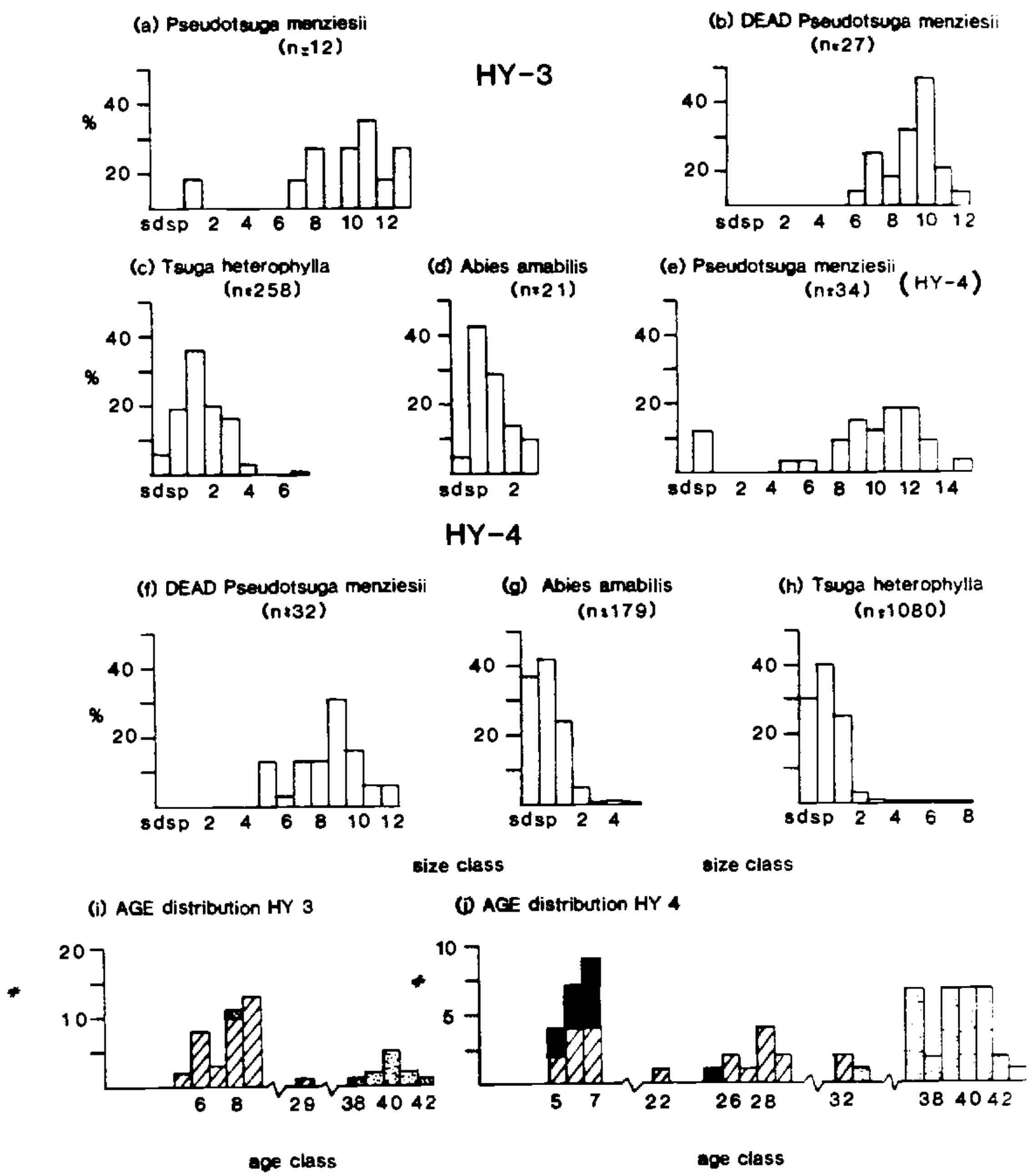


TABLE 8: Number of trees (≥ 1.4 m tall) in relative height classes on each sample plot at the 4 study sites (for plots HY-1 and HY-2 see Chapter II). The height classes are: I, overtopped; II, below main canopy; III, lower main canopy; IV, upper main canopy; and V, emergent.

PLOT	HY-3					HY-4					HY-5					GL-1				
PLOT SIZE (m^2)	1944					2916					1944					4800				
HEIGHT CLASS	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
SPECIES																				
Pseudotsuga menziesii	1				11	4				30		2		2		1			1	
Tsuga heterophylla	146	31	49	17		710	25	8	13		72	33	15	2		74	30	21	19	
Abies procera	1			1		1							20	76			1	4	27	26
Abies amabilis	15	1	3	1		102	7	1	3		3	1	3	3		49	10	8	14	

PLOT	GM-1					GM-2					SM-1					SM-2				
PLOT SIZE (m^2)	2268					3564					2916					2160				
HEIGHT CLASS	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
SPECIES																				
Pseudotsuga menziesii			1	3		1	3	7	29		14	39	111	1				1	2	13
Tsuga heterophylla	42	19	13	22		153	45	49	32		315	5				17	55	44	46	
Abies procera			2	2				4	30		9			9						
Abies amabilis	40	5	22	42		39	3	16	36		8								1	
Thuja plicata											7	1								
Castanopsis chrysophylla											3									



HY-3

(a) Pseudotsuga menziesii (n=12)

(b) DEAD Pseudotsuga menziesii (n=27)

(c) Tsuga heterophylla (n=258)

(d) Abies amabilis (n=21)

(e) Pseudotsuga menziesii (n=34) (HY-4)

HY-4

(f) DEAD Pseudotsuga menziesii (n=32)

(g) Abies amabilis (n=179)

(h) Tsuga heterophylla (n=1080)

(i) AGE distribution HY 3

(j) AGE distribution HY 4

FIGURE 11: Size- and age-class histograms for main canopy tree species in plots HY-3 and HY-4. The size-classes are: sd, seedlings; sp, saplings; 1, trees of 5-14 cm dbh; 2, dbh 15-24 cm; 3, dbh 25-34 cm; etc. n is the number of trees ≥ 0.1 m tall. The age-classes are: 1, 1-10 years; 2, 11-20 years; 3, 21-30 years; etc. ▨, Tsuga heterophylla; ░, Pseudotsuga menziesii; ☐, Abies procera; ■, Abies amabilis.

TABLE 9: Percentage of saplings and stems ≥ 5 cm dbh of tree species established on elevated surfaces (logs, stumps, trunk buttresses, or upturned root plates) at the 4 study sites.

	PLOT							
SPECIES	HY-3	HY-4	HY-5	GL-1	GM-1	GM-2	SM-1	SM-2
Pseudotsuga menziesii	0.0	0.0	50.0	0.0	50.0	10.0	0.6	0.0
Tsuga heterophylla	57.6	52.9	63.1	79.2	65.3	72.0	82.2	25.9
Abies procera		0.0	34.4	0.0	0.0	16.7	5.6	
Abies amabilis	20.0	15.0	10.0	25.9	35.8	34.8	50.0	0.0
Thuja plicata							37.5	

TABLE 10: Number of seedlings (< 1.4 m tall) of dominant tree species per hectare at the 4 study sites. The numbers in parentheses refer to percentages of seedlings rooted on stumps, fallen logs, upturned root plates and trunk buttresses. Mean understory cover for each plot is also included.

	PLOT							
SPECIES	HY-3	HY-4	HY-5	GL-1	GM-1	GM-2	SM-1	SM-2
Tsuga heterophylla	77 (60.0)	1 111 (80.0)	864 (94.0)	546 (98.1)	66 (93.0)	258 (100.0)	3 158 (90.6)	9 (100.0)
Abies amabilis	5 (0.0)	226 (2.0)	87 (53.0)	306 (51.0)	362 (8.5)	637 (26.0)	168 (36.7)	9 (0.0)
Abies procera	5 (0.0)	10 (0.0)				6 (0.0)	233 (60.3)	
Thuja plicata							21 (66.7)	

PLOT	HY-1	HY-2	HY-3	HY-4	HY-5	GL-1	GM-1	GM-2	SM-1	SM-2
MEAN UNDERSTORY COVER (%)	3.4	28.3	4.6	26.6	13.2	61.0	13.1	12.5	63.8	4.2

Plot HY-4

Many live, emergent *Pseudotsuga menziesii* are present in adjacent plot HY-4 (Table 8). A main canopy is almost absent from this stand; both *Tsuga heterophylla* and *Abies amabilis* are abundant and form a dense tier of overtopped to below main canopy trees at 4-6 meters (Table 8, Fig. 10b). *Vaccinium alaskense*, *Chimaphila* spp., *Achlys triphylla* and *Smilacina stellata* are locally common in open areas.

Apart from 4 saplings that established following the 1893 fire, all other *Pseudotsuga* form a relatively even-sized population (Fig. 11e). As in plot HY-3 these trees range in age, in this instance from 361-430 years; one anomalous tree in the 321-330 year age-class may have established after the c. 1662 fire (Fig. 11j). Some of the large dead *Pseudotsuga* were probably killed by the 1893 fire (Table 7, Fig. 11f). Small *Abies amabilis* and *Tsuga heterophylla* are abundant (Fig. 11g, h), many *Tsuga* are on elevated surfaces (Table 9). All 12 *Tsuga heterophylla* > 43 cm dbh were aged and were from 211-320 years old (Fig. 11j). Twenty *Abies amabilis* and *Tsuga heterophylla* 2-10 cm dbh ranged in age from 42-67 years (Fig. 11j).

The largest *Pseudotsuga* probably arose following the c. 1527 fire (Table 7); only a few were killed in 1893 (Fig. 11e, f, j). The density of the surviving canopy probably delayed regeneration (Fig. 11j) and may indicate that the old-growth *Pseudotsuga* took a while to die and fall after the fire. Recently, many old trees have died, creating canopy openings which *Abies amabilis* and *Tsuga heterophylla* are filling.

Plot HY-5

Plot HY-5 differs structurally from the other plots at Hyatt Soapgrass; *Abies procera* dominates the main canopy at 35-40 m, with some *Tsuga heterophylla* and a few *Abies amabilis* in the lower main canopy (Table 8, Fig. 10c). Most *Tsuga* and many *Abies procera* occur on elevated surfaces, as do most small *Tsuga heterophylla* in canopy openings (Table 9, 10). *Vaccinium alaskense* is locally abundant in openings.

Both *Tsuga heterophylla* and *Abies amabilis* have similar size-class distributions (Fig. 12a, b); Many older trees of both species were of similar age to the dominant *Abies procera* (Fig. 12a, b, d, k). Live *Pseudotsuga menziesii* are rare in HY-5 (Table 8). *Pseudotsuga* stumps, many of similar diameter to the live populations in plots HY-1, HY-3 and HY-4, are numerous (Fig. 12c). *Abies procera* is relatively uniform in size and age (Fig. 12d, k).

The even-aged nature of this young forest, and fire scars in plot HY-1 c. 250 m distant suggest that the 1893 fire destroyed old-growth *Pseudotsuga*, allowing establishment of dense *Abies procera*.

Gordon Lakes

Plot GL-1

On the north-facing slopes above Gordon Lakes, old-growth forests of *Abies procera* and *Pseudotsuga menziesii* are interrupted by *Alnus sinuata* communities that occur in snow chutes. In plot GL-1, emergent *Abies procera* are up to 55 m tall with the main canopy 5-10 m shorter (Table 8, Fig. 10d). In part of the plot, *Oplopanax horridum* is abundant along a seep; under the old-growth *Abies procera*, *Oxalis oregana* and *Smilacina stellata* form a dense mat (Fig. 10d).

Two cohorts of *Abies procera* are present (Fig. 12e, l). *Pseudotsuga menziesii* stumps measured up to 2 meters in diameter; live *Pseudotsuga* were rare (Table 8, Fig. 12f). *Abies amabilis* and *Tsuga heterophylla* are represented by a range of sizes and ages (Fig. 12g, h, l). Numerous *Abies procera* and *Abies amabilis* established c. 110 years ago, but died (Table 7, Fig. 12i, j).

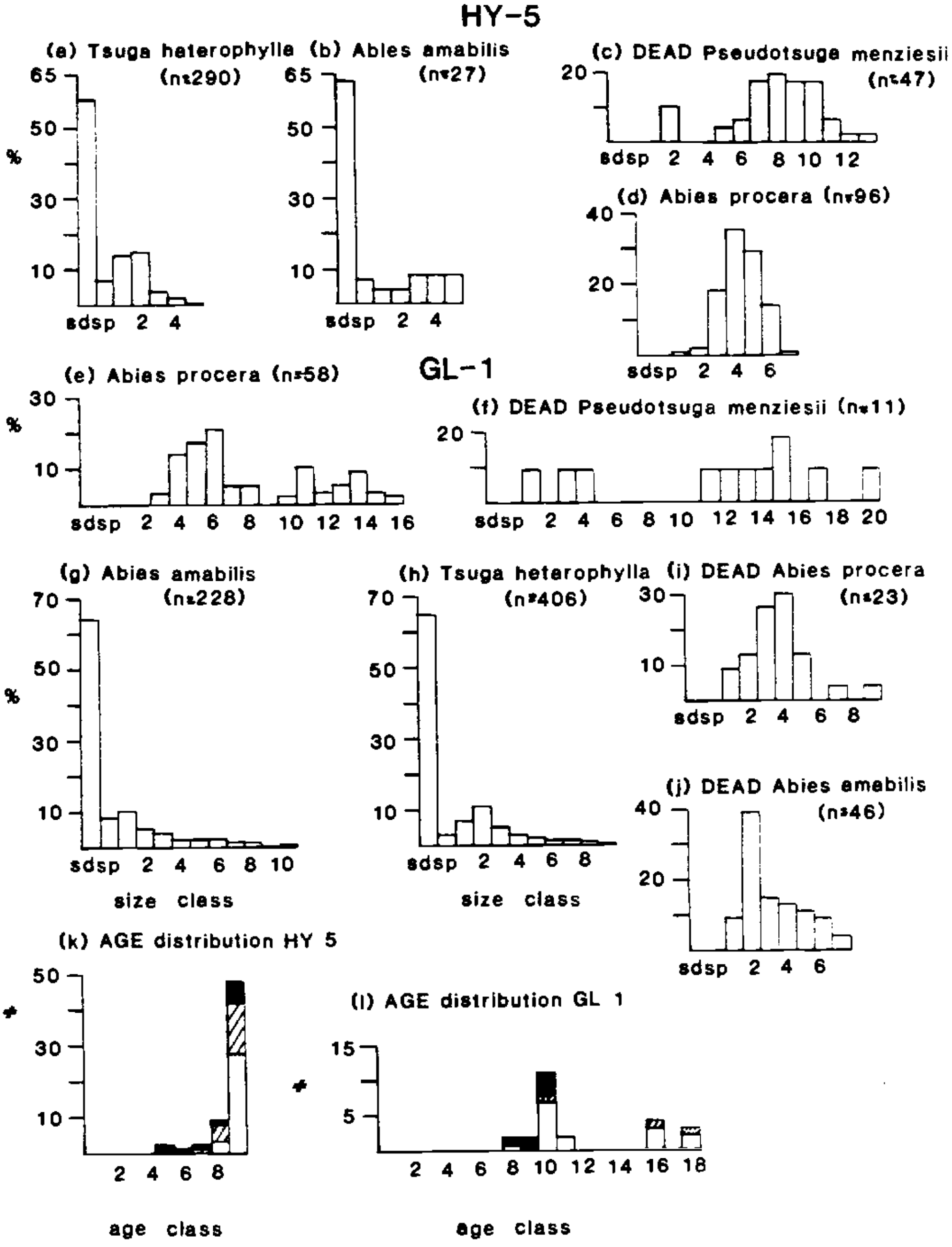


FIGURE 12: Size- and age-class histograms for main canopy tree species in plots HY-5 and GL-1. The size- and age classes and *n* are the same as in FIG. 11.

Approximately 175-180 years ago, a fire initiated the canopy trees (Table 7). Increases in annual ring widths on several large *Abies procera* and *Pseudotsuga menziesii* and the age of the younger main canopy trees suggest a fire c. 107 years ago in part of the plot; a stand of *Tsuga heterophylla*, *Abies procera* and *Abies amabilis* resulted. Several *Abies amabilis* have fire scars from a localised fire c. 86 years ago.

Gordon Meadows

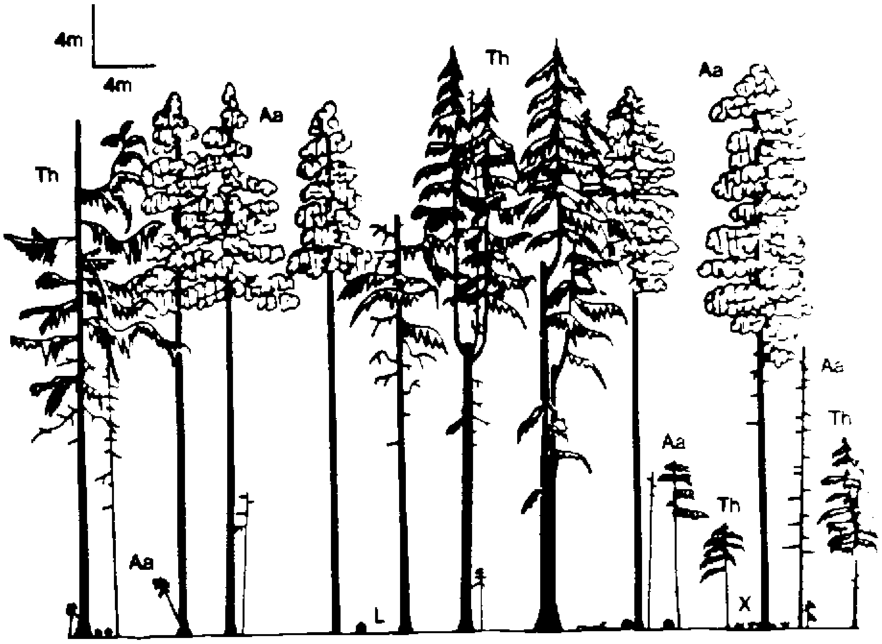
Plots GM-1 and GM-2 support varying mixtures of *Tsuga heterophylla*, *Abies procera*, *Abies amabilis* and *Pseudotsuga menziesii*; occasional old-growth *Pseudotsuga* are also present in the area.

Plot GM-1

Plot GM-1 is dominated by *Tsuga heterophylla* and *Abies amabilis* (Table 8). Most of the large *Tsuga* have multiple stems, probably a result of wind damage (Fig. 13a). *Abies procera* are rare and there is one old-growth *Pseudotsuga* 125 - 134 cm dbh (Table 8). *Tsuga heterophylla* and *Abies amabilis* seedlings are generally < 20 cm tall, and a few saplings of both species are scattered through the stand. Understory plants are uncommon (Fig. 13a).

Three distinct cohorts of *Abies amabilis* are evident (Fig. 14a, l): main canopy trees (c. 110-160 years), lower main canopy trees (15-34 cm dbh, c. 90-110 years), and subcanopy individuals (< c. 90 years old) regenerating under a relatively closed canopy. Similarly, *Tsuga heterophylla* has many size-classes (seedlings to trees 114 cm dbh), and probably 3 age-classes < 160 years old (Fig. 14b, l). There are also trees much older than this, at least c. 235-485 years old (Fig. 14l). Several old *Tsuga* and many smaller ones recently died (Fig. 14c). Large numbers of dead *Abies amabilis* include a range of sizes (Fig. 14d), many in patches where 1 or 2 live trees are rapidly attaining main canopy stature.

(a) PLOT GM 1



(b) PLOT GM 2

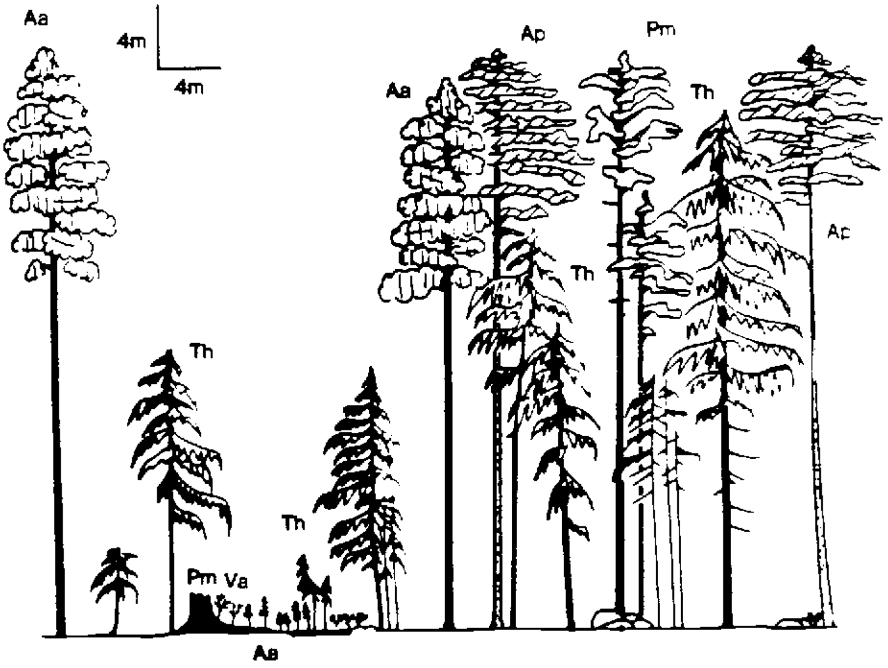


FIGURE 13: Profiles of (a) plot GM-1, and (b) plot GM-2. Pm, *Pseudotsuga menziesii*, Th, *Tsuga heterophylla*; Aa, *Abies amabilis*; Ap, *Abies procera*; L, log; Va, *Vaccinium alaskense*; X, *Xerophyllum tenax*.

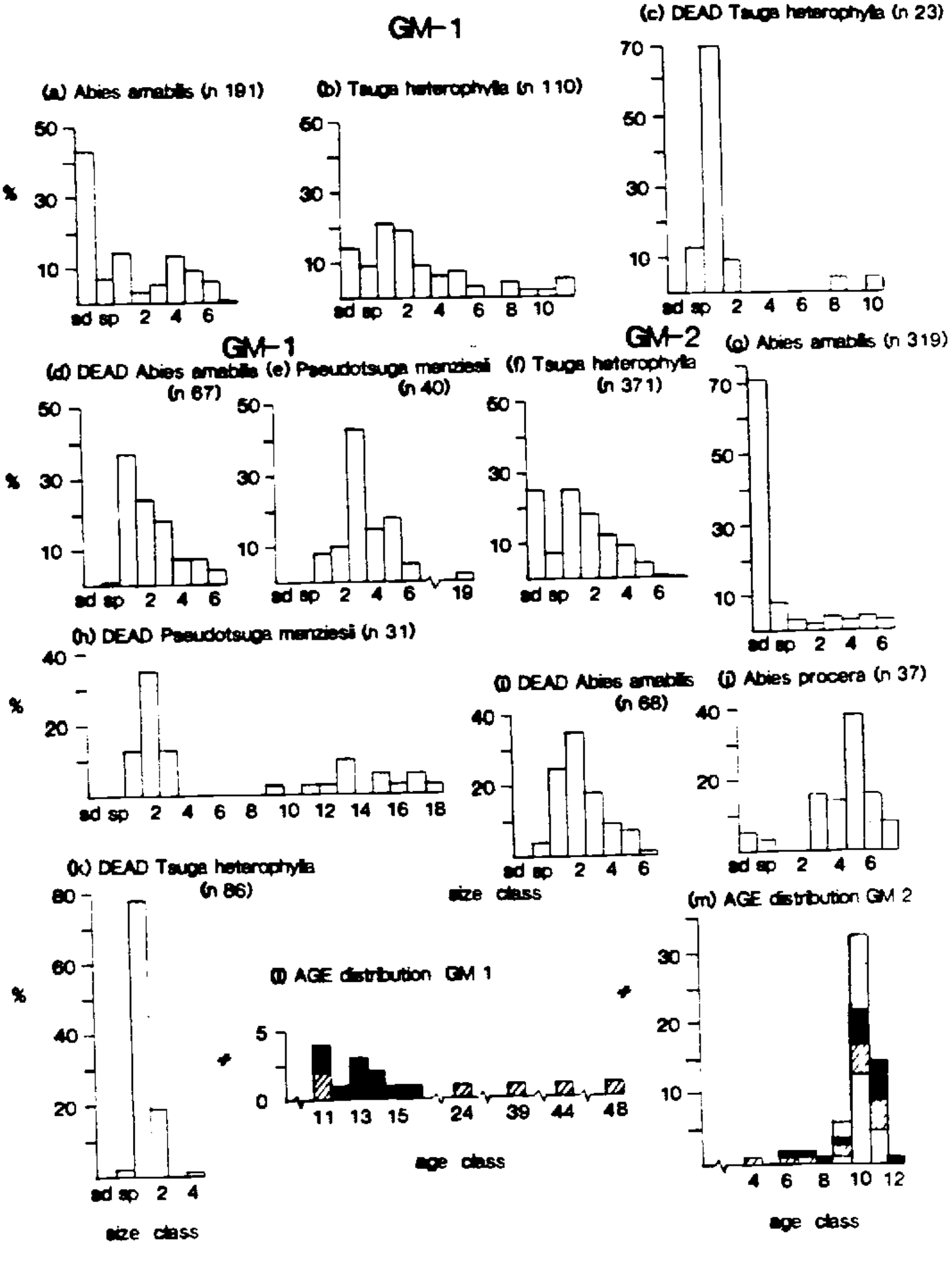


FIGURE 14: Size- and age-class histograms for main canopy tree species in plots GM-1 and GM-2. The size- and age-classes and n are the same as in FIG. 11.

Several recent ground fires have affected this stand. Age cohorts beginning at c. 160 years and c. 110 years are probably the result of such fires (Table 7). In an adjacent windthrow, the large gaps created are filled with small *Abies amabilis* and *Tsuga heterophylla*, the latter commonly on fallen logs.

Plot GM-2

The c. 1874 fire that allowed establishment of all 4 main canopy tree species in plot GM-1, affected a larger area in plot GM-2. The main canopy is dominated by a mixture of species, but the lower tiers almost solely by *Tsuga heterophylla* and *Abies amabilis* (Table 8, Fig 13b). In canopy openings created by the fall of large *Pseudotsuga* snags, *Tsuga heterophylla* of intermediate height are common, the shrub *Vaccinium alaskense* is abundant and herb cover often high (Fig 13b). As in plots HY-1, GL-1, and GM-1, *Abies amabilis* below the main canopy are less common than *Tsuga heterophylla* (Table 8) perhaps reflecting a lesser ability to persist as a subcanopy tree (also see Chapter II). Many seedlings and trees are located on elevated surfaces, especially *Tsuga heterophylla* (Table 9, 10).

Apart from one *Pseudotsuga menziesii* > 750 years old, most trees arose following a fire in c. 1874 (Table 7, Fig. 14e, m). *Tsuga heterophylla* and *Abies amabilis* from seedlings to stems 64 cm dbh are common but both are predominantly two-aged (Fig. 14f, g, m). Both species began to establish with the *Pseudotsuga*, but probably continued longer (Fig. 14m). The *Pseudotsuga menziesii* that died as this stand matured (stumps 5-34 cm dbh) and the previous population of this species (stumps c. 85-184 cm dbh) may represent several cohorts (Fig. 14h). Many *Abies amabilis* of intermediate diameter (and height) along with a few main canopy trees have died (Fig. 14i). The *Abies procera* are mostly even-aged (Fig. 14j, m). Dead *Tsuga heterophylla* are mostly small stems (Fig. 14k).

Soapgrass Mountain

On the southern slopes of Soapgrass Mountain, mature forest of similar structure is widespread, presumably the result of major fires. Where these fires did not totally destroy the forest, old-growth stands similar to plot HY-1 are common. Plots were located on a 15° slope where fires (< 200 years ago) had totally (SM-1) and partially destroyed (SM-2) the previous forest.

Plot SM-1

Pseudotsuga menziesii dominates plot SM-1 (Table 8) and many below the main canopy are dying or dead (Fig. 15a). Below the main canopy, *Tsuga heterophylla* dominates, although a few saplings or small stems of other species are present (Table 8); small individuals are often on elevated surfaces, especially *Tsuga* (Table 9, 10). *Acer circinatum* is locally abundant above an almost complete herb cover (Fig. 15a).

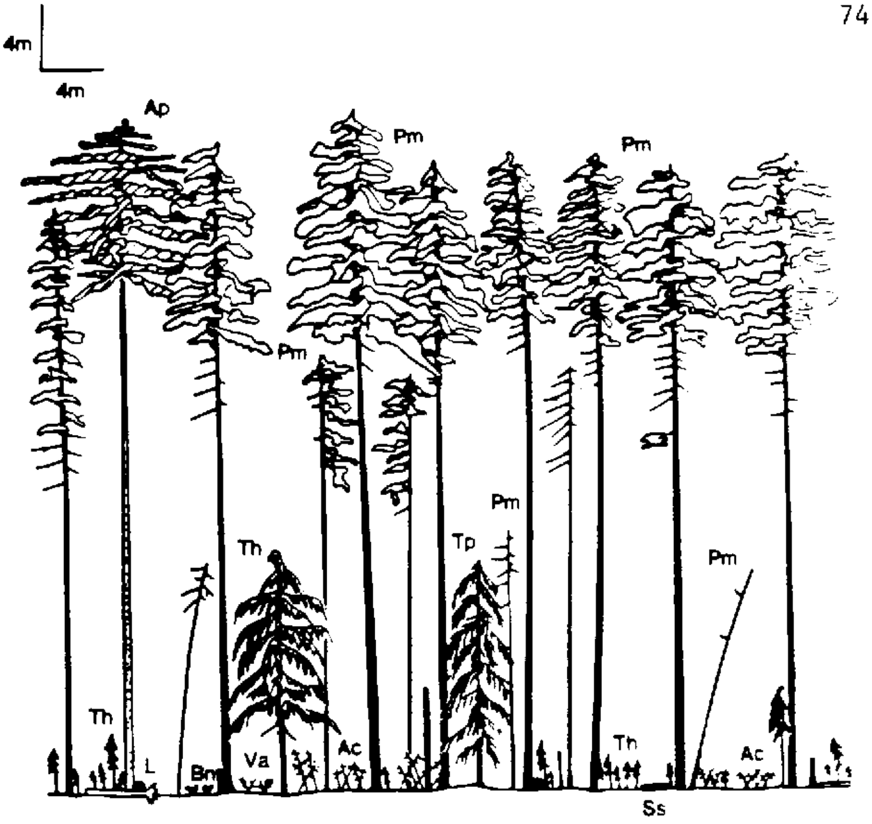
The *Pseudotsuga menziesii* vary in size but are a relatively even-aged population (Fig. 16a, k). *Tsuga heterophylla*, *Abies procera*, *Thuja plicata* and *Abies amabilis* are mostly small (Fig 16b, c, d, f), although a few larger individuals are as old as some dominant *Pseudotsuga* (Fig. 16k). Dead *Pseudotsuga menziesii* represent members of both the present and past cohorts (Fig. 16e).

Plot SM-2

A few emergent *Pseudotsuga menziesii* dominate plot SM-2 above a dense canopy of *Tsuga heterophylla* (Table 8, Fig. 15b). Lower strata are solely *Tsuga*, many dead or dying, resulting in many spars and down logs (Table 8, Fig. 15b and 16i). Few *Tsuga* are located on elevated surfaces (Table 9). Tree seedlings and understorey plants are extremely rare (Table 10) and if present, generally < 20 cm tall.

One *Pseudotsuga menziesii* established at the same time as the *Tsuga heterophylla* but the rest belong to a much older population

(a) PLOT SM 1



(b) PLOT SM 2

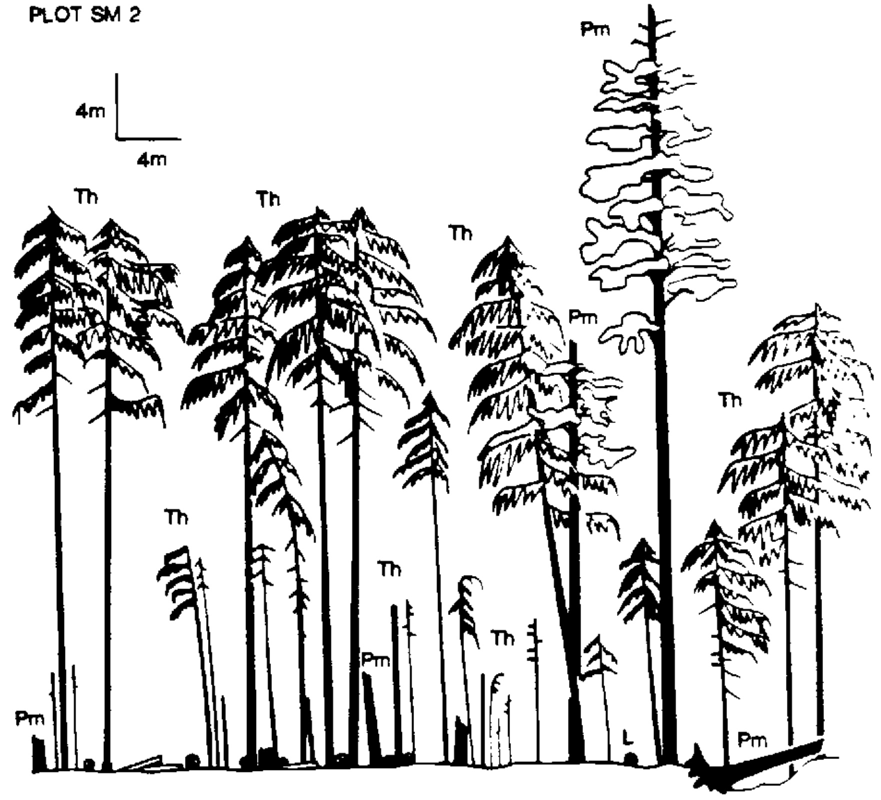


FIGURE 15: Profiles of (a) plot SM-1, and (b) plot SM-2.
Pm, *Pseudotsuga menziesii*; Th, *Tsuga heterophylla*;
Tp, *Thuja plicata*; Ac, *Acer circinatum*; Va, *Vaccinium alaskense*;
Bn, *Berberis nervosa*; L, log; Ss, *Smilacina stellata*.

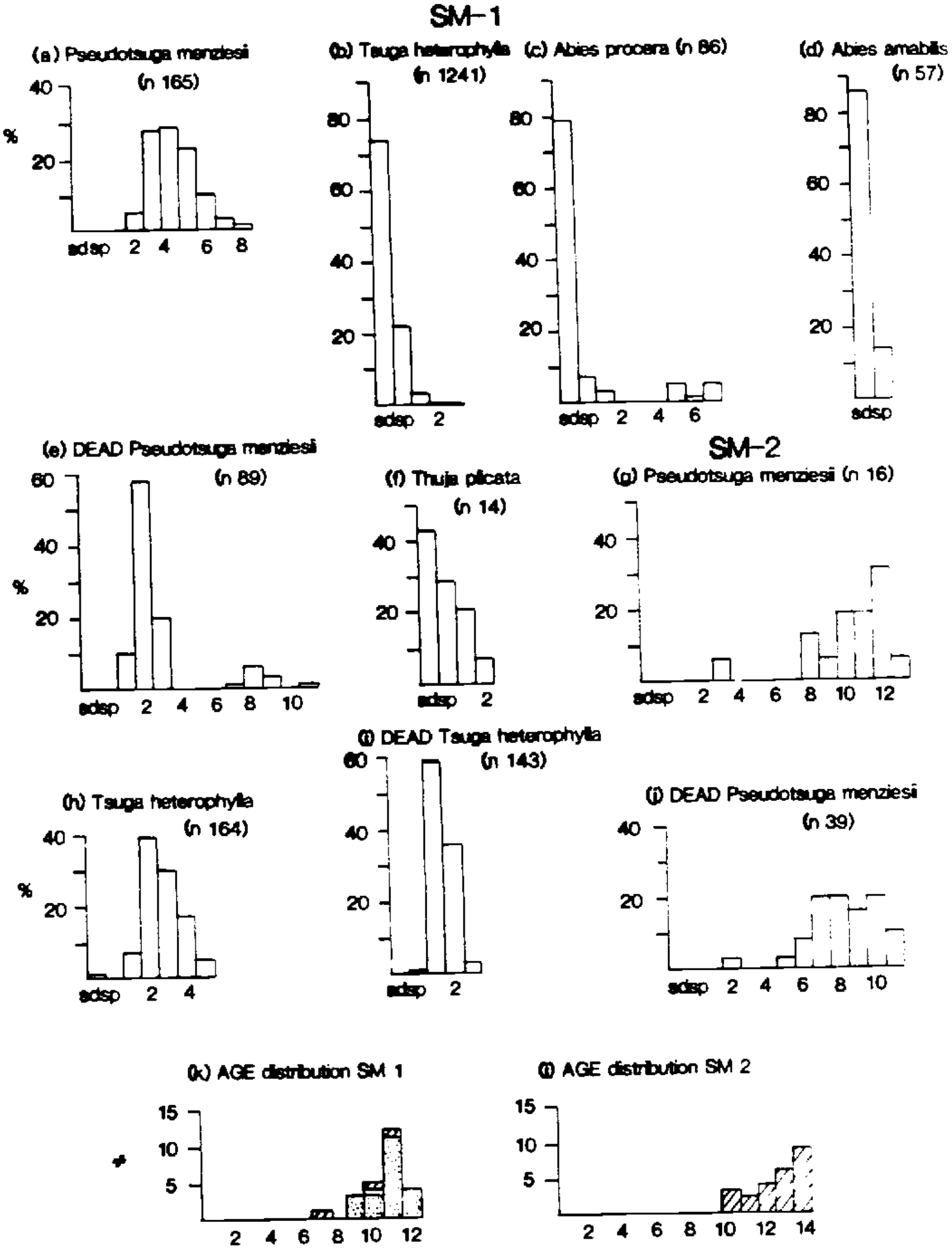


FIGURE 16: Size- and age-class histograms for main canopy tree species in plots SM-1 and SM-2. The size- and age-classes and n are the same as in FIG. 11.

(Fig. 16g). Five of these Pseudotsuga are 465-559 years old and may represent one or more cohorts that established after a fire. Tsuga heterophylla is even-aged with many dead individuals (Fig. 16h, i, l). Most of the old-growth Pseudotsuga population has died (Fig. 16g, j).

Spatial pattern

To examine the dynamics of regeneration further, spatial dispersions of species were analysed. Often, the spatial arrangement of individuals may reflect the regeneration process that produced such a pattern (e.g. Law 1981, Williamson 1975). For example, small clumps of young trees may reflect establishment in canopy openings created by treefalls, whereas larger patches of trees of similar size may indicate a larger disturbance such as fire.

The patterns of young individuals may differ from those of older trees of the same species, due to influences of competition and environment and to the distribution of safe sites at the time of their establishment. Consequently, separate analyses were made of individuals of different sizes and ages. In many instances similar patterns were found for similar sized trees of a species in the various plots; therefore, only examples of the various patterns are illustrated.

Hyatt Soapgrass

All Pseudotsuga menziesii in HY-3 and HY-4 were pooled for one analysis (Fig. 17a). Trees > 48 cm dbh are uniformly distributed at quadrat sizes up to 225 m^2, except where they occur in groups of 2-3 equally spaced trees as indicated by an I_δ value of 0.99 at 36 m^2. Analysis of dead and live trees > 48 cm dbh (n = 100) also revealed a uniform distribution of stems at small quadrat sizes (I_δ = 0.44 at 9 m^2 and I_δ = 0.71 at 36 m^2) but at larger quadrat sizes stems were randomly distributed. The uniform distributions at small quadrat sizes are due to the large area

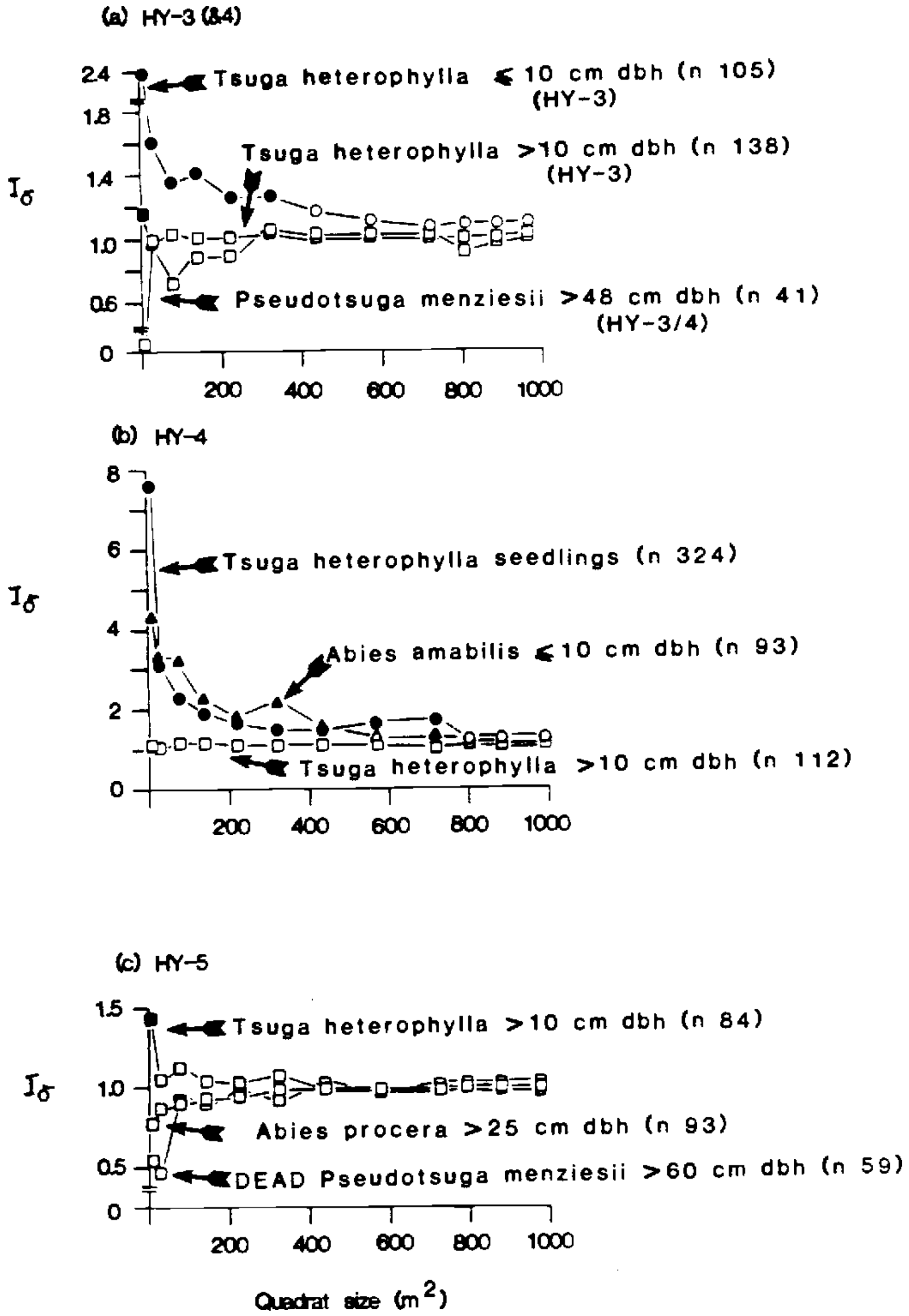


FIGURE 17: Values of Morisita's index, I_δ, at different quadrat sizes for species of different size-classes in plots HY-3, HY-4, and HY-5. Filled symbols are I_δ values significantly > 1.0 ($P < 0.05$) according to an F test of Morisita (1959).

required by an individual old-growth tree that leads to equal spacing with age. After the 1893 fire in this plot many old-growth trees died but the variable burn pattern allowed survival of small groups.

Tsuga heterophylla $\leq$ 10 cm dbh in HY-3 are clumped at all quadrat sizes from 9-324 m^2 (Fig. 17a). Stems of Tsuga > 10 cm dbh, on the other hand, are clumped only at 9 m^2 and random at all other quadrat sizes (Fig. 17a). This suggests that as the Tsuga population ages, mortality is high, and the degree of aggregation rapidly declines.

Tsuga heterophylla seedlings and small trees in plot HY-4 are significantly clumped at all quadrat sizes from 9-729 m^2 (Fig. 17b). Small clumps reflect establishment on raised woody substrates (Table 10) and larger ones, success in canopy openings. Tsuga heterophylla > 10 cm dbh, trees that survived the 1893 fire and the fastest growing younger trees, are randomly distributed at all quadrat sizes (Fig. 17b).

Abies amabilis seedlings are clumped at quadrat sizes up to 324 m^2, although there are fewer seedlings per clump than for Tsuga (I_δ = 4.2 at quadrat size 9 m^2). Abies amabilis $\leq$ 10 cm dbh are clumped from 9-729 m^2, similar to small Tsuga (Fig. 17b). Abies amabilis > 10 cm dbh were too few for analysis (n = 20) but appeared to occur in clumps of 4-6 trees of c. 225 m^2.

In HY-5 Abies procera > 25 cm dbh are uniformly distributed (Fig. 17c). Tsuga heterophylla seedlings are clumped from 9-324 m^2 (I_δ = 13.9 at 9 m^2 to I_δ = 2.9 at 324 m^2) reflecting the many seedlings on logs, primarily in 2 large canopy openings. Tsuga heterophylla both $\leq$ 10 and > 10 cm dbh are clumped at small quadrat sizes indicating patches of 2 or 3 trees on or around Pseudotsuga menziesii stumps (Fig. 17c). Dead Pseudotsuga > 60 cm dbh have a uniform distribution from 9-144 m^2 and are random at larger quadrat sizes (Fig. 17c).

Gordon Lakes

Abies procera < 84 cm dbh occur as several clumps of 225 and 400 m^2 with a uniform distribution of individuals within each clump resulting from high mortality within each patch (Fig. 18a). This is confirmed by the contagious distribution within clumps for live *Abies procera* < 84 cm dbh pooled with dead stems < 54 cm dbh (Fig. 18a). *Abies procera* > 95 cm dbh (including 2 recently dead trees) are randomly distributed but grouped into two patches in opposite corners of the plot ($I_{\delta} = 1.15$ at 1225 m^2, Fig. 18b).

Tsuga heterophylla seedlings occur in clumps up to 900 m^2, stems $\leq$ 10 cm dbh are clumped up to 625 m^2, and trees > 10 cm dbh, from 25-400 m^2.

Abies amabilis seedlings are in clumps 25-900 m^2 and stems $\leq$ 10 cm dbh occur in patches up to 400 m^2. Trees > 10 cm dbh are aggregated at 25 m^2 with a secondary peak at 400 m^2 due to several larger clumps (Fig. 18b). Analysis of live and dead *Abies amabilis* > 10 cm dbh revealed that aggregation within small clumps has declined as the clumps have aged.

Gordon Meadows

Tsuga heterophylla seedlings and trees $\leq$ 10 cm dbh, relatively uncommon in plot GM-1, were pooled for analysis. They occur in clumps from 9-144 m^2, as do stems > 10 cm dbh.

Abies amabilis seedlings and trees $\leq$ 10 cm dbh occur in patches from 9 m^2 to 144 m^2 (Fig. 19a). Trees > 10 cm dbh are clumped only at 81 m^2 (Fig. 19a), probably representing groups of trees that established in openings created by fire or windthrow.

In plot GM-2 *Pseudotsuga menziesii* > 10 cm are uniformly dispersed but show a tendency towards 36-81 m^2 clumps (Fig. 19b). In contrast live individuals (> 10 cm dbh) and dead trees (< 92 cm dbh) combined show an aggregated distribution (Fig. 19b). *Pseudotsuga* stumps have a similar dispersion to that of live trees. i.e. uniform at small quadrat sizes ($I_{\delta} = 0$ at 9 and 36 m^2) and

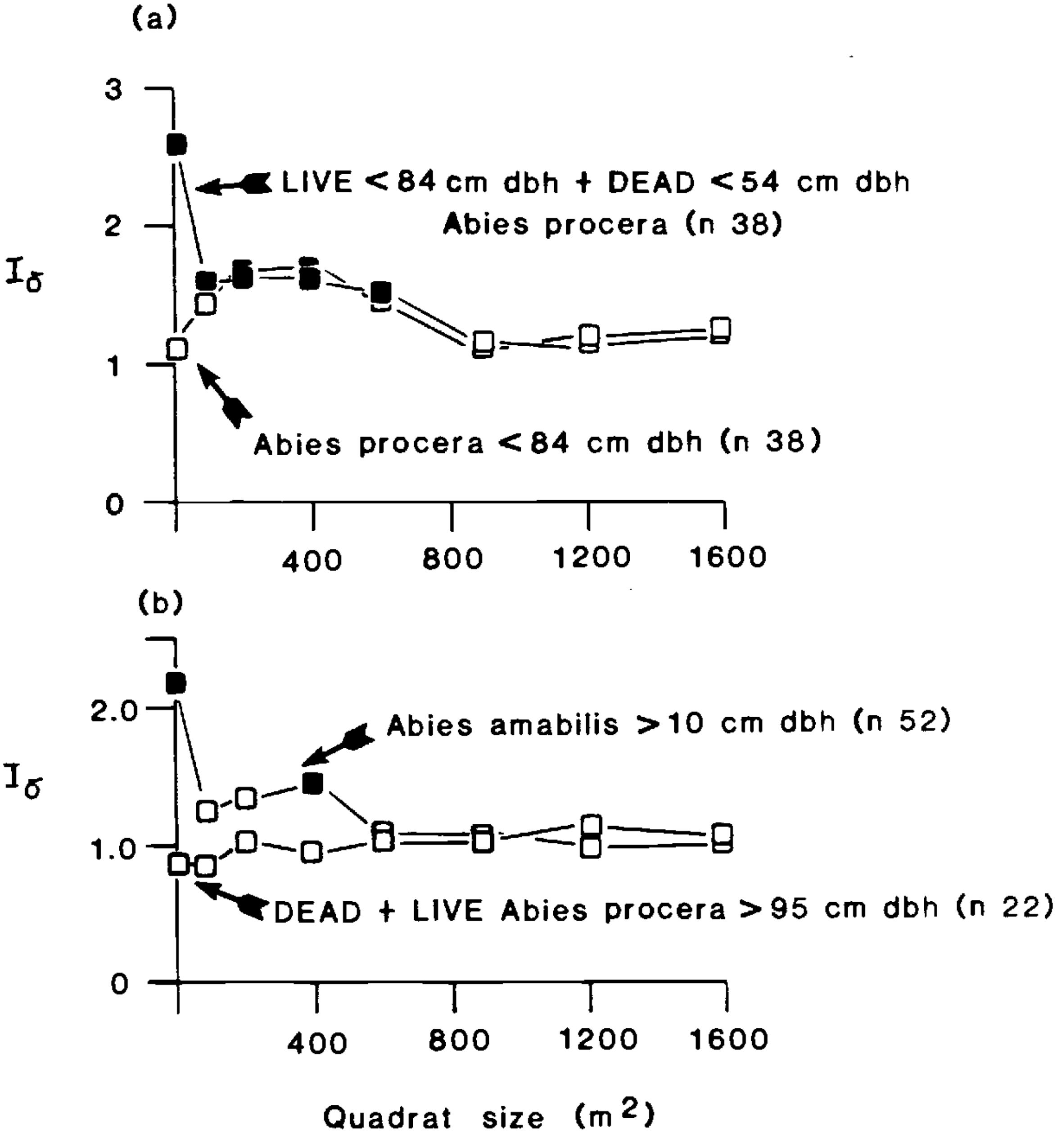


FIGURE 18: Values of Morisita's index, I_δ, at different quadrat sizes for species of different size-classes in plot GL-1. Filled symbols are I_δ values significantly > 1.0 ($P < 0.05$) according to an F test of Morisita (1959).

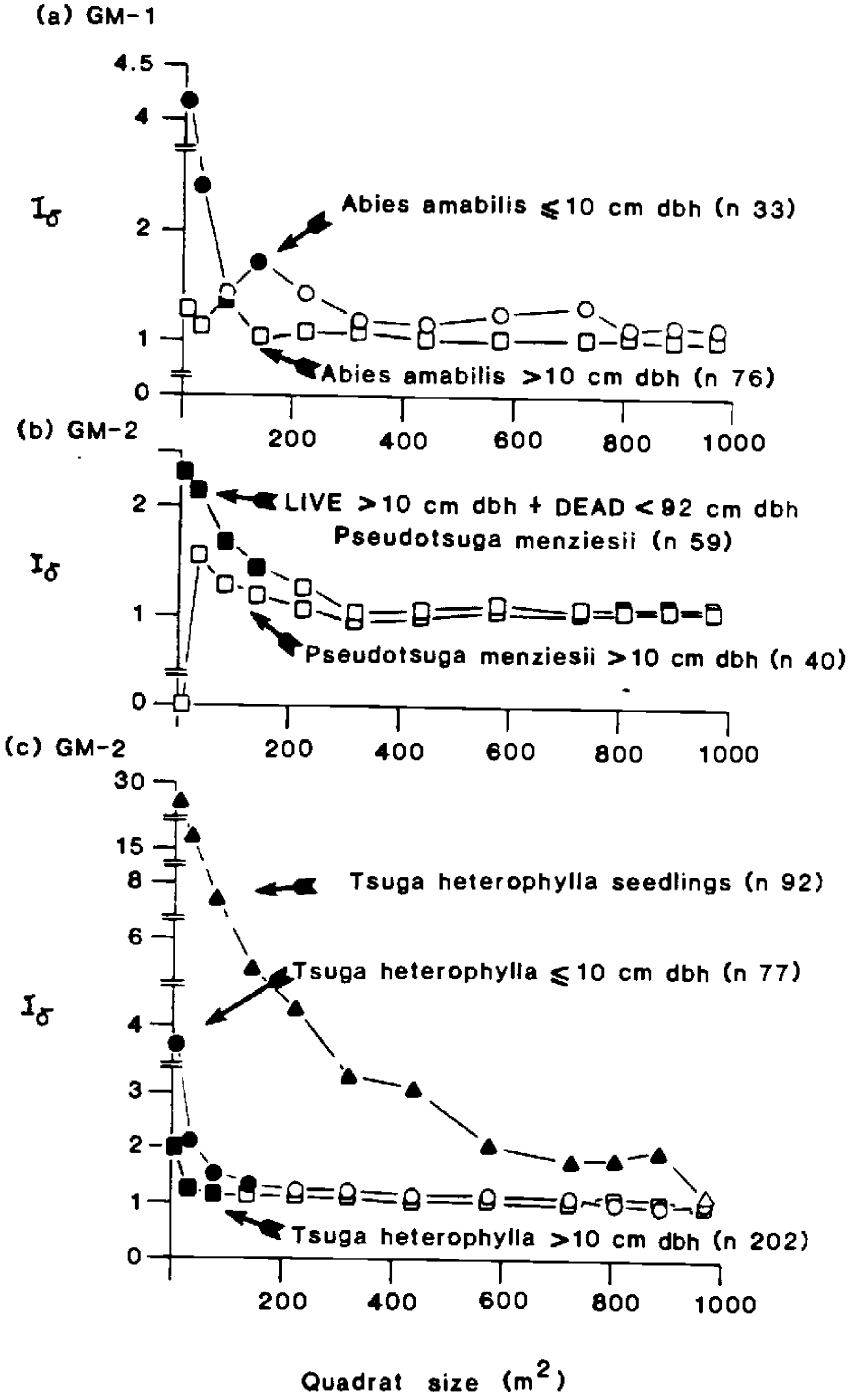


FIGURE 19: Values of Morisita's index, I_δ, at different quadrat sizes for species of different size-classes in plots GM-1 and GM-2. Filled symbols are I_δ values significantly > 1.0 ($\underline{P} < 0.05$) according to an F test of Morisita (1959).

a tendency to form clumps at 81 m^2 ($I_\delta = 1.3$). It is likely that the current Pseudotsuga population established in aggregations at least partially due to the distribution of Pseudotsuga stumps.

Live Abies procera occur in discrete clumps c. 36-225 m^2; there is a uniform distribution of trees in each of the smaller (36 m^2) clumps. Live and dead trees combined show a greater density of trees in the past (eg. $I_\delta = 5.0$ at 9 m^2 for live and dead trees, $I_\delta = 1.3$ for live trees).

Tsuga heterophylla seedlings are densely clumped at all quadrat sizes from 9-891 m^2 (Fig. 19c). Stems $\leq$ 10 cm dbh occur in smaller clumps, 9-144 m^2 and trees > 10 cm dbh are aggregated only at quadrat sizes 9-81 m^2 (Fig. 19c). These dispersions illustrate the thinning effect with age.

Abies amabilis seedlings occur in clumps of a similar size to those of Tsuga, although with fewer seedlings per clump. Trees $\leq$ 10 cm dbh are intensely clumped at small quadrat sizes and also occur in larger clumps up to 225-324 m^2; trees > 10 cm dbh are aggregated up to 324 m^2.

Soapgrass Mountain

Live Pseudotsuga menziesii in plot SM-1 are uniformly distributed at 9 and 36 m^2 while aggregated distributions occur at small quadrat sizes for dead Pseudotsuga 5-34 cm dbh (Fig. 20a). Many of the trees that died were in dense clumps and now 1 or 2 trees remain where 5 or more previously formed clumps at 9 m^2. Tsuga heterophylla seedlings and trees $\leq$ 10 cm dbh occur in patches, 9-576 and 9-729 m^2, respectively (Fig. 20a). Abies amabilis seedlings and trees $\leq$ 10 cm dbh occur in patches 9-81 m^2 (Fig. 20b), while for Abies procera seedlings, clumping occurs from 9-324 m^2 (Fig. 20b).

In plot SM-2, Tsuga heterophylla > 10 cm dbh are randomly distributed at all quadrat sizes (Fig. 20c), although an analysis of dead and live large Tsuga illustrates clumping from 9 m^2 to at least 540 m^2 and possibly higher (Fig. 20c).

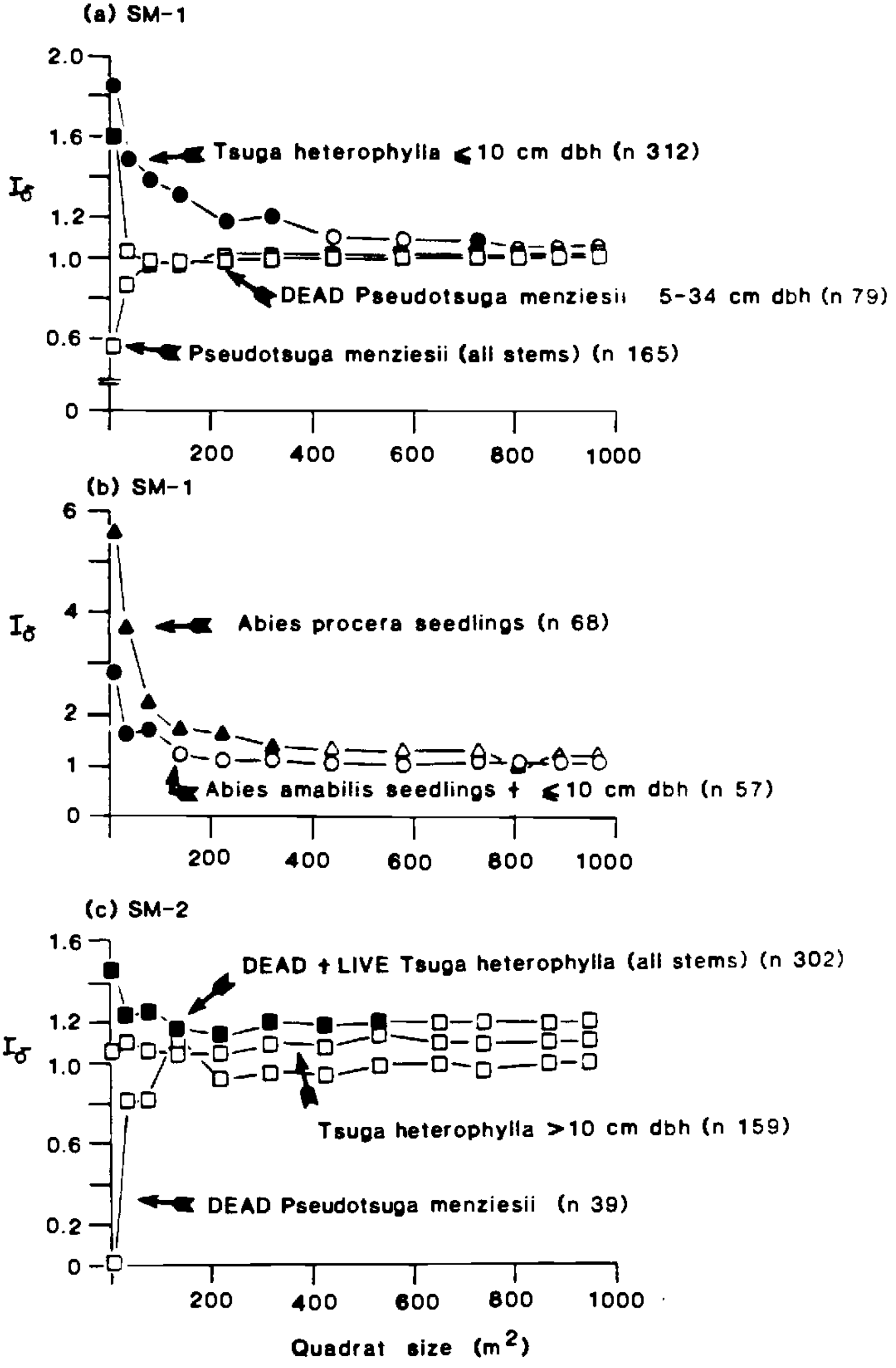


FIGURE 20: Values of Morisita's index, I_δ, at different quadrat sizes for species of different size-classes in plots SM-1 and SM-2. Filled symbols are I_δ values significantly $>$ 1.0 ($P < 0.05$) according to an F test of Morisita (1959).

Pseudotsuga stumps were uniformly distributed at 9-81 m^2 but showed a tendency to form clumps at 144 m^2 suggesting mortality of patches following fire (Fig. 20c). Dead and live trees combined were uniformly distributed at small quadrat sizes (< 225 m^2) and random at all larger quadrat sizes.

Association

Several consistent patterns emerged from the chi-square association tests (Table 11). The most common positive associations were between *Tsuga heterophylla* and *Abies amabilis* seedlings and stems of both species ≤ 10 cm dbh. Chi-square tests between seedlings and/or stems ≤ 10 cm dbh and canopy gaps (as assessed from the 3 x 3 or 5 x 5 m contiguous quadrats) often showed a positive association, especially for the Gordon Lakes and Gordon Meadows plots (Table 11). In some instances trees of *Tsuga heterophylla* and *Abies amabilis* ≤ 10 and > 10 cm dbh co-occur.

In contrast, *Abies amabilis* and *Tsuga heterophylla* seedlings are frequently negatively associated with *Tsuga heterophylla* > 10 cm dbh. Also stems > 10 cm dbh of *Abies amabilis* and *Tsuga heterophylla* occur separately more often than expected due to chance. Small *Abies amabilis* and *Tsuga heterophylla* are often positively associated with *Pseudotsuga menziesii*, and *Tsuga heterophylla* trees may also be positively associated with dead *Pseudotsuga*.

Other associations are peculiar to particular stands. For example, in plot HY-5, *Tsuga heterophylla* > 10 cm dbh are negatively associated with *Abies procera* at the smallest quadrat size.

Tree seedlings

Numbers of tree seedlings (especially *Tsuga heterophylla* and *Abies amabilis*) are low in plots with many *Tsuga* in the canopy (Table 8, 10). Plot HY-1 has few seedlings (288 *Tsuga* and 194 *Abies amabilis* per ha) as do HY-3, GM-1 and SM-2. In contrast,

TABLE 11: Significant positive (+) and negative (-) associations of live and dead trees at different quadrat sizes (by species and size-class) and canopy openings (gaps) at the 4 study sites based on a X^2 test applying Yates' correction (Greig-Smith 1983).

SPECIES AND SIZE-CLASS		PLOT									
		HY-1	HY-2	HY-3	HY-4	HY-5	GL-1	GM-1	GM-2	SM-1	SM-2
T. heterophylla seedlings	*A. amabilis* seedlings	(1)+++	+++			++	++		+++		
T. heterophylla ≤ 10 cm dbh	*A. amabilis* ≤ 10 cm dbh	+	+		+					++	
T. heterophylla seedlings	*T. heterophylla* ≤ 10 cm dbh								+	+	
A. amabilis seedlings	*A. amabilis* ≤ 10 cm dbh				+		+		++		
T. heterophylla seedlings	*A. amabilis* ≤ 10 cm dbh								+		
A. amabilis seedlings	*T. heterophylla* ≤ 10 cm dbh								+	+	
A. amabilis ≤ 10 cm dbh	*A. amabilis* > 10 cm dbh		+				+				
T. heterophylla ≤ 10 cm dbh	*T. heterophylla* > 10 cm dbh		+		+		+				
A. amabilis seedlings	*T. heterophylla* > 10 cm dbh	-	-			-			--		
T. heterophylla seedlings	*T. heterophylla* > 10 cm dbh	-	--	--					-		
A. amabilis seedlings	*A. amabilis* > 10 cm dbh								-		
A. amabilis > 10 cm dbh	*T. heterophylla* > 10 cm dbh	-			-		-	-	-		
A. amabilis seedlings	LIVE *P. menziesii* (2)	+									
A. amabilis ≤ 10 cm dbh	LIVE *P. menziesii* (2)	+	+		+						
T. heterophylla > 10 cm dbh	LIVE *P. menziesii* (2)		+		+						
A. amabilis > 10 cm dbh	DEAD *P. menziesii* (2)	-									
T. heterophylla ≤ 10 cm dbh	DEAD *P. menziesii* (2)	+	++								
T. heterophylla > 10 cm dbh	DEAD *P. menziesii* (2)		+			+					
LIVE *P. menziesii* (2)	DEAD *P. menziesii* (2)		+								-
LIVE *T. heterophylla* (2)	DEAD *T. heterophylla* (2)										+
T. heterophylla seedlings	*A. procera* (2)								+		
T. heterophylla ≤ 10 cm dbh	*A. procera* (2)	+				+					
T. heterophylla > 10 cm dbh	*A. procera* (2)					-					
A. amabilis seedlings	*A. procera* seedlings									++	
T. heterophylla seedlings	Gaps	+					+		+++		
T. heterophylla ≤ 10 cm dbh	Gaps				-			+	+		
A. amabilis seedlings	Gaps						+		+++		
A. amabilis ≤ 10 cm dbh	Gaps						+		+		

(1) $P < 0.05$ at block sizes 1, 2 and 3. For HY-1 and GL-1 these are 25 m^2, 100 m^2, and 225 m^2; for all other plots they are 9 m^2, 36 m^2, and 81 m^2.

(2) Size-classes for these species may vary between plots and are the same as those presented in the spatial analyses.

the more open stands and Pseudotsuga dominated stands have many more seedlings; an exponential decline in numbers of Tsuga seedlings occurs with an increase in Tsuga in the main canopy (Fig. 21).

Height of Abies amabilis seedlings under a Pseudotsuga or Pseudotsuga/Abies procera canopy exceeds that under a Tsuga canopy, but height was greatest in canopy openings (Table 12). Tsuga seedlings were taller than Abies amabilis where both were measured. Many seedlings (especially Tsuga) were located on elevated surfaces under mixed canopies or in canopy openings but rarely under Tsuga canopies on these sites (Table 12). These patterns concur with the data from the larger plots.

Understory vegetation

Plots with a high Tsuga heterophylla canopy component (HY-3, GM-1, GM-2, SM-2 and HY-1) tended to have low understory cover (Table 10); generally the more open stands (HY-4 and GL-1) and those dominated by Pseudotsuga (HY-2 and SM-1) have much more luxuriant and complete understory cover.

Differences in the shrub and herb composition and cover exceed those in seedling regeneration. At Gordon Meadows, all 12 major understory species are significantly more frequent in canopy openings than under a Tsuga canopy, and most are more common under a mixed canopy (Table 13). Few species were more common in canopy openings than under a mixed canopy although Clintonia uniflora and Smilacina stellata were especially frequent in canopy openings. Cover differences among the canopy conditions were more marked than differences in frequency (Table 13). Few species have > 1 percent cover under a Tsuga canopy whereas almost all of the 12 common species had > 1 percent cover under both of the other canopy conditions. Cover of many species was greatest in canopy openings (Table 13).

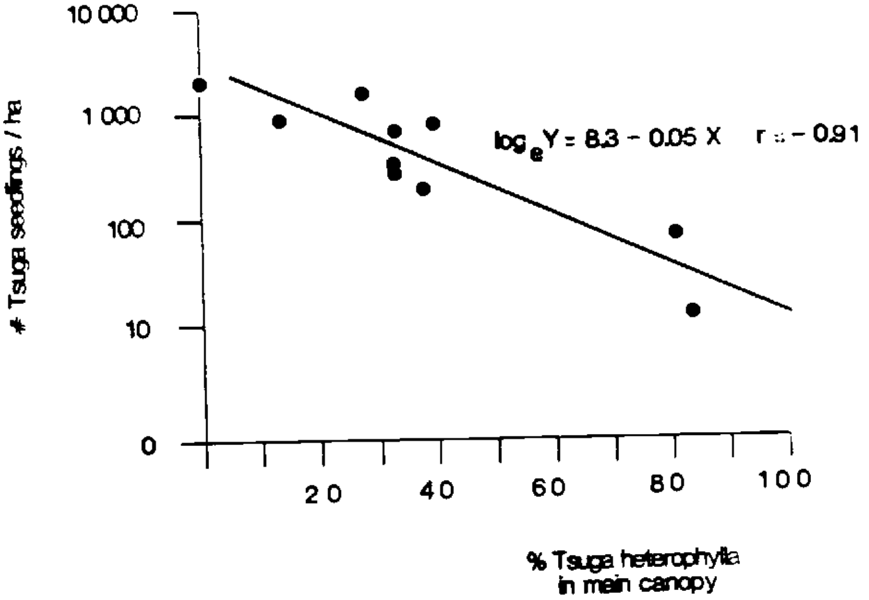


FIGURE 21: Numbers of *Tsuga heterophylla* seedlings/ha in the ten sample plots as a function of the percentage of main canopy trees that are *Tsuga heterophylla*.

TABLE 12: Mean maximum height (±S.E.) of tree seedlings in 1 x 1 m quadrats under different canopy conditions at Gordon Meadows and Soapgrass Mountain. *n* is the number of quadrats sampled and the numbers in parentheses refer to percentages of seedlings on elevated surfaces.

MEAN MAXIMUM HEIGHT (m)

AREA	SPECIES	CANOPY CONDITION		
		Tsuga heterophylla (*n* = 100)	*P.menziesii*/ *A.procera* (*n* = 50)	canopy openings (*n* = 50)
Gordon Meadows	*Abies amabilis*	11.3 ± 6.3	20.0 ± 3.2	27.7 ± 4.9
		(0.0)	(21.6)	(14.3)
	Tsuga heterophylla	-	*	37.5 ± 2.5
				(100.0)

AREA	SPECIES	*Tsuga heterophylla* (*n* = 100)	*Pseudotsuga menziesii* (*n* = 100)
Soapgrass Mountain	*Abies amabilis*	5.6 ± 0.6	23.6 ± 6.6
		(0.0)	(42.1)
	Tsuga heterophylla	-	61.5 ± 7.4
			(86.3)

* seedlings present but absolute frequency < 5

TABLE 13: Frequency and cover of common species in 1 x 1 m quadrats under different canopy conditions at Gordon Meadows (only species with a percent frequency > 25 are listed; differences were subjected to a χ^2 test using the absolute frequencies and applying Yates' correction (Greig-Smith 1983)). Pairwise statistical comparisons were made between *Tsuga* and each of the other canopy conditions. * indicates a significant difference from *Tsuga heterophylla* at $P < 0.05$; + indicates < 1 percent cover; *n* is the number of quadrats sampled.

SPECIES	PERCENT FREQUENCY *Tsuga heterophylla* (*n* = 100)	CANOPY CONDITION *P.menziesii*/ *A.procera* (*n* = 50)	 canopy openings (*n* = 50)	 *Tsuga heterophylla* (*n* = 100)	PERCENT COVER (±S.E.) *P.menziesii*/ *A.procera* (*n* = 50)	 canopy openings (*n* = 50)
Tree seedlings, shrubs						
Abies amabilis	3	38 *	42 *	not	measured	
Vaccinium alaskense	63	82 *	92 *	1.6 ± 0.3	22.3 ± 3.7	43.7 ± 4.5
Rubus lasiococcus	32	86 *	88 *	1.7 ± 0.5	16.9 ± 3.2	16.6 ± 2.7
Herbs, ferns						
Clintonia uniflora	21	38 *	78 *	+	4.5 ± 1.1	9.4 ± 1.5
Cornus canadensis	26	88 *	84 *	+	20.6 ± 2.9	26.9 ± 3.5
Smilacina stellata	9	12	50 *	+	4.2 ± 2.3	13.0 ± 3.1
Pteridium aquilinum	9	34 *	46 *	+	5.2 ± 1.8	10.7 ± 2.9
Tiarella unifoliata	8	16	30 *	+	+	4.4 ± 2.0
Trillium ovatum	21	46 *	32 *	+	1.8 ± 0.6	2.0 ± 0.9
Viola spp. (1)	41	88 *	90 *	+	5.3 ± 1.0	2.4 ± 0.5
Coptis laciniata	5	44 *	54 *	+	12.1 ± 3.1	11.2 ± 2.9
Pedicularis racemosa	4	12 *	30 *	+	1.6 ± 0.9	5.2 ± 1.8
All species (2)						
Total number of species	23	33 *	27			
Total of absolute frequencies / *n*	2.6	7.3 *	8.2 *			

(1) 3 species were recognised; *Viola glabella*, *V. sempervirens* and *V. orbiculata*.

(2) includes 20 additional species which occurred in < 25 percent of the quadrats under any canopy condition. The species are: *Tsuga heterophylla*, *Vaccinium membranaceum*, Rosa *gymnocarpa*, *Ribes lacustre*, *Chimaphilaumbellata*, *Rubus* ursinus, *Anemone lyallii*, *Achlys triphylla*, Vancouveria *hexandra*, *Campanula scouleri*, Xerophyllum *tenax*, *Pyrola secunda*, *Listera* borealis, Hieracium *albiflorum*, Valeriana *sitchensis*, *Osmorhiza chilensis*, *Goodyera oblongifolia*, *Streptopus roseus*, *Linnaea borealis*, *Polystichum munitum*.

Species richness was greater under openings or mixed canopies than under a Tsuga canopy (Table 13). No species grew exclusively under Tsuga but several rare ones were limited to one or both of the other canopy conditions.

Of the 14 common species at Soapgrass Mountain, 13 were significantly more frequent under a Pseudotsuga canopy (Table 14). Understory plant cover was much greater under a Pseudotsuga menziesii canopy. The total number of species found under a Pseudotsuga canopy approached twice as many as under a Tsuga canopy.

Tree canopy density

A comparison of the percentage frequency of canopy openings, as assessed for each unit quadrat, illustrates interplot differences in light conditions. At Hyatt Soapgrass, stands with a high old-growth Pseudotsuga component (HY-1 and HY-4) have many canopy openings; younger stands (HY-2 and HY-5) have few (Table 15). In plot HY-3 many of the trees have not yet reached the upper main canopy, so many canopy openings were assessed, but at the lower main canopy and below main canopy levels the forest is relatively closed, resulting in low values for direct radiation. At Gordon Lakes and Gordon Meadows, the strong influence of cohorts of younger trees also results in few canopy openings. However, at Soapgrass Mountain, although the number of gaps is small there are significantly more in plot SM-1 than in SM-2, most likely due to differences in canopy density between Pseudotsuga and Tsuga (Table 16).

Light conditions vary within and between areas. Plots with many Tsuga in the canopy may have low total diffuse plus direct radiation and direct radiation only (e.g. plots GM-1, GM-2, and SM-2), whereas other plots often have high values (e.g. plots HY-2 and HY-5, Table 15). These data, coupled with the variable occurrence of canopy openings, show that diverse canopy conditions exist in mixed stands.

The detailed light measurements at Gordon Meadows and Soapgrass Mountain, however, show differences in light conditions under

TABLE 14: Frequency and cover of common species in 1 x 1 m quadrats under different canopy conditions at Soapgrass mountain (only species with a percent frequency > 30 are listed (except for tree seedlings); differences were subjected to a X^2 test using the absolute frequencies and applying Yates' correction (Greig-Smith 1983)). * indicates a significant difference from *Tsuga heterophylla* at *P* < 0.001; + indicates < 1 percent cover; - indicates absence; *n* is the number of quadrats sampled.

	PERCENT FREQUENCY		PERCENT COVER (±S.E.)	
	CANOPY	CONDITION		
SPECIES	*Tsuga heterophylla* (*n* = 100)	*Pseudotsuga menziesii* (*n* = 100)	*Tsuga heteophylla* (*n* = 100)	*Pseudotsuga menziesii* (*n* = 100)
Tree seedlings, shrubs				
Abies amabilis	8	13	not	measured
Tsuga heterophylla	-	23 *	not	measured
Vaccinium alaskense	16	45 *	+	7.8 ± 1.6
Vaccinium membranaceum	18	44 *	+	3.3 ± 0.8
Chimaphila umbellata	4	71 *	+	12.5 ± 1.8
Rubus ursinus	7	93 *	+	2.5 ± 0.3
Rubus lasiococcus	1	41 *	+	3.2 ± 0.6
Herbs, ferns				
Clintonia uniflora	-	49 *	-	8.0 ± 1.5
Cornus canadensis	7	52 *	+	2.6 ± 2.0
Smilacina stellata	7	76 *	+	5.1 ± 3.1
Pteridium aquilinum	2	52 *	+	6.6 ± 1.3
Viola spp. (1)	8	67 *	+	4.5 ± 0.7
Linnaea borealis	3	63 *	+	6.5 ± 1.0
Pyrola secunda	-	32 *	-	+
All species (2)				
Total number of species	25	44 *		
Total of absolute frequencies / *n*	1.5	9.6 *		

(1) 3 species were recognised; *Viola glabella*, *V. sempervirens*, *V. orbiculata*.

(2) includes 28 additional species which occurred in < 30 percent of the quadrats under either canopy condition. The species are: *Abies procera*, *Pseudotsuga menziesii*, *Vaccinium parvifolium*, *Acer circinatum*, *Berberis nervosa*, *Rubus nivalis*, *Rosa gymnocarpa*, *Chimaphila menziesii*, *Spiraea* sp. (probably *S. betulifolia*), *Symphoricarpos mollis*, *Pyrola picta*, *Galium oreganum*, *Listera borealis*, *Polystichum munitum*, *Tiarella unifoliata*, *Vancouveria hexandra*, *Xerophyllum tenax*, *Hieracium albiflorum*, *Oxalis oregana*, *Streptopus roseus*, *Campanula scouleri*, *Corallorhiza mertensiana*, *Anemone deltoidea*, *Achlys triphylla*, *Trillium ovatum*, *Pedicularis racemosa*, *Goodyera oblongifolia*, *Coptis laciniata*.

TABLE 15: Mean light conditions for all plots determined from hemispherical canopy photographs and the percentage frequency of gaps based on the assessment of 5 x 5 m (plots HY-1, HY-2 and GL-1) and 3 x 3 m (all other plots) contiguous quadrats in each plot. Percentages followed by a different letter in the same column are significantly different at $\underline{P} < 0.05$ according to a X^2 test (using the absolute frequencies and applying Yates' correction; Greig-Smith 1983). $\underline{n}$ is the number of photographs analysed; N is the number of contiguous quadrats assessed; only plots within a study area were compared.

PLOT	n	PERCENT TOTAL DIFFUSE AND DIRECT RADIATION	PERCENT DIRECT RADIATION	N	PERCENT FREQUENCY GAPS
HY-1	24	31.3	14.5	320	35 b
HY-2	18	51.5	21.0	144	19 c
HY-3	6	43.1	9.3	216	30 b
HY-4	6	47.8	16.0	324	46 a
HY-5	6	40.9	11.8	216	16 c
GL-1	6	33.5	7.7	160	19
GM-1	6	32.5	6.3	252	18
GM-2	5	30.8	5.7	396	12
SM-1	6	36.2	11.2	324	9 a
SM-2	6	31.6	5.3	240	1 b

TABLE 16: Mean light conditions for different canopy conditions at Gordon Meadows and Soapgrass Mountain determined from analysis of hemispherical photographs. Percentages in each column followed by a different letter are significantly different at *P* < 0.05 according to a Mann-Whitney U test. Only within area comparisons were made. *n* is the number of photographs analysed.

PLOT AND CANOPY CONDITION	*n*	PERCENT TOTAL DIFFUSE AND DIRECT RADIATION		PERCENT DIRECT RADIATION	
GM-2 Gaps	11	43.6		9.6	a
GM-2 *Tsuga heterophylla*	13	44.9		6.1	b
GM-2 *Pseudotsuga*/*Abies procera*	11	46.6		8.7	a
SM-1 *Pseudotsuga menziesii*	11	36.6.	a	11.4	a
SM-2 *Tsuga heterophylla*	8	31.1	b	4.8	b

different canopies. If only direct radiation from May - September is considered, the influence of Tsuga in and below the main canopy is apparent. At Gordon Meadows there are no significant differences in total diffuse and direct radiation under the different canopy conditions (Table 16). However, if direct beam radiation only is considered there is a c. 50 percent increase in gaps and under a Pseudotsuga /Abies procera canopy compared to under a Tsuga canopy. A similar pattern occurs at Soapgrass Mountain, although in this area there are significant differences in total radiation also.

DISCUSSION

In general, forest structures at all study sites indicate that regeneration of Pseudotsuga menziesii and Abies procera depends on drastic disturbance. On the other hand, the relative importance of Abies amabilis and Tsuga heterophylla gradually increases in the absence of fire. These successional trends demonstrate the accordance criterion, widely used to interpret regeneration of forests (Braun 1950, Whittaker 1974). According to this criterion, regeneration is a relatively continuous process and trees of all sizes must be present for accordance to be complete. In the present study, however, species with negative exponential diameter distributions may be even-aged (e.g. Tsuga in plots HY-1, HY-4, HY-5, GL-1, GM-2). Thus, as pointed out by Watt (1947), the replacement of canopy dominants may be discontinuous or cyclic as well as a continuous process.

The present structure and composition of individual stands is the result of a complex disturbance history. In the study area, many fires burned during the last 5 centuries (Table 7). Many did not destroy all dominant trees, allowing establishment of other species besides Pseudotsuga. These burns produced a mosaic of stands varying in composition and structure. Many man-caused fires may have been set at seasons different from natural burns; this may change the present complex stand structures from those common previously. In addition to fires, smaller disturbances such as windthrow, and fungal or insect attack have had important influences on the structure and composition of these forests. Also, massive blowdowns resulting from the Columbus Day storm in 1962 and other major storms in 1880 and 1921 (Ludlum 1971) may enhance the shift from Pseudotsuga to Tsuga and Abies amabilis by removal of the overstory, allowing release of understory seedlings and saplings.

The spatial patterns described for various species also reflect their responses to various scales and intensities of disturbance. For example, if an area of forest is almost totally destroyed by fire, as in plot SM-1 or HY-5, and this results in a relatively even-aged stand, then the trees in this stand may have characteristic spatial dispersions. For Pseudotsuga menziesii and Abies procera in this example, this probably means a uniform distribution at small quadrat sizes and random at all larger quadrat sizes. The tendency towards a uniform distribution reflects the development of more even spacing between trees as the stand ages. If a mixed species stand results (e.g. plot GM-2) or if an area of forest is only partially destroyed by fire, then a number of different patterns may result, depending not only on the composition and structure of the surviving vegetation but also on the nature of the resulting regeneration. For example, in plot HY-1 a fire resulted in the regeneration of primarily Tsuga heterophylla and Abies procera in the openings between scattered old-growth Pseudotsuga menziesii. The clumped spatial patterns of Tsuga and Abies at various quadrat sizes reflects their establishment on suitable substrates and under favorable canopy conditions in differently sized openings.

The species that initially establishes following a disturbance may determine, to a large extent, the rate and nature of subsequent regeneration. For example, Abies procera and Abies amabilis possess heavy seeds, with rates of spread more limited than the light seeded Tsuga heterophylla and Pseudotsuga menziesii (Minore 1979). Absence of Abies spp. from a stand initially may influence stand structure for decades, if not centuries. If Pseudotsuga establishes first, other species may regenerate within 100 years or less; if, however, Tsuga dominates reproduction, other tree species may be excluded for a longer period of time (also see Chapter II). The effect of a dense Tsuga canopy is to inhibit new invasion or suppress the growth of those already present. The resulting succession is consistent with the 'inhibition' model of Connell and Slatyer (1977). Conversely, the presence of a main canopy of Pseudotsuga may facilitate the regeneration of Tsuga and other shade tolerant species. Egler (1954) in his 'initial floristic composition' model suggested that the species arriving at a site first significantly affects succession.

Several key processes in regeneration depend on the species composition in the main canopy. Firstly, the canopy species determines the light availability in the understory and the amount and type of precipitation that reaches it (Atzet and Waring 1970, Rothacher 1963). The differences between Pseudotsuga menziesii (and Abies procera) and Tsuga heterophylla tree canopies probably result in differences in soil moisture and light in the understory and are manifested by fewer small trees and understory herbs under the Tsuga. A second important factor is the abundance, size and location of canopy openings. In many old-growth stands where trees range from several meters to 50-60 meters tall, canopy openings may not be discrete. However, younger stands often have a relatively uniform canopy and openings are obvious and discrete. Large, old-growth trees and snags that remain after fire produce openings in the developing forest as they decay or are blown over.

A third important contributor to regeneration is effectiveness of woody debris not consumed by fire. This may be especially important as a substrate for successful establishment of Tsuga heterophylla, and to a lesser extent, Abies amabilis and the other species. In canopy openings down logs from windfalls, stumps, upturned root plates and trunk buttresses are all potential establishment sites for tree seedlings. Tsuga seedlings thrive on rotten wood throughout the Pseudotsuga forests of Oregon and Washington (Christy 1982, Christy and Mack 1984, Fonda and Bliss 1969, Franklin 1966, Franklin et al. 1981, Long 1976, Thornburgh 1969); logs hold moisture well when the forest floor is drying out during summer (Kotar 1972). In the Abies amabilis zone raised sites for Tsuga seedlings also provide: (1) an earlier, longer snow-free season; and (2) a substrate above where debris accumulates (Kotar 1972, Long 1976, Thornburgh 1969). Logs also have different nutrient availabilities than soil, which may affect establishment (Sollins 1982). Abies amabilis seedlings are deeper rooted and so not as severely affected by moisture stress and more rigid, so less likely to be flattened by debris deposited during snowmelt.

Canopy openings are rarely occupied by Pseudotsuga menziesii, except on dry sites where it frequently forms all-aged stands (Means 1982b). Abies procera seedlings and saplings were found in several Pseudotsuga dominated stands, suggesting that it may establish for several decades after initial stand formation and also persist in canopy openings. Individual trees that capitalize on canopy openings may be new arrivals following gap formation or trees that were present beforehand. In either instance, they must be able to grow rapidly to dominate over new invaders or other competitors such as shrubs. Often, however, many become suppressed; both Tsuga and Abies amabilis are very shade tolerant and may persist under a relatively closed canopy (Minore 1979). When a gap is created either species can rapidly occupy it. At lower elevations in the transition zone, Tsuga often dominates gaps owing to its faster growth rate (Kotar 1972). At higher elevations, Abies amabilis, due to its seedling morphology and physiology, is more often the gap occupant. The numbers of small Tsuga are often limited by the abundance and state of decay of woody debris.

In old-growth Pseudotsuga forest, Christy (1982) found that both removing root competition and increasing light availability increased seedling growth but there was no apparent synergistic effect; the greatest increases in growth were accomplished by reducing root competition (Christy 1982). The greater frequency and height of seedlings in gaps and under Pseudotsuga canopies than under Tsuga canopies in the present study suggests that resources for establishment and growth are less limiting there. Canopy fish-eye photographs revealed differences in direct beam radiation which may be important to tree seedlings. *Tsuga* had higher average daily rates of photosynthesis than *Abies* at all light intensities in the Washington Cascades (Thornburgh 1969); it may be that minimum compensation points necessary for survival and growth, are lower and the relative abilities to respond to release greater for *Tsuga* than *Abies amabilis* seedlings. Occasional sunflecks may provide most energy for photosynthesis under these dense multilayered canopies (Emmingham and Waring 1973, Hodges 1967); if so, measurements of direct light may be more useful than total radiation.

Stand characteristics which control tree regeneration similarly affect the abundance of understory shrubs and herbs. This has important implications for forest management. Plant communities in this area are classified using cover of key shrub and herb species (Dyrness et al. 1974, Hemstrom et al. 1982). Certain key species vary greatly in importance as a result of stand history as well as a consequence of the habitat characteristics. For example, under a dense *Tsuga heterophylla* canopy, many herb species are poorly represented (Tables 13, 14, Alaback 1982), the canopy effect overriding the influence of the substrate. It is important, therefore, to determine to what degree understory composition responds to stand history vs. differences in site before these communities can be related to habitat types (sensu Daubenmire and Daubenmire 1968).

Forest succession

Forests with widely-spaced large trees in an uneven-aged matrix of other species reflect the effects of succession (Jones 1945). As in earlier descriptions, I found that *Pseudotsuga menziesii* and *Abies procera* will be replaced by *Tsuga heterophylla* and/or *Abies amabilis* in the absence of fire. In all the old-growth stands aged, the dominant *Pseudotsuga* displayed a range in age, from at least 50 to 100 years; such an age span has been attributed elsewhere to a delay in regeneration owing to a lack of seed source following large fires and repeated disturbances (Franklin and Hemstrom 1981). The range in age of Pseudotsuga in younger stands was generally not as great as in the older stands, a pattern also noted by Munger (1930, 1940).

Tsuga heterophylla and Abies amabilis are "equilibrium" species (Pickett 1976), in the sense that, once established, they can persist as long as the physical habitat remains relatively stable. On the other hand, Pseudotsuga menziesii and Abies procera are "opportunist" species, establishing in large numbers and growing rapidly in open environments created by massive disturbance. Catastrophic disturbances are frequent enough to prevent complete, widespread successional replacement of the long-lived Pseudotsuga by the shade-tolerant species in the transition zone of the central western Oregon Cascade Range, and probably also in similar forests elsewhere in the Cascade Range in Oregon and Washington. On the other hand, where species-composition, disturbance or environment differ, the dynamics of forest regeneration may differ.

The old-growth forests described are not in a steady-state condition. There is a shift from Pseudotsuga to shade-tolerant species in the absence of disturbance and a number of successional pathways possible resulting from repeated disturbance (also see Chapter II). This is not unique to the region; many forests in other parts of the world reflect periodic, catastrophic disturbances such as fire, windstorms, mass movements and vulcanism (Ashton 1976, McKelvey 1953, Veblen and Ashton 1978, Wardle 1974, Whitmore 1974). In such disturbed situations, a non-equilibrium view of succession, the concept of patch dynamics, is useful (Pickett 1980, Pickett and Thompson 1978). Its important components are (1) the pattern of patch creation in time and space, (2) patch size and structure, and (3) the changes in individual patches due to species availabilities, adaptations, and interactions (Pickett 1980). This approach incorporates the unpredictability in rate of change and species-composition common during succession; it is not necessary to assume an orderly progression toward an idealized end-point.

Models of vegetation change that emphasize continuous change and do not require stable end-points have been termed kinetic schemes (Drury and Nisbet 1971). The differential growth and survival of the species available in spatially and temporally varying environments produce vegetation change (Drury and Nisbet 1971, 1973). While plants change the environment, frequently the more significant changes are the result of periodic disturbances. The importance of such disturbances in the western Oregon Cascade Range, with their apparent effects on forest structure and regeneration demonstrated here, suggest that forest succession in the region should be interpreted using a kinetic scheme.

IV. TREE REPLACEMENT PATTERNS IN THE ABSENCE OF FIRE IN OLD-GROWTH *PSEUDOTSUGA* FORESTS OF THE WESTERN CASCADE RANGE, OREGON

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ABSTRACT

In the absence of holocaustic fire in mid-elevation old-growth forests of the Western Oregon Cascades, the shade intolerant *Pseudotsuga menziesii* and *Abies procera* are replaced by the shade tolerant *Tsuga heterophylla* and *Abies amabilis*. Seedlings of the shade tolerant species may be present under a *Pseudotsuga* canopy and respond to formation of openings in the canopy but are rare or absent under overstory *Tsuga*. Rarely do understory trees reach the main canopy in the absence of disturbance. Small disturbances, such as single or several tree windfalls, create canopy openings where *Abies amabilis* often regenerates; *Tsuga heterophylla* may also be important when rotten logs provide suitable substrates. The differences in canopy species, and presence of canopy openings result in the regeneration of relatively even-aged groups of trees. The abundance and vigor of small trees in openings increase in larger openings which have higher levels of direct radiation during the growing season.

These interactions demonstrate the need for any successional scheme to include the effects of different canopy tree species, in addition to various disturbances, as factors controlling the rate and nature of forest succession.

INTRODUCTION

Vegetation change has often been regarded as a community-controlled process and the importance of microenvironmental modification by plants (autogenic change) stressed (Clements 1916, Whittaker 1975). Many recent models of succession, however, emphasize the importance of periodic disturbances, producing allogenic change which continues even after a "stable" community has established (e.g. Drury and Nisbet 1971, Pickett 1980, Connell and Slatyer 1977). Type, scale, frequency and intensity of disturbance vary among different types of vegetation. For example, widespread mass movements in tropical forests may initiate large scale succession (e.g. Garwood, Janos and Brokaw 1979), whereas the effects of tree falls in hardwood forests of the eastern United States may be more subtle (e.g. Runkle 1981).

Most of the older stands in the western Cascade Range of Oregon are not in a steady state (*sensu* Whittaker 1975) because the species regenerating beneath the canopy are not yet canopy dominants (Chapter III). Extensive forests dominated by old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and at higher elevations, noble fir (*Abies procera* Rehd.), resulted from periodic catastrophic fires (Hemstrom and Franklin 1982, Franklin and Hemstrom 1981). At least two large fire episodes have occurred in the western Cascade Range in the last 5 centuries, initiating c. 140 and 450 year old age-classes of *Pseudotsuga menziesii* (Franklin and Hemstrom 1981). In the absence of further fire in such areas, the *Pseudotsuga* would eventually be replaced by shade-tolerant species such as western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) (Franklin and Hemstrom 1981). In many areas, however, periodic fires of low intensity prevent the replacement of shade-intolerant species by *Tsuga heterophylla* and *Abies amabilis*; in others partial burns have allowed the establishment of stand mosaics of varying composition and structure (Chapters II, III).

Without repeated fire, regeneration processes may differ from areas where periodic fires burned. The objective of the present study is to describe and interpret forest regeneration in old-growth stands in the absence of fire. Particular emphasis is given to: (1) the influence of disturbance (allogenic change) and (2) the role of interactions among tree species (autogenic change) in the dynamics of these forests.

STUDY SITES

The area studied is in the South Santiam River drainage in the central Western Cascade Range of Oregon (latitude 44° 25'S, longitude 122° 20'W) at elevations of c. 1000 - 1300 m. Here, Tsuga heterophylla and Abies amabilis are both potential climax species; this area is referred to as a transition between the Tsuga heterophylla zone and the higher elevation Abies amabilis zone (Franklin and Dyrness 1973).

Two areas were selected for detailed study (Table 17), both having relatively undisturbed old-growth transition-zone forests, with large, old-growth Pseudotsuga menziesii in a matrix of variously-sized Tsuga heterophylla and Abies amabilis. Canopy dominants often exceed 450 years old, with no evidence of fire for at least 4-5 centuries. A well developed shrub tier [Alaska huckleberry (Vaccinium alaskaense Howell), vine maple (Acer circinatum Pursh) and Pacific rhododendron (Rhododendron macrophyllum D. Don ex G. Don)] is often present and numerous herbaceous species are usually abundant.

In each area, two rectangular plots were sampled (Table 17). These four plots represent several structural types, differentiated by the colonizing species following fire and by presence of more recent disturbance. Plots BP-1 and BP-2 (T14S R4E, Sect. 25), located at the base of a glacial cirque, are characteristic of forests where Pseudotsuga and Tsuga established together following fire (Fig. 22 a). Plot SC-1 (T14S R5E, Sect. 18) is dominated by Pseudotsuga with fewer Tsuga in the upper main canopy (Fig. 22 b), a

TABLE 17: Study site characteristics.

LOCATION AND PLOT	CANOPY DOMINANTS	STAND AGE * (years)	ELEVATION (m)	SAMPLE PLOT DIMENSIONS (m)	ASPECT	SLOPE (°)
Bear Pass						
BP-1	*Pseudotsuga menziesii*, *Tsuga heterophylla*	500	1170	80 x 100	NE	5-10
BP-2	*Pseudotsuga menziesii*, *Tsuga heterophylla*	500	1200	30 x 120	Flat-NE	0- 5
Squaw Creek						
SC-1	*Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies amabilis*	450/830	1260	60 x 100	E-SE	10
SC-2	*Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies amabilis*	800	1190	50 x 100	NW	5-10

* Approximate age based on the emergent *Pseudotsuga menziesii*.

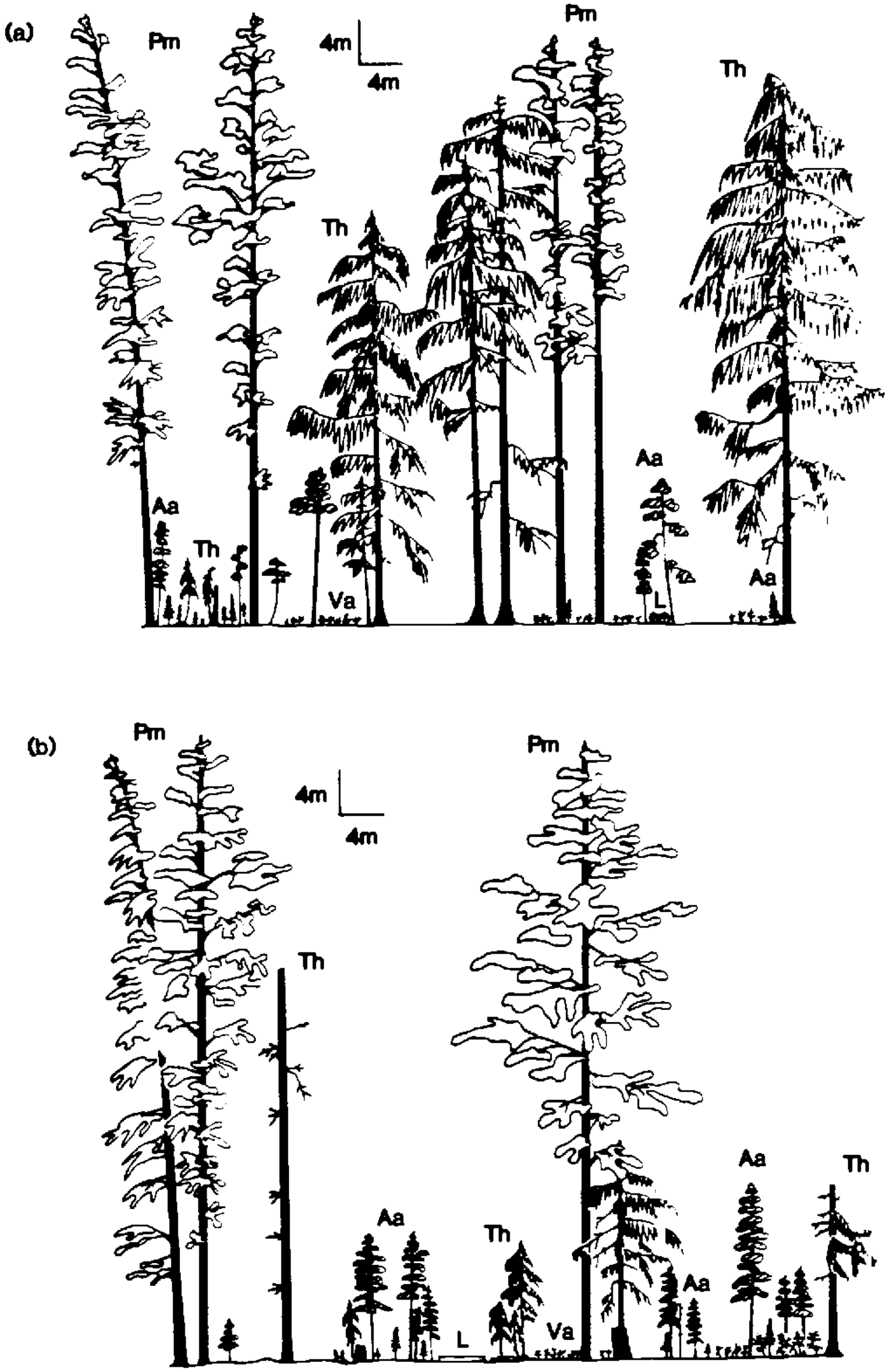
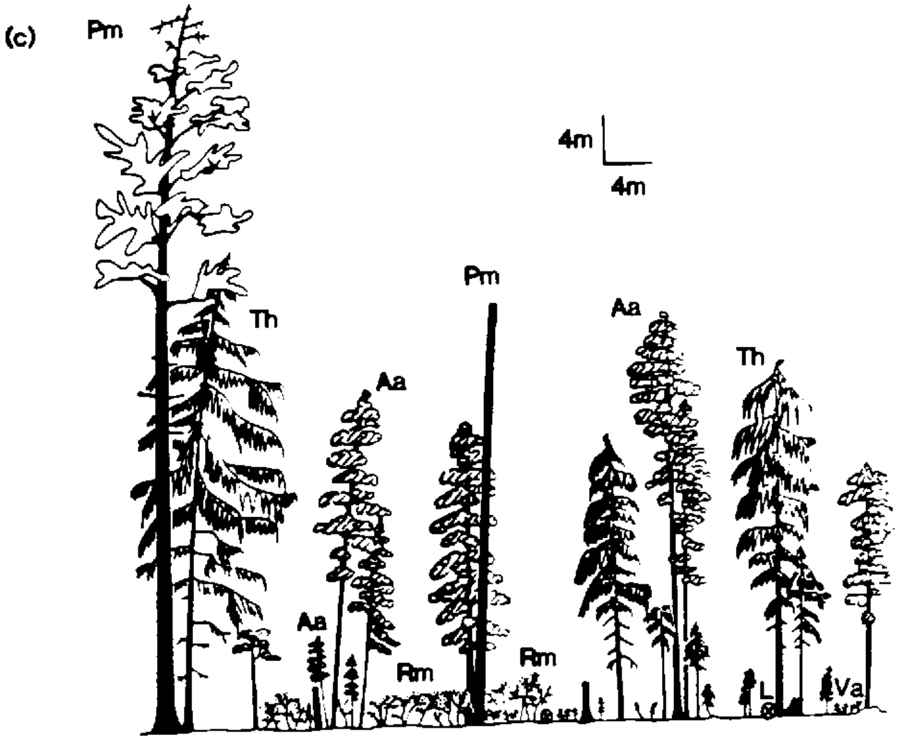


FIGURE 22: Profiles of (a) plot BP-1, (b) plot SC-1, and (c) plot SC-2. Aa, Abies amabilis; Ac, Acer circinatum; L, Log; Oo, Oxalis oregana; Pm, Pseudotsuga menziesii; Rm, Rhododendron macrophyllum; Th, Tsuga heterophylla; Va, Vaccinium alaskense.

Figure 22: continued



structure more common where Pseudotsuga colonized first following fire and Tsuga established later. Plot SC-2 (T14S R5E, Sect. 17 & 20) contains few old-growth Pseudotsuga, with the canopy dominated by Tsuga and Abies amabilis (Fig 22. c), a structure suggesting prolonged succession in the absence of fire.

METHODS

Analysis of forest structure

Use of size-class analysis to interpret forest dynamics assumes a consistently positive relationship between diameter and age of different trees within a species. My other studies (Chapters II, III) indicated that, in many stands subjected to recurrent partial fires, age is often weakly correlated with diameter. In these other stands Tsuga heterophylla and Abies amabilis regenerate after fire or in the absence of fire underneath a Pseudotsuga or Abies procera canopy or in canopy openings (Chapters II, III). When fires do not occur in an area for several centuries, as in the plots in the present study, regeneration of Tsuga and Abies amabilis may depend on which species dominates the main canopy or the abundance of canopy openings (Chapter III). Both with and without fire, clumps of trees with different growth rates develop and hence, have different diameter/age relationships.

To test the diameter/age relationship, increment cores were extracted at a height of 1 m from 26-33 trees in each area or plot. Several trees from each 5 cm size class from 5 - 60 cm dbh were cored. Plots BP-1 and BP-2 were adjacent, so only one sample was collected for both plots. For SC-2, stumps in an adjacent clearcut also were aged, some of which were included for an age/diameter regression analysis. Age estimates for the main canopy trees (Table 17) in each area were also obtained from stumps on adjacent clearcuts.

The diameter of all trees $\geq$ 5 cm dbh was measured in the plots. The numbers of saplings (trees < 5 cm dbh but $\geq$ 1.4 m tall) were also recorded. Saplings and trees which showed obvious signs of having established on an elevated surface such as a log, stump, trunk buttress, or upturned root plate were noted. Stumps, dead standing trees and dead saplings were also counted, measured and, if possible, identified to species. Size-class diagrams for each tree species in each plot were prepared to depict the frequency of saplings and of stems in 10 cm size-classes beginning at 5 cm dbh.

To investigate the vertical component of forest structure, trees $\geq$ 5 cm dbh were assigned to relative canopy-height classes: emergent, upper main canopy, lower main canopy, below main canopy, and overtopped. These crown-class categories do not necessarily indicate vigor of an individual tree nor its probability of success to maturity. This is due to the presence of *Tsuga heterophylla* and *Abies amabilis* with different growth rates and varying tolerances to low light conditions. Vertical structure was also depicted by vegetation profiles drawn for forest strips 60 x 5 m.

Spatial relationships

Current vegetation pattern often reflects the origin of the pattern. Therefore, the spatial dispersion of trees was assessed by mapping all individuals $\geq$ 1.4 m tall in 5 x 5 m contiguous quadrats. A variation of the nested quadrat technique (Greig-Smith 1964, Kershaw 1973) and Morisita's (1959) index (I_δ) were used to determine the departure of tree species from a random distribution. The application of this technique has been described in Chapter II. Morisita's index is given by:

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

where q = the number of quadrats, n_i = the number of individuals in the *i*th quadrat, and N = the total number of individuals in all quadrats. I_δ = 1.0 when the population is randomly dispersed, where randomness implies an equal probability of each individual occurring in any one quadrat. If the individuals are aggregated, $I_\delta > 1.0$, and if evenly distributed or hyperdispersed, $I_\delta < 1.0$. The significance of values of Morisita's index > 1.0 was evaluated by an F test (Morisita 1959).

Spatial patterns of young trees often differ strongly from those of older trees; the spatial distributions of tree species of different size-classes were therefore assessed separately. Morisita's index was computed for different species and size-classes for quadrats of increasing size, beginning with quadrats of 5 x 5 m. The quadrat sizes for plot BP-1, for example, were 5 x 5 m (25 m^2), 10 x 10 m (100 m^2), 15 x 15 m (225 m^2), 20 x 20 m (400 m^2), and so on. For quadrat sizes < 50 x 50 m (plot BP-1), < 25 x 25 m (plot SC-2), and < 30 x 30 m (plots BP-2 and SC-1) the original quadrats were grouped into perfect squares; larger blocks of quadrats were rectangles. In instances where the quadrat sizes were not evenly divisible into the total area, I_δ was computed for the largest subareas of a given size. In these cases the average index was calculated from the results obtained from different subareas of the total grid of 5 x 5 m quadrats. Since the index may vary erratically when few individuals are present, it was only calculated for sample groups $\geq$ 15.

To determine which size-classes to use in the spatial analyses, age information and other structural attributes were considered. For example, in plot BP-1 Tsuga heterophylla > 55 cm dbh formed a distinct group of large, main canopy trees, so their dispersion was analysed separately from smaller Tsuga trees. Similarly, stems of Tsuga $\leq$ 10 cm dbh in the same plot frequently occurred in canopy openings, so their dispersion was probably produced by a different regeneration process; these were analysed separately. In most cases large size-classes were used, because there was considerable variation in the diameter/age relationship.

Occurrence of different species together was investigated at various quadrat sizes, using a chi-square test (Mueller-Dombois and

Ellenberg 1974). The test was applied only to species sufficiently abundant to provide adequate cell frequencies in 2 x 2 contingency tables, but not so abundant as to be present in all quadrats.

Understory sampling

On each unit quadrat (5 x 5 m) in all plots the total cover of understory species (excluding tree species) was estimated in percentage cover classes of < 1, 1-5, 6-25, 26-50, 51-75, and 76-100. Separate estimates using the same classes were also made for the total cover of Acer circinatum and Rhododendron macrophyllum, which were abundant in several plots.

In plots SC-1 and SC-2, tree seedlings (> 5 cm tall but < 1.4 m tall) were counted in 100 2 x 1 m randomly located quadrats.

Canopy openings

To investigate the importance of canopy openings for tree regeneration in unburned old-growth stands, detailed sampling was performed at Bear Pass. In each of 10 variously sized openings and 10 adjacent areas with a relatively closed canopy, pairs of 10 x 10 m plots were established. The plots in openings were located to include patches of regeneration, because the seedlings and saplings were not distributed evenly over the entire canopy opening. In each plot all saplings were counted. Within these plots, five 2 x 1 m quadrats were randomly located and all seedlings counted within them. The overstory dominant for each seedling plot was recorded, as was the total understory cover of all species in percentage classes < 1, 1-5, 6-25, 26-50, 51-75, and 76-100. Whether seedlings or saplings showed obvious signs of having established on an elevated surface was recorded.

In each canopy opening plot, the last 5 years height growth was measured on 6-11 small Abies amabilis. Abies amabilis terminates each year's growth with a whorl of branches and a terminal bud scar, so height increments are easily measured. From the center of each

10 x 10 m plot, a hemispherical canopy fish-eye photograph was taken at a height of 1 m, to assess differences in total diffuse and direct radiation (Veblen, Veblen and Schlegel 1979). Since heavy snowpacks of 1-2 m are common in these forests from December-May, and bury most seedlings and saplings, percentage direct radiation only for the growing season (May-September) was calculated.

As an indirect measure of root competition, the basal area of all trees > 10 cm dbh was calculated in a circle of 15 m radius from the center of each 10 x 10 m canopy opening plot.

RESULTS

Forest structure

All least squares linear regressions of age over diameter at breast height show significant correlations (Fig. 23). In all plots, however (especially at Bear Pass), the presence of groups of *Abies amabilis* of similar age but different diameter, due to periods of suppression and release, reduces the strength of the relationship. Thus, although a good correlation exists between age and diameter, the strength of the relationship depends on how many of these differently aged groups are present. The frequency of individuals in large size-classes (i.e. 10 cm dbh) in the whole plot was therefore used to approximate the age structures of the tree populations in each plot.

Tsuga heterophylla at Bear Pass has size-class distributions that are interpreted to indicate all-aged populations (Fig. 24 a, e). Ages of several large old-growth *Tsuga*, on an adjacent 12 year old clearcut, ranged from 452-488 years. There are at least a few trees in all size-classes up to 1 m dbh but at least 40% of stems in both populations are saplings in canopy openings. Thus, although trees are present in all size-classes many trees in the populations are either saplings or large old-growth trees. *Abies amabilis* is represented by many saplings and small stems with few larger individuals (Fig. 24 b, f). The size-class distributions

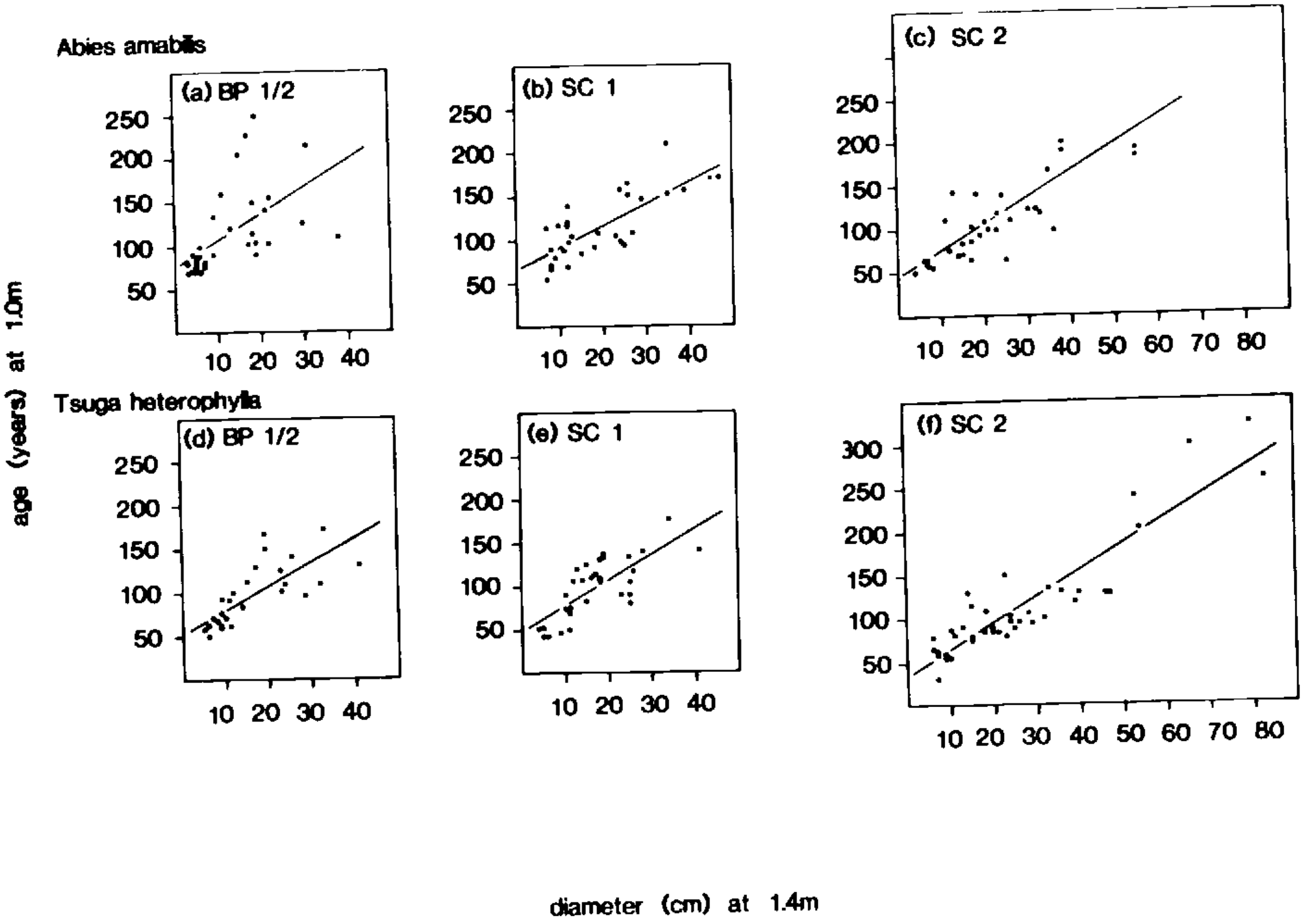


FIGURE 23: Relationship of age to diameter at a height of 1 m for *Abies amabilis* and *Tsuga heterophylla* in the study plots. Equations are: *Abies amabilis* (a) $y = 76.0 + 3.00\ x$, $r = 0.56$; (b) $y = 68.4 + 2.45\ x$, $r = 0.76$; (c) $y = 51.3 + 2.64\ x$, $r = 0.81$; *Tsuga heterophylla* (d) $y = 56.2 + 2.60\ x$, $r = 0.73$; (e) $y = 49.4 + 2.92\ x$, $r = 0.75$; (f) $y = 34.8 + 3.00\ x$, $r = 0.91$. $P < 0.001$ for all equations.

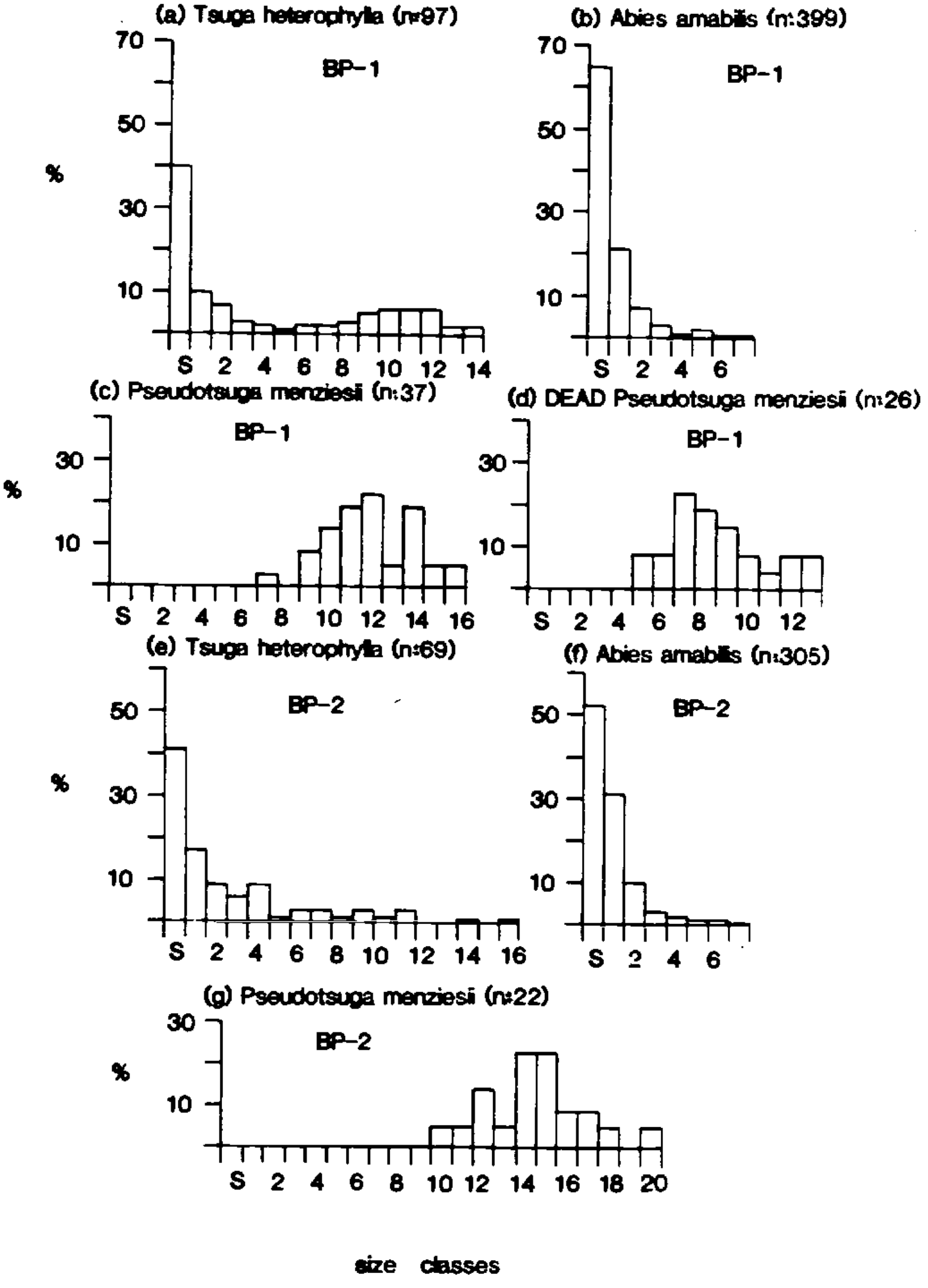


FIGURE 24; Size-class frequency histograms for main canopy tree species in plots BP-1 and BP-2. The size-classes are: S, saplings; 1, trees of dbh 5-14 cm; 2, dbh 15-24 cm; 3, dbh 25-34 cm; etc. n = number of trees ≥ 1.4 m tall.

of *Pseudotsuga menziesii* (Fig. 24 c, d, g) are similar to other old-growth stands in the central Oregon Cascades (Franklin and Hemstrom 1981, Chapters II, III) and probably represent populations that established over several decades following catastrophic fire. Ages of several *Pseudotsuga* on the adjacent clearcut were c. 450-500 years. A recently dead 148 cm dbh western white pine (*Pinus monticola* Dougl. ex D. Don) may be of the same origin.

Pseudotsuga menziesii and *Tsuga heterophylla* probably established together following holocaustic fire approximately 500 years ago. The *Pseudotsuga* grew faster than the *Tsuga* producing more emergent trees (Fig. 22 a, Table 18). *Abies amabilis* are more abundant than *Tsuga* in the regeneration tiers (Table 18), especially in BP-2 where several large patches of trees 10-20 cm dbh occupy former canopy openings.

In plot SC-1 over 60% of *Abies amabilis* are < 15 cm dbh but this species and *Tsuga heterophylla* have size class distributions similar to the plots at Bear Pass (Table 18, Fig. 25 a, b). *Pseudotsuga menziesii* has modes at several size classes (Fig. 25 c); two trees > 245 cm dbh may be of the c. 800 year old age class as in plot SC-2. Sizes of dead trees indicate mortality within patches of young *Abies*, and of many main canopy *Tsuga*, which may have reached the species' maximum longevity (Fig. 25 d, e).

Several *Pseudotsuga* stumps on an adjacent clearcut were 425-470 years old and 4 *Tsuga* were all 350-400 years. Probably *Pseudotsuga* established following fire; *Tsuga* more likely invaded subsequently. Two *Pinus monticola* 95-114 cm dbh (one recently dead) probably established with the *Pseudotsuga*.

In plot SC-2 the main canopy and all lower tiers have abundant *Tsuga* and *Abies* (Table 18); Pacific yew (*Taxus brevifolia* Nutt.) [and the occasional giant chinkapin (*Castinopsis chrysophylla* (Dougl.) A. DC.)] are present in the understory. *Tsuga* and *Abies* have reverse J-shaped size-class distributions indicative of a reproducing population (Fig. 26 a, b; Whittaker 1974, Hett and Loucks 1976). *Pseudotsuga menziesii* are rare and large, suggesting

TABLE 18: Number of trees ≥ 1.4 m tall in relative height classes in the 4 plots. The height classes are: I, overtopped; II, below main canopy; III, lower main canopy; IV, upper main canopy; and V, emergent.

	PLOT AND HEIGHT CLASS									
	BP-1					BP-2				
SPECIES	I	II	III	IV	V	I	II	III	IV	V
Pseudotsuga menziesii				4	33				1	21
Tsuga heterophylla	51	11	4	29	2	44	8	8	9	
Abies amabilis	359	25	14	1		264	28	11	2	
	SC-1					SC-2				
	I	II	III	IV	V	I	II	III	IV	V
Pinus monticola					1					
Pseudotsuga menziesii				3	19				5	6
Tsuga heterophylla	140	9	12	3		153	17	13	11	
Abies amabilis	183	55	31	2		418	43	21	10	
Taxus brevifolia						9				

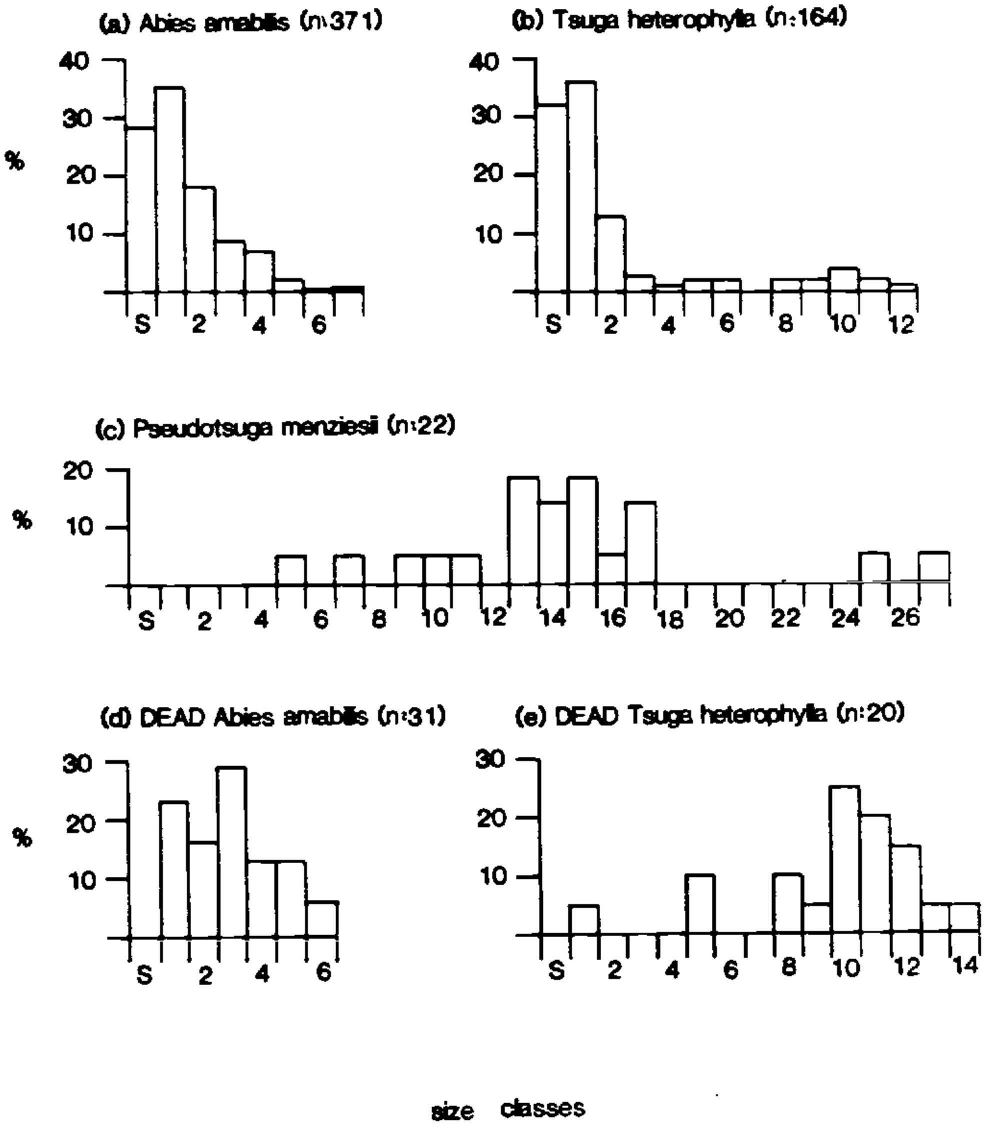


FIGURE 25: Size-class frequency histograms for main canopy tree species in plot SC-1. The size-classes and n are the same as in FIG. 3.

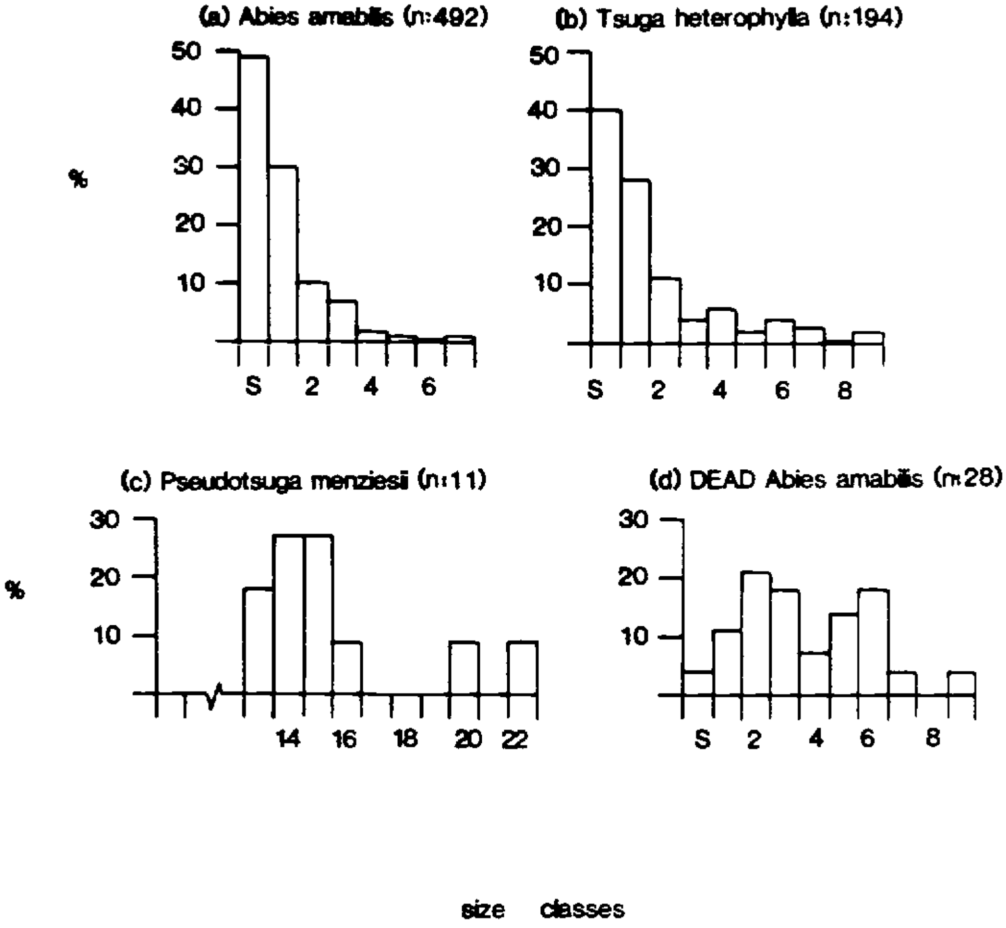


FIGURE 26: Size-class frequency histograms for main canopy tree species in plot SC-2. The size-classes and n are the same as in FIG. 3.

a very old population (Table 18, Fig. 26 c). Three stumps > 2 m dbh in an adjacent clearcut were c. 790-830 years old. It is possible that Pseudotsuga 125-164 cm dbh are younger, similar in age to those in plot SC-1. Many Abies amabilis of intermediate diameter within regeneration patches are dead (Fig. 26 d).

In all plots ≥ 80% of Tsuga heterophylla established on elevated surfaces; fewer Abies amabilis and Taxus brevifolia regenerated on these microsites (Table 19).

TABLE 19: Percentages of saplings and stems ≥ 5 cm dbh of important tree species established on elevated surfaces (logs, stumps, trunk buttresses, or upturned root plates) in the 4 plots.

	PLOT			
SPECIES	BP-1	BP-2	SC-1	SC-2
Tsuga heterophylla	88	94	80	81
Abies amabilis	16	35	35	18
Taxus brevifolia	-	-	-	22

Spatial dispersion of tree species

Large Pseudotsuga menziesii are uniformly distributed at small quadrat sizes and randomly at larger quadrat sizes (Fig. 27 a, c, 28 b, d). In plots BP-2 and SC-1, however, Pseudotsuga menziesii although showing a tendency towards a uniform distribution at 25 m^2, appear to occur in several clumps at 400-625 m^2 and 100 & 400 m^2 respectively (Fig. 27 c, 28 b). Small Tsuga heterophylla are often extremely clumped at quadrat sizes up to 900 m^2 (Fig. 27 b, 28 a, c). Intermediate-sized Tsuga heterophylla may be distributed in smaller clumps (Fig. 27 b, 28 a, c) whereas large stems are often evenly distributed at small quadrat sizes and randomly at larger quadrat sizes (Fig. 27 b, 28 b). Small Abies

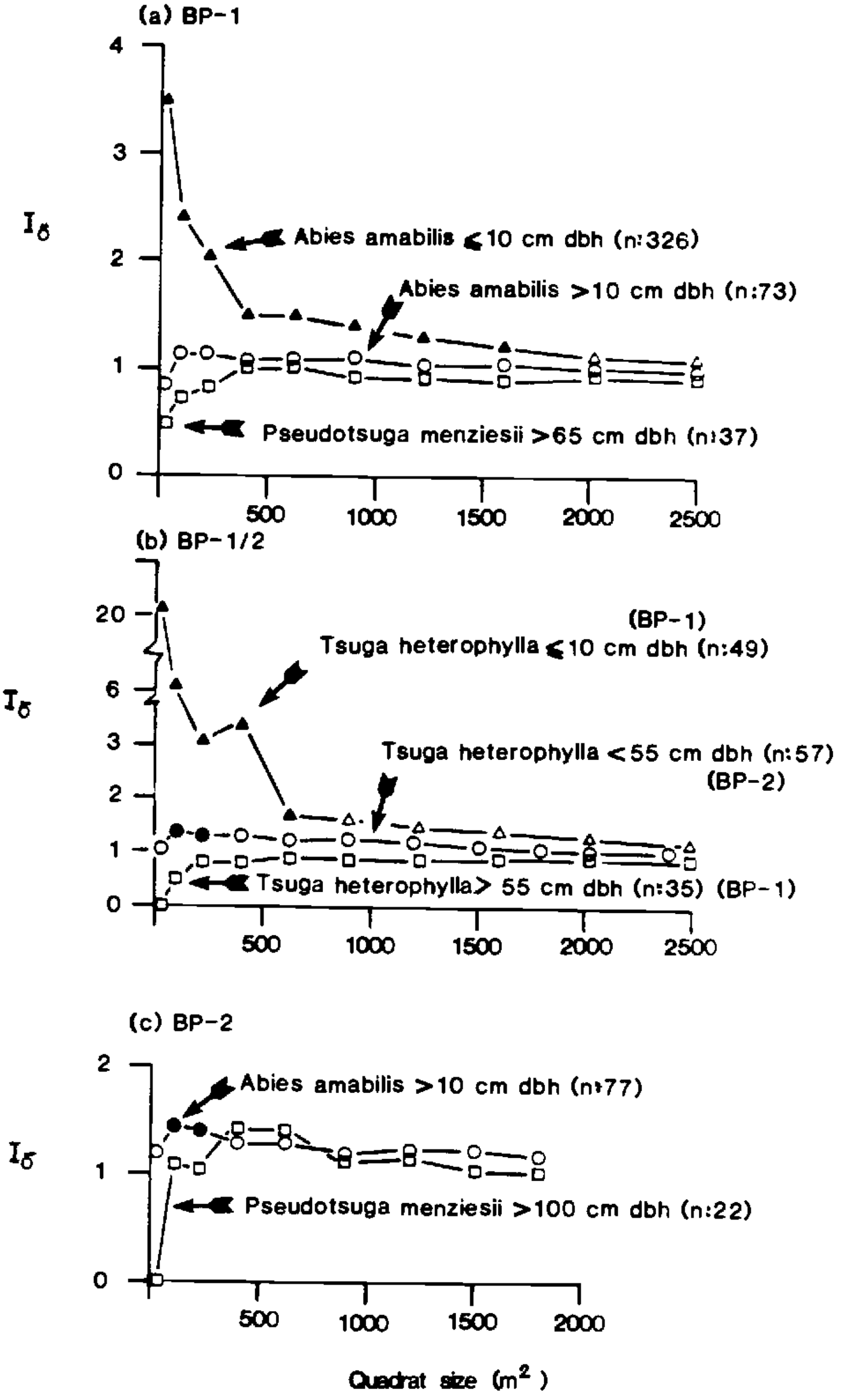


FIGURE 27: Values of Morisita's index, I_δ, at different quadrat sizes for species of different size-classes at Bear Pass. Filled symbols are I_δ values significantly > 1.0 ($P < 0.05$) according to an F test of Morisita (1959).

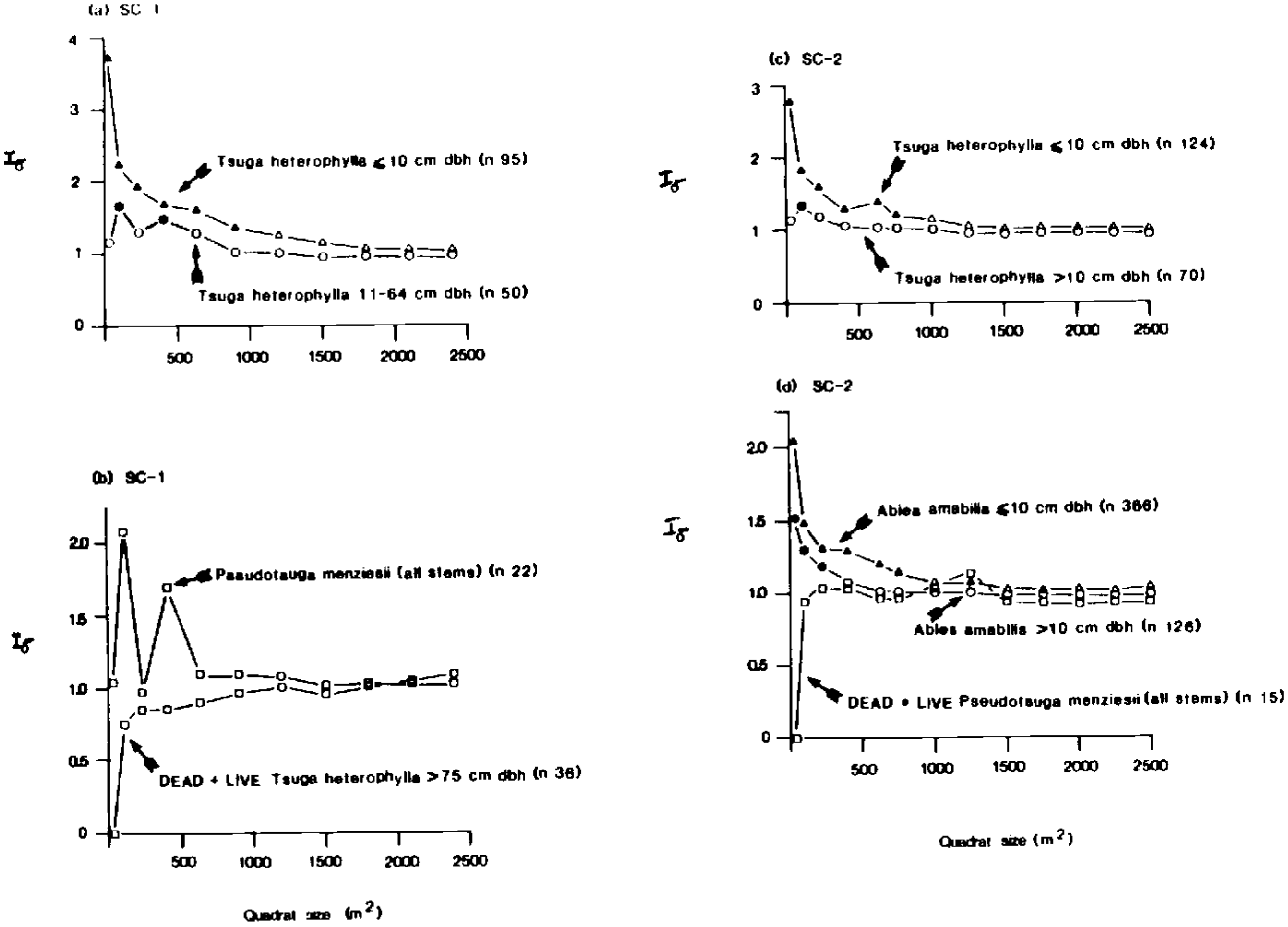


FIGURE 28: Values of Morisita's index, I_σ, at different quadrat sizes for species of different size-classes at Squaw Creek. Filled symbols are I_σ values significantly > 1.0 ($P < 0.05$) according to an F test of Morisita (1959).

amabilis are highly clustered at various quadrat sizes up to 1600 m^2 (Fig. 27 a, 28 d). Larger stems of Abies may be aggregated in small patches but tend to randomness at larger quadrat sizes (Fig. 27 a, c, 28 d).

A stem map of the northern 50 x 50 m of plot SC-2 illustrates the change in the degree of aggregation of trees with age (Fig. 29). For example, dense clumps of Abies amabilis $\leq$ 10 cm dbh are apparent whereas stems > 10 cm dbh are not as highly clumped. The random distributions of both Tsuga heterophylla > 50 cm dbh and Pseudotsuga menziesii (all stems) at quadrat sizes > 100 m^2 are also noticeable.

Forest development in the absence of massive disturbance such as fire also involves interactions between individuals of the same and different species. In plots BP-1 and SC-2 where there is a large component of Tsuga in the main canopy, small stems ($\leq$ 10 cm dbh) of Tsuga heterophylla and Abies amabilis are consistently negatively associated with the main canopy Tsuga (Table 20). Conversely, in several instances, small Tsuga heterophylla are often found under the less dense crowns of main canopy Pseudotsuga, as indicated by positive associations. The negative associations for Tsuga and Abies stems $\leq$ 10 cm dbh and larger diameter trees of the same species reflect single species patches.

Understory vegetation

There are almost twice as many seedlings of both Tsuga and Abies in plot SC-2 as in SC-1, many on elevated surfaces (Table 21). Plot SC-2 was divided for some analyses, since there are more seedlings in the portion that contains 9 of the 11 old-growth Pseudotsuga (SC-2A, illustrated in Fig. 29) than in SC-2B, where the canopy is dominated by Tsuga and Abies.

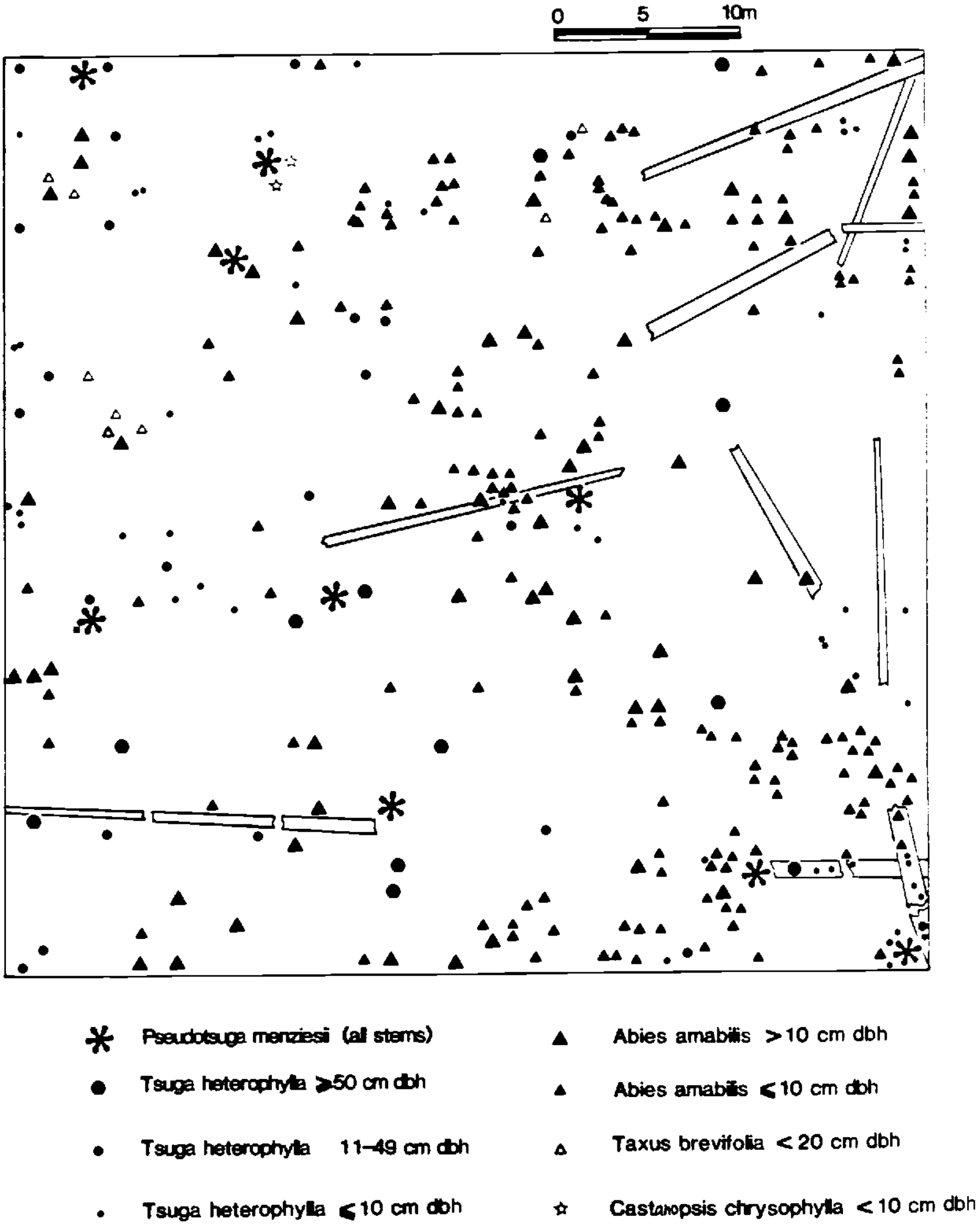


FIGURE 29: Stem map of plot SC-2A.

TABLE 20: Significant positive (+) and negative (-) associations between different species and size-classes in the study plots, based on a χ^2 test applying Yates' correction (Greig-Smith 1964).

PLOT	SPECIES COMPARISONS	BLOCK SIZE (m^2)	TYPE OF ASSOC'N	χ^2	*n*	*P*<
BP-1	*T*.*heterophylla* ≤ 10 cm dbh : *T*.*heterophylla* > 55 cm dbh	100	-	8.1	80	.005
		225	-	8.7	30	.005
	A.*amabilis* ≤ 10 cm dbh : *T*.*heterophylla* > 55 cm dbh	25	-	14.7	320	.001
		100	-	11.2	80	.001
BP-2	*A*.*amabilis* > 10 cm dbh : *T*.*heterophylla* > 55 cm dbh	100	-	4.2	36	.05
	P.*menziesii* > 100 cm dbh : *T*.*heterophylla* ≤ 55 cm dbh	25	+	4.6	144	.05
SC-1	*P*.*menziesii* (all stems) : *T*.*heterophylla* ≤ 10 cm dbh	25	+	14.3	240	.001
	T.*heterophylla* 11-64 cm dbh: *T*.*heterophylla* > 75 cm dbh	225	+	4.8	24	.05
	P.*menziesii* (all stems) : *T*.*heterophylla* > 75 cm dbh (DEAD)	100	-	3.9	60	.025
	P.*menziesii* (all stems) : *A*.*amabilis* > 10 cm dbh	100	-	5.2	24	.05
SC-2	*T*.*heterophylla* ≤ 10 cm dbh : *T*.*heterophylla* > 10 cm dbh	225	-	4.0	18	.05
	A.*amabilis* ≤ 10 cm dbh : *T*.*heterophylla* > 10 cm dbh	225	-	4.0	18	.05
	A.*amabilis* ≤ 10 cm dbh : *T*.*heterophylla* ≤ 10 cm dbh	225	-	4.0	18	.05
	A.*amabilis* > 10 cm dbh : *T*.*heterophylla* > 10 cm dbh	25	-	10.1	200	.005

TABLE 21: Numbers of seedlings per ha (±S.E.) in the 2 study plots at Squaw Creek. Numbers in parentheses refer to percentages of seedlings on elevated surfaces.

	PLOT			
SPECIES	SC-1	SC-2	SC-2A	SC-2B
Tsuga heterophylla	2450 ± 780 (95.9)	4750 ± 1602 (98.9)	6400 ± 2955	3100 ± 1236
Abies amabilis	2250 ± 548 (71.1)	4400 ± 683 (38.6)	6100 ± 1091	2700 ± 759

The mean understory cover in all plots is high; the Squaw Creek plots have much greater understory shrub cover (Table 22). Plot SC-2 supports more *Rhododendron* and *Acer* beneath the *Pseudotsuga* canopy (SC-2A) than the *Abies*-*Tsuga* canopy (SC-2B) (Table 22). These shrubs occur in dense clumps, interspersed with relatively open areas where regeneration of *Tsuga* and *Abies* is abundant.

TABLE 22: Mean understory cover (%) excluding *Rhododendron macrophyllum* and *Acer circinatum* for the 4 study plots and mean cover (%) of *Rhododendron* and *Acer*. *n* is the number of 2 m^2 quadrats assessed. SC-2A is the *Pseudotsuga* dominated half of plot SC-2, and SC-2B is dominated by *Tsuga* and *Abies amabilis* .

	PLOT				
	BP-1 (*n*=320)	BP-2 (*n*=144)	SC-1 (*n*=240)	SC-2A (*n*=100)	SC-2B (*n*=100)
Mean understory cover	50.8	65.9	62.7	48.8	69.6
Mean *Rhododendron* cover	+	+	+	30.6	11.2
Mean *Acer* cover	+	+	13.2	12.4	1.8

+ = < 1 percent mean cover

Importance of canopy openings

The composition of the main canopy influences understory cover and tree seedling regeneration in old-growth Cascade forests (Chapter III). At Bear Pass there is a much denser understory under a *Pseudotsuga menziesii* canopy and in canopy openings, and more tree seedlings in openings, than under a *Tsuga heteropyhlla* canopy (Table 23). The difference in tree regeneration is further demonstrated by a comparative sample of canopy openings and closed canopy situations (Table 24). Also, success to the sapling stage for both species appears to be related to establishment on elevated surfaces; the percentages of saplings on these sites are higher than those for seedlings (Table 24).

TABLE 23: Relationship between overstory dominant (or canopy opening) and mean understory cover (%) and mean number of seedlings per plot for seedling plots at Bear Pass. *n* is the number of 1 x 2 m plots located under each overstory dominant. Numbers within one column followed by different letters are significantly different according to Duncan's New Multiple Range test (P < 0.01).

OVERSTORY DOMINANT	*n*	MEAN UNDERSTORY COVER (%)	MEAN NUMBER SEEDLINGS
Pseudotsuga menziesii	18	64 a	3 a
Tsuga heterophylla	50	28 b	2 a
Canopy opening	30	68 a	9 b
Abies amabilis *	2	88	2

* no statistical comparisons were made with this species.

TABLE 24: Numbers of tree seedlings and saplings per 1000 m^2 in 10 canopy openings and under 10 adjacent closed canopies at Bear Pass. Numbers in parentheses refer to the percentages on elevated surfaces.

	CANOPY OPENINGS		CLOSED CANOPIES	
SPECIES	seedlings	saplings	seedlings	saplings
Tsuga heterophylla	1440 (77.8)	18 (94.4)	150 (46.7)	2 (100.0)
Abies amabilis	2090 (26.8)	95 (45.3)	570 (10.5)	4 (0.0)
Thuja plicata Donn ex D. Don (western redcedar)	10 (0.0)			

TABLE 25: Mean light conditions for canopy openings and adjacent closed canopies at Bear Pass. *n* is the number of photographs analysed. Values in a given column followed by different letters are significantly different according to a Mann-Whitney U test ($P < 0.01$).

	% DIFFUSE AND DIRECT BEAM RADIATION	% DIRECT BEAM RADIATION
CANOPY OPENINGS (*n* = 10)	53 a	18 a
CLOSED CANOPIES (*n* = 10)	42 b	9 b

Canopy openings are common in all stands: at Bear Pass 36-40% and at Squaw Creek 53-60% of all 5 x 5 m quadrats were in openings. There was significantly more total direct, and diffuse plus direct, radiation in canopy openings than beneath relatively closed canopy (Table 25). Openings transmit twice as much direct beam radiation during the growing season as closed canopies.

The numbers and height growth of seedlings or saplings increase with the amount of direct radiation received during the growing season (Fig. 30).

Smaller canopy openings (judged by their higher adjacent basal area) had fewer seedlings and saplings; a least squares regression of basal area and numbers of seedlings and saplings combined for the 10 canopy openings revealed an inverse relationship (Y (numbers of seedlings and saplings per plot) = 99.8 - 6.43 X (basal area, m^2 ha^{-1}), $r = 0.76$, $P < 0.01$).

DISCUSSION

Forest structure and tree spatial distributions are modified by: (1) disturbances by phenomena largely external to the vegetation and (2) intra- and interspecific plant interactions. The variability in forest structures and spatial patterns described here and the importance of canopy openings for tree regeneration illustrate the importance of small scale disturbances. Also, the complex pattern imposed on the forest mosaic by the effects of different canopy tree species demonstrates the need for any forest successional scheme also to include plant interactions as factors controlling the rate and nature of forest succession.

Importance of minor disturbances

Canopy openings form in these very old, unburned conifer forests when branches break, creating small openings, and when large trees fall or snap off as a result of disease, wind, the weight of snow or some combination of factors. The crown size of the fallen tree is important; for example, large Tsuga would form a larger gap than

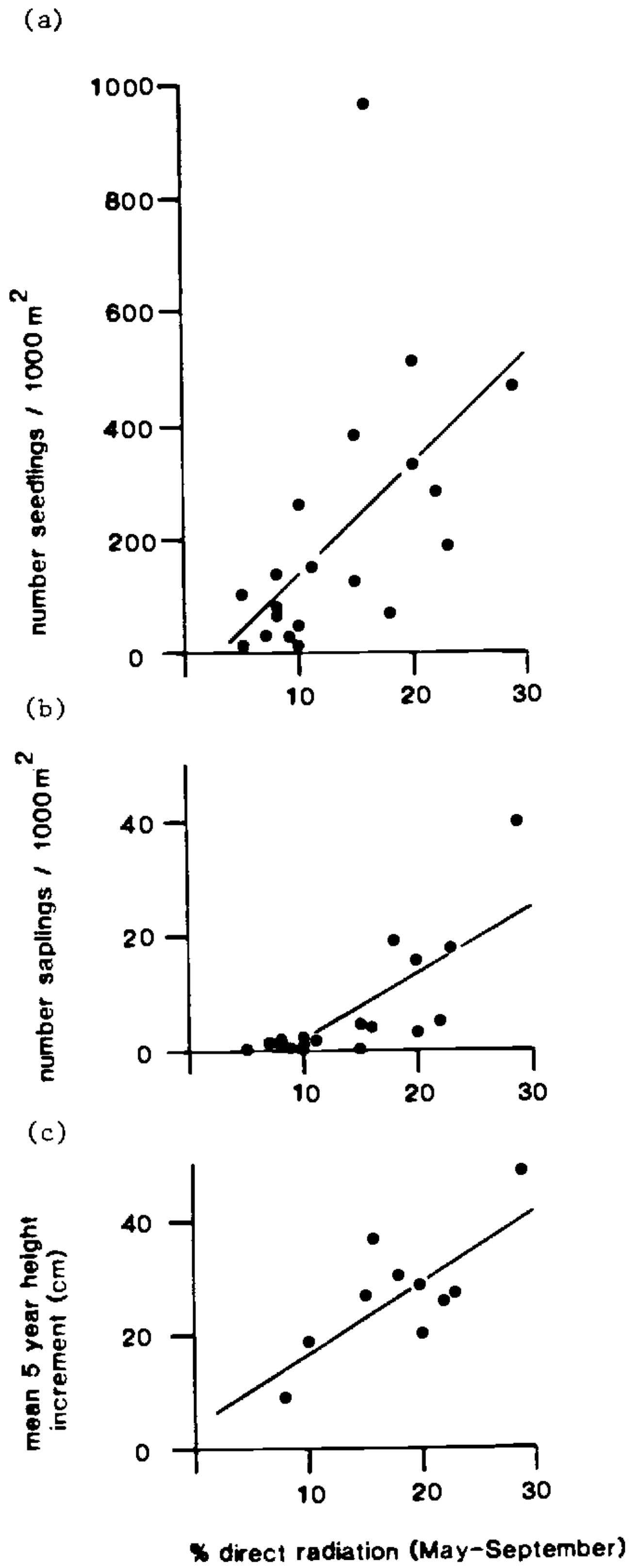


FIGURE 30: Relationship of percentage direct beam radiation (May-September) at Bear Pass to: (a) numbers of seedlings of all tree species, (b) numbers of saplings of all tree species, and (c) mean 5 year height increment of <u>Abies amabilis</u> saplings and small stems. The regression equations are (a) $y = 19.32\ x - 48.3$, $r = 0.56$, $\underline{P} < 0.02$; (b) $y = 1.17\ x - 9.9$, $r = 0.79$, $\underline{P} < 0.001$; (c) $y = 1.28\ x + 4.0$, $r = 0.76$, $\underline{P} < 0.02$.

Pseudotsuga of similar height, due to *Tsuga*'s wide, spreading crowns.

In the *Abies amabilis* zone forests of the Cascades of Washington, trees grow faster in openings than under a closed canopy; gaps were considered necessary for *Abies amabilis* and *Tsuga heterophylla* to reach the main canopy (Long 1976, Kotar 1972). Canopy openings in the Oregon and Washington coastal *Picea sitchensis* (Bong.) Carr. (Sitka spruce)/ *Tsuga heterophylla* forests are important for the regeneration of both species, and may be essential for *Picea* (Quaye 1982). Canopy openings modify the composition and distribution of understory shrubs and herbs and tree regeneration in partially burned old-growth forests near the present study area (Chapter III). Variously sized patches of saplings and small diameter stems commonly form mosaics of relatively even-sized groups in old-growth forests lacking the influence of repeated fire, such as those studied. The role of canopy openings in these situations, however, has received little recognition.

In plots BP-1 and BP-2, the toppling of large *Pseudotsuga* and *Tsuga* has created sizeable openings in the overstory canopy. Abundant small *Abies amabilis* and, to a lesser extent, *Tsuga heterophylla* develop in such gaps, forming clusters of individuals 600-1600 m^2 in area (Fig. 27 a, b). In plot SC-1, canopy openings occur where large *Tsuga heterophylla* have fallen or snapped. As at Bear Pass, these openings now support distinct clumps of *Abies amabilis* and *Tsuga* regeneration. The forest in plot SC-2 is now more "opening" than closed forest canopy; once all the old-growth *Pseudotsuga* fall, openings created by windfall of the shorter *Tsuga* and *Abies amabilis*, which produce a dense lower canopy, will become extremely important for subsequent regeneration.

At Bear Pass, canopy openings were rarely fully occupied by tree regeneration; commonly it was in distinct patches, rarely in the center of openings. Many seedlings and small trees were recent arrivals following gap creation, but often, especially in small openings, small diameter *Abies* and *Tsuga* were present prior to gap formation. Many of these showed increased height growth following gap creation, which declined as the surrounding main canopy tree crowns expanded into the opening. However, small *Abies* and *Tsuga* in many larger openings showed large persistent increases in height growth.

A persistent deep winter snowpack modifies the effects of canopy openings created by windthrow. *Tsuga heterophylla* seedlings are more susceptible to damage from snow than those of *Abies amabilis* (Kotar 1972, Long 1976, Thornburgh 1969). As a result, *Tsuga* survive on elevated surfaces where the effects of snow load are reduced. In summer, low soil moisture, where exacerbated by competition with understory shrubs and herbs, may often be too severe for *Tsuga* seedlings to survive except on rotten logs (Kotar 1972). Since the snow-free season is very short, it may take many years for canopy openings to fill completely.

Plant interactions

Aspects of life history of the species affect regeneration. *Pseudotsuga menziesii* regenerates primarily after fire except on dry sites (Means 1982b), and rarely colonizes canopy openings in old-growth stands. *Tsuga heterophylla* and *Abies amabilis*, on the other hand, are very shade tolerant and may persist in the understory as suppressed individuals for many years (Franklin and Hemstrom 1981). Hence, they may establish under a relatively closed canopy and grow faster when the canopy thins or is removed. Many of the sapling-sized individuals of *Abies amabilis* in the canopy openings I sampled were probably present before the openings were created. Many 3-7 cm dbh trees in openings that formed over the last 10-20 years were 70-90 years old.

The composition of the pioneer vegetation following fire also influences tree regeneration patterns for several centuries. If the post-fire tree reproduction is largely *Pseudotsuga menziesii*, *Tsuga heterophylla* usually invades the stand within the first century of development, if a seed source is nearby (Chapters II, III). If *Pseudotsuga* and *Tsuga* establish together following the fire, then there will be little subsequent regeneration beneath the dense Tsuga canopies (Chapter III). If the post-fire stand is mainly Tsuga heterophylla, regeneration may be excluded until dominant trees die.

Regeneration is successful in canopy openings because light levels are generally higher and root competition lower than in the surrounding forest. Root trenching in the eastern hardwood forests, to eliminate root competition, produced astounding responses in the understory, demonstrating the importance of competition for soil moisture (Toumey and Kienholz 1931, Korstian and Coile 1938). Increasing light further enhanced height growth of understory plants (including tree seedlings). An experimental study in low elevation Tsuga heterophylla forests of the western Oregon Cascades (Christy 1982) also found root competition to be important, but demonstrated the synergistic effect of root competition and light. These responses, coupled with radiation estimates from the fish-eye photographs in the present study, suggest that growth of individuals to main canopy stature may depend on a combination of factors.

At Bear Pass, seedlings and saplings usually grow in clumps away from the center of canopy openings. It is possible that some patches of these shade tolerant species established in canopy openings that subsequently closed, where they now persist as suppressed trees; this was certainly true for some individuals in several of the smaller gaps studied. Regeneration is most likely with: (1) early snow melt and therefore a longer growing season; (2) presence of suitable substrates for establishment (e.g. logs, especially for Tsuga seedlings, Christy and Mack 1984); (3) favourable soil moisture conditions due, in part, to reduced root competition; and (4) greater available light.

Although these explanations were not all tested in the present study, the available evidence suggests that root competition and light are important. Available soil moisture is related not only to the roots of the surrounding trees but also to the amount of precipitation reaching the soil, which varies with canopy density and composition (Rothacher 1963, Voigt 1960), and the substrate (log versus soil). The dense crowns of *Tsuga heterophylla* probably intercept more rainfall than those of *Pseudotsuga*.

Direct beam radiation in canopy openings is associated with more and faster growing seedlings and saplings (Fig. 30). Similar relationships have been documented previously (Chapter III, Veblen, Ashton and Schlegel 1979). Occasional sunflecks may be important for photosynthesis and, thus, direct light is apparently more important for the development of understory plants, including tree seedlings, than the amount of total light (Hodges 1967, Emmingham and Waring 1973).

Understory vegetation often affects tree regeneration. For example, dense thickets of understory bamboo in the mid-elevation forests of the Chilean Andes often prevent the successful establishment of the main canopy beech (*Nothofagus* spp.) (Veblen et al. 1981). In many old-growth Cascade forests, including those in this study, *Rhododendron macrophyllum*, *Acer circinatum* and several *Vaccinium* species are important shrubs, especially where stands have not been severely disturbed by fire for centuries (e.g. plot SC-2). The abundance of elevated surfaces afforded by rotten logs may be critical for successful establishment in these situations, especially for *Tsuga heterophylla*, since seedlings may be raised above the competing understory.

V. CONCLUSIONS

1. A combination of techniques was better than any single method for inferring patterns of forest stand development in transition zone forests of the central western Oregon Cascade Range. Trees in a stand often have different growth rates, resulting in a weak relationship between diameter and age for all 4 species. Age data and the study of spatial dispersion added critical information which could not be gained from study of tree size distributions alone.

2. The population structures and regeneration patterns described are strongly influenced by natural disturbances and species life histories. Periodic fires of variable intensity and extent initiate a mosaic of relatively even-aged patches of different conifer species, the mixture reflecting the result of stochastic factors, life history attributes, and the nature of the disturbance.

3. Which species first dominates a site after disturbance strongly affects subsequent regeneration. If *Pseudotsuga menziesii* or *Abies procera* dominate early, then *Tsuga heterophylla* and often *Abies amabilis* will invade rapidly. If, however, *Tsuga heterophylla* establishes first, regeneration will be minimal until canopy openings are formed.

4. Several key regeneration processes depend on the composition of the main canopy. Firstly, available light, which differs under different canopy species, influences the abundance of tree seedlings and herbaceous species. Secondly, windfalls of old trees, branches, and snags often create canopy openings that are colonized by new seedlings or filled by previously suppressed individuals. The abundance of decaying logs and stumps as substrates for establishment of tree seedlings of some species, especially *Tsuga heterophylla*, is also important.

5. In the absence of holocaustic fire in mid-elevation forests of the western Oregon Cascades, the shade intolerant *Pseudotsuga* and *Abies procera* are replaced by the shade tolerant *Tsuga* and *Abies amabilis*. Small disturbances, such as single or several tree windfalls, are especially important for the formation of canopy openings where both the latter species may regenerate. Greater numbers of seedlings and saplings were found in openings that receive higher levels of direct beam radiation during the growing season, than in small openings or areas of closed canopy.

6. These interactions demonstrate the need for any successional scheme to include the effects of different canopy species, in addition to various disturbances, as factors controlling the rate and nature of forest succession. The vegetation, in such a disturbed situation, could be viewed as a non-equilibrium system in which patches of different size and structure are the result of the interactions of species availabilities, adaptations, chance, and a complex disturbance regime.

BIBLIOGRAPHY

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce - western hemlock forests of southeast Alaska. Ecology 63:1932-1948.

Anderson, M.C. 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. Journal of Ecology 52:27-41.

Ashton, D.H. 1976. The development of even-aged stands of Eucalyptus regnans F. Muell. in central Victoria. Australian Journal of Botany 24:397-414.

Atzet, T., and R.H. Waring. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Canadian Journal of Botany 48:2163-2167.

Braun, E.L. 1950. Deciduous forests of eastern North America. Blackiston, Philadelphia.

Brewer, R., and P.G. Merritt. 1978. Windthrow and tree replacement in a climax beech-maple forest. Oikos 30:149-152.

Buchholz, K., and J.L. Pickering. 1978. DBH - distribution analysis: an alternative to stand age analysis. Bulletin of the Torrey Botanical Club 105:282-288.

Burke, C.J. 1979. Historic fires in the central western Cascades, Oregon. M.S. thesis, Oregon State University, Corvallis, Oregon.

Childs, T.W. 1970. Laminated root rot of Douglas-fir in western Oregon and Washington. United States Department Of Agriculture Forest Service Research Paper, PNW-102. Washington D.C.

Christensen, N.L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. American Midland Naturalist 97:176-188.

Christy, E.J. 1982. Population dynamics of understory Tsuga heterophylla, western hemlock, in the Cascade Mountains, Oregon. Ph.D. thesis, Washington State University, Pullman, Washington.

Christy, E.J., and R.N. Mack. 1984. Variation in demography of juvenile Tsuga heterophylla across the substrate mosaic. Journal of Ecology 72:75-91.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution, Washington. Publication no. 242.

Connell, J.H., and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111:1119-1144.

Daubenmire, R. 1968. Plant Communities: A Textbook of Synecology. Harper & Row, New York.

Daubenmire, R., and J.B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station, Washington State University, Pullman, Washington.

Deevey, E.S. 1947. Life tables for natural populations of animals. Quarterly Review of Biology 22:283-314.

Drury, W.H., and I.C.T. Nisbet. 1971. Inter-relations between developmental models in geomorphology, plant ecology, and animal ecology. General Systems 16:57-68.

Drury, W.H., and I.C.T. Nisbet. 1973. Succession. Journal of the Arnold Aboretum 54:331-368.

Dyrness, C.T., Franklin, J.F., and W.H. Moir. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. Bulletin no. 4, Coniferous Forest Biome, Ecosystem Analysis Studies, U.S./International Biological Program.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4:412-417.

Emmingham, W.H., and R.H. Waring. 1973. Conifer growth under different light environments in the Siskiyou Mountains of southwestern Oregon. Northwest Science 47:88-99.

Fonda, R.W., and L.C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecological Monographs 39:271-301.

Forcier, L.K. 1975. Reproductive strategies and co-occurrence of climax tree species. Science 189:808-810.

Fowells, H.A. 1965. Silvics of Forest Trees of the United States. United States Department of Agriculture Handbook no. 271. Washington, D.C.

Fox, J.F. 1977. Alternation and coexistence of tree species. American Naturalist 111:69-89.

Franklin, J.F. 1964a. Some notes on the distribution and ecology of noble fir. Northwest Science 38:1-13.

Franklin, J.F. 1964b. Ecology and silviculture of the true fir-hemlock forests of the Pacific Northwest. Proceedings of the Society of American Foresters 1964 pp. 28-32.

Franklin, J.F. 1966. Vegetation and soils in the subalpine forests of the southern Washington Cascade Range. Ph.D, thesis, Washington State University, Pullman, Washington.

Franklin, J.F., and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. United States Department of Agriculture Forest Service General Technical Report PNW-8. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Franklin, J.F., and M.A. Hemstrom. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. Pages 212-229 in West, D.C., Shugart, H.H., and D.B. Botkin, editors. Forest Succession. Springer-Verlag, New York.

Franklin, J.F., Cromack Jr, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and G. Juday. 1981. Ecological characteristics of old-growth Douglas fir forests. United States Department of Agriculture Forest Service General Technical Report PNW-118. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Franklin, J.F., and R.H. Waring. 1980. Distinctive features of the northwestern coniferous forest: Development, structure, and function. Pages 59-86 in R.H. Waring, editor. Forests: Fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon.

Garwood, N.C., Janos, D.P., and N. Brokaw. 1979. Earthquake-caused landslides: a major disturbance to tropical forests. Science 205:997-999.

Gashwiler, J.S. 1970. Further study of conifer seed survival in a western Oregon clearcut. Ecology 51:849-854.

Gray, B. 1975. Size-composition and regeneration of Araucaria stands in New Guinea. Journal of Ecology 63: 273-289.

Greig-Smith, P. 1964. Quantitative Plant Ecology. Second edition. Butterworths, London, England.

Greig-Smith, P. 1983. Quantitative Plant Ecology. Third edition. University of California Press, Berkeley, California.

Harcombe, P.A., and P.L. Marks. (1978). Tree diameter distributions and replacement processes in southeast Texas forests. Forest Science 24: 153-166.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York.

Harper, J.L. 1982. After description. Pages 11-25 in E.I. Newman, editor. The Plant Community as a Working Mechanism. Blackwell Scientific Publications, Oxford, England.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area. Quaternary Research 3:329-382.

Hemstrom, M.A., and J.F. Franklin. 1982. Fire and other disturbances of the forests of Mount Rainier National Park. Quaternary Research 18:32-51.

Hemstrom, M.A., Emmingham, W.H., Halverson, N.M., Logan, S.E., and C. Topik. 1982. Plant association and management guide for the Pacific silver fir zone, Mt Hood and Willamette National Forests. United States Department of Agriculture Forest Service R6-Ecol 100. Pacific Northwest Region.

Hett, J.M. 1971. A dynamic analysis of age in sugar maple seedlings. Ecology 52:1071-1074.

Hett, J.M., and O.L. Loucks. 1968. Application of life-table analyses to tree seedlings in Quetico Provincial Park, Ontario. Forestry Chronicle 44:29-32.

Hett, J.M., and O.L. Loucks. 1976. Age structure models of balsam fir and eastern hemlock. Journal of Ecology 64:1029-1044.

Hibbs, D.E. 1979. The age structure of a striped maple population. Canadian Journal of Forest Research 9:504-508.

Hitchcock, C.L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hodges, J.D. 1967. Patterns of photosynthesis under natural environmental conditions. Ecology 48:234-242.

Isaac, L.A. 1930. Seed flight in the Douglas-fir region. Journal of Forestry 28:492-499.

Isaac, L.A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forestry Foundation, Washington, D.C.

Jones, E.W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. New Phytologist 44:130-148.

Kershaw, K.A. 1973. Quantitative and dynamic Plant Ecology. Second edition. American Elsevier, New York, New York, USA.

Kilgore, B.M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. Pages 58-89 in Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., and W.A. Reiners, Technical Coordinators. Fire regimes and ecosystem properties. United States Department of Agriculture Forest Service General Technical Report WO-26. Washington D.C.

Knowles, P., and M.C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. Ecology 64:1-9.

Korstian, C.F., and T.S. Coile. 1938. Plant competition in forest stands. Duke University School Forestry Bulletin 3. 125 pp.

Kotar, J. 1972. Ecology of Abies amabilis in relation to its altitudinal distribution and in contrast to its common associate Tsuga heterophylla. Ph.D. thesis, University of Washington, Seattle, Washington.

Lahey, J.F. 1973. Climates. Pages 43-54 in Highsmith Jr, R.M., and R. Bard, editors. Atlas of the Pacific Northwest. Fifth edition. Oregon State University Press, Corvallis, Oregon.

Law, R. 1981. The dynamics of a colonizing population of Poa annua. Ecology 62:1267-1277.

Leak, W.B. 1964. An expression of diameter distribution for unbalanced, uneven-aged stands and forests. Forest Science 10:39-50.

Leak, W.B. 1975. Age distribution in virgin red spruce and northern hardwoods. Ecology 56:1451-1454.

Long, J.N. 1976. Forest vegetation dynamics within the Abies amabilis zone of a western Cascades watershed. Ph.D. thesis, University of Washington, Seattle, Washington.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169-1184.

Ludlum, D.M. 1971. Weather record book: United States and Canada. Weatherwise, Inc., Princeton, N.J.

Lynott, R.E., and O.P. Cramer. 1966. Detailed analysis of the 1962 Columbus Day windstorm in Oregon and Washington. Monthly Weather Review 94:313-339.

McKelvey, P.J. 1953. Forest colonisation after recent volcanicity at west Taupo. New Zealand Journal of Forestry 6:435-448.

Marks, P.L. 1974. The role of pin cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44:73-88.

Martin, R.E. 1982. Fire history and its role in succession. Pages 92-99 in J.E. Means, editor. Forest succession and stand development research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Means, J.E. 1982a. (editor) Forest succession and stand development research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Means, J.E. 1982b. Development history of dry coniferous forests in the central western Cascade Range of Oregon. Pages 142-158 in J.E. Means, editor. Forest succession and stand development research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Meyer, H.A. 1952. Structure, growth, and drain in balanced uneven-aged forests. Journal of Forestry 50:85-92.

Minore, D. 1979. Comparative autecological characteristics of Northwestern tree species - a literature review. United States Department of Agriculture Forest Service General Technical Report PNW-87. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Morisita, M. 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. Memoirs of the Faculty of Science , Kyushu University, Fukuoka, Japan. Series E Biology 2:215-235.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of Vegetation Ecology. Wiley, New York.

Muller, R.N. 1982. Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. Ecology 63:1901-1917.

Munger, T.T. 1930. Ecological aspects of the transition from old forests to new. Science 72:327-332.

Munger, T.T. 1940. The cycle from Douglas-fir to hemlock. Ecology 59:799-809.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3:153-168.

Peck, D.L., Griggs, A.B., Schlicker, H.G., Wells, F.B., and H.M. Dole. 1964. Geology of the central and northern parts of the western Cascade Range in Oregon. United States Geological Survey. Professional Paper 449.

Peet, R.K. 1976. Successional patterns and tree population structure in Rocky Mountain forests. Bulletin of the Ecological Society of America 57:60.

Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. American Naturalist 110:107-119.

Pickett, S.T.A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107:238-248.

Pickett, S.T.A., and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13:27-37.

Pielou, E.C. 1977. Mathematical Ecology. Wiley, New York, New York, USA.

Quaye, E.C. 1982. The structure and dynamics of old-growth Sitka spruce (Picea sitchensis) forest of the Oregon Coast Range. Ph.D. thesis, Oregon State University, Corvallis, Oregon.

Ross, M.S., Sharik, T.L., and D.W. Smith. 1982. Age-structure relationships of tree species in an Appalachian oak forest in southwest Virginia. Bulletin of the Torrey Botanical Club 108:287-298.

Rothacher, J. 1963. Net precipitation under a Douglas-fir forest. Forest Science 9:423-429.

Runkle, J.R. 1979. Gap phase dynamics in climax mesic forests. Ph.D. thesis, Cornell University, Ithaca, New York.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041-1051.

Silvertown, J.W. 1982. Introduction to Plant Population Ecology. Longman, London.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, 2nd edition. W.H. Freeman and Company, San Francisco.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in Oregon and Washington. Canadian Journal of Forest Research 12:18-28.

Spurr, S.H., and B.V. Barnes. 1980. Forest Ecology, 2nd edition. Wiley and Sons, New York.

Stewart, G.H., and T.T. Veblen. (1982). Regeneration patterns in southern rata (Metrosideros umbellata) - kamahi (Weinmannia racemosa) forest in central Westland, New Zealand. New Zealand Journal of Botany 20:55-72.

Thornburgh, D.A. 1969. Dynamics of the true fir-hemlock forests of western Washington. Ph.D. thesis, University of Washington, Seattle, Washington.

Toumey, T.W., and T. Kienholz. 1931. Trenched plots under forest canopies. Yale University School Forestry Bulletin 30:1-31.

Veblen, T.T. 1979. Structure and dynamics of Nothofagus forests near timberline in south-central Chile. Ecology 60:937-945.

Veblen, T.T., and D.H. Ashton. 1978. Catastrophic influences on the vegetation of the Valdivian Andes. Vegetatio 36:149-167.

Veblen, T.T., Ashton, D.H., and F.M. Schlegel. 1979. Tree regeneration strategies in a lowland Nothofagus-dominated forest in south-central Chile. Journal of Biogeography 6:329-340.

Veblen, T.T., Veblen, A.T., and F.M. Schlegel. 1979. Understorey patterns in mixed evergreen-deciduous Nothofagus forests in Chile. Journal of Ecology 67:809-823.

Veblen, T.T., and G.H. Stewart. 1982. On the conifer regeneration gap in New Zealand: the dynamics of Libocedrus bidwillii stands on South Island. Journal of Ecology 70:413-436.

Veblen, T.T., Donoso, Z.C., Schlegel, F.M., and B. Escobar, R. 1981. Forest dynamics in south-central Chile. Journal of Biogeography 8:211-247.

Voigt, G.K. 1960. Distribution of rainfall under forest stands. Forest Science 6:2-10.

Wardle, J.A. 1974. The life history of mountain beech (Nothofagus solandri var. cliffortioides). Proceedings of the New Zealand Ecological Society 21:21-26.

Waring, R.H., and J.F. Franklin. 1979. The evergreen coniferous forests of the Pacific Northwest. Science 204:1380-1386.

Waring, R.H., Holbo, H.R., Bueb, R.P., and R.L. Fredriksen. 1978. Documentation of Meteorological Data from the Coniferous Biome Primary Station in Oregon. United States Department of Agriculture Forest Service, General Technical Report, PNW-73. Washington D.C.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Weaver, H. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific Slope. Journal of Forestry 41:7-14.

Wells, F.G., and D.L. Peck. 1961. Geological map of Oregon west of the 121st meridian. United States Geological Survey Miscellaneous Geological Investigations Map I-32.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229-299.

Whitmore, T.C. 1974. Change with time and the role of cyclones in tropical rainforest on Kolombangara, Solomon Islands. Paper no. 46 Commonwealth Forestry Institute, University of Oxford.

Whitmore, T.C. 1982. On pattern and process in forests. Pages 45-59 in E.I. Newman, editor. The plant community as a working mechanism. Special publication number 1 of the British Ecological Society. Blackwell Scientific Publications, Oxford, England.

Whittaker, R.H. 1974. Climax concepts and recognition. Pages 139-154 in R. Knapp, editor. Vegetation Dynamics. Handbook of Vegetation Science 8. Junk, The Hague, Netherlands.

Whittaker, R.H. 1975. Communities and Ecosystems. Second edition. MacMillan and Collier-MacMillan, New York, New York, USA.

Williamson, G.B. 1975. Pattern and seral composition in an old-growth beech-maple forest. Ecology 56:727-731.

Woods, K.D., and R.H. Whittaker. 1981. Canopy-understory interaction and the internal dynamics of mature hardwood and hemlock-hardwood forests. Pages 305-323 in West, D.C., Shugart, H.H., and D.B. Botkin, editors. Forest Succession. Springer-Verlag, New York.

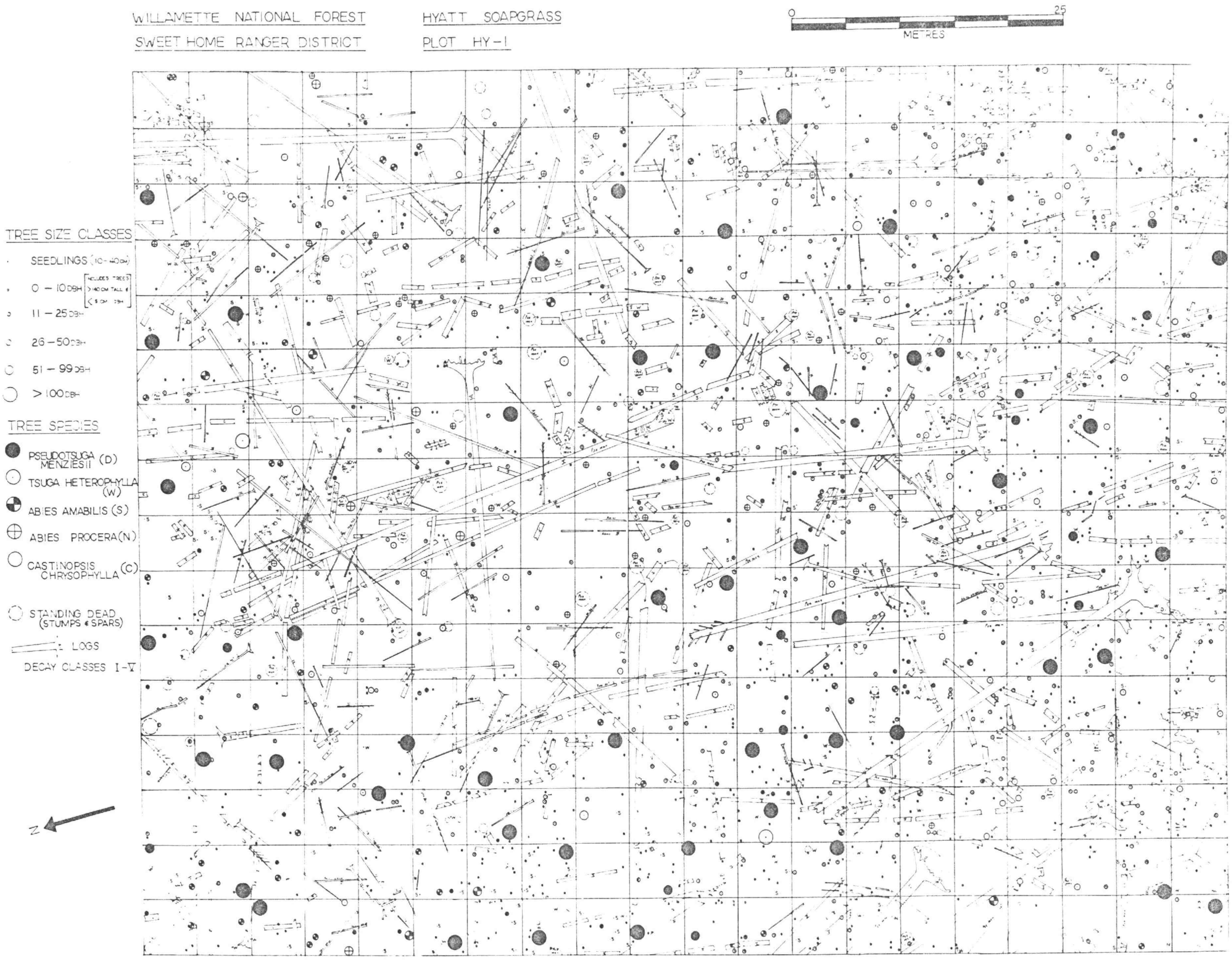
Wright, H.A. 1978. The effect of fire on vegetation in ponderosa pine forests, a state-of-the-art review. Texas Technical University Range and Wildlife review information series 2:21.

Zobel, D.B., and J.A. Antos. 1982. Adventitious rooting of eight conifers into a volcanic tephra deposit. Canadian Journal of Forest Research 12:717-719.

Zobel, D.B., McKee, A., Hawk, G.M., and C.T. Dyrness. 1976. Relationships of environment to composition, structure and diversity of forest communities of the central western Cascades of Oregon. Ecological Monographs 46:135-156.

WILLAMETTE NATIONAL FOREST
SWEET HOME RANGER DISTRICT

HYATT SOAPGRASS
PLOT HY-1



WILLAMETTE NATIONAL FOREST
SWEET HOME RANGER DISTRICT

HYATT SOAPGRASS
PLOT HY-2