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The structure of natural Douglas-fir forests in Western Washington and Western Oregon

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Contents

Abstract

The structure of 5 natural Douglas-fir stands, located on relatively good sites within the *Tsuga heterophylla* zone in western Washington and western Oregon, was analysed in 1984. Stand ages ranged from 50 to 1000 years. Vertical diagrams and crown projection maps were used to identify developmental phases. The results were presented in such a way that the spatial coherence between the forest components was maintained, while describing the characteristics of trees, eco-units and the forest mosaic for each plot in detail. From the results general developmental trends were deduced. The structure of natural Douglas-fir forests appeared to be very heterogeniously and diversified in all developmental phases.

Keywords: Pseudotsuga menziesii, Douglas-fir, vertical diagram, structure, stand development.

1. Introduction

Though the northern temperate forest regions are well known floristically, our knowledge of the structure and dynamics of their primeval forests is rather scanty. In Europe temperate forests have been so devastated and changed by man that very few natural stands are left for baseline studies (*Leibundgut*, 1982; *Mayer* et al. 1987). In the Pacific Northwest area the situation is much better: about 5 percent of the original landscape, occupied by old growth forest ecosystems that have developed over a long period of time and essentially free of human disturbance, is protected in reserves (*Franklin* et al., 1981). Also there is still a considerable area covered by second growth stands that have developed naturally without human interference after the railroad loggings in the 1920's.

Natural forests are particularly valuable in ecosystem research since typical components, processes and interactions in natural stands may be absent from the artificially simplified managed forest stands (*Franklin* et al., 1981). For practical forest management more fundamental knowledge of natural forest ecosystems as baselines against which to measure the health of our managed forests is needed (*Fabijanowski*, 1978; *Vyskot*, 1978; *Mlinsek*, 1978; *Mayer*, 1978; *Mayer* et al. 1987). Knowledge of the structure and dynamics of natural forests is especially important since structure and the change of structures over time are features directly related to silviculture and forest management (*Hillgarter*, 1978; *Leibundgut*, 1982; *Oliver* et al. 1986; *Oldeman*, in prep.).

1.1 Objectives

The main objective of this study was to analyse the structure of a number of natural Douglas-fir stands (*Pseudotsuga menziesii* (Mirb.) Franco) forming a chronosequence of ages ranging from 50-1000 years, on more or less comparable sites.

2. Methods

The general features of each development phase of the forest are studied by analysing the size, structure and distribution of the tree components and of the eco-units which build the forest mosaic. When these qualities are known at different ages a general idea of forest growth and development can be obtained.

In this study a structure-based system hierarchy was used, from which the levels of forest components, eco-unit and forest mosaic were studied (Table 1). The basic idea behind this hierarchy is, that each system studied should fit within the framework of a system at a higher hierarchical level, and can be explained in terms of its subsystems.

Forest components

At the basic level forest components are distinguished. The architecture and functioning of trees and other forest components is explained by their organs. In case of tree components the subsystems are e.g. branch system, root system or reproductive system. Tree components form the building blocks of eco-units, which are considered to be their supersystem.

A set of functionally related components may be brought together in a *compartment*. A compartment is considered to be any set of abiotic or biotic components in a living system, that is delimited as a recognisable functional ensemble. It can be useful to identify compartments to provide a possibility for well-ba-

Table 1: System hierarchy used in the present study, which is primarily based on structures. (simplified after Oldeman (in prep.)

	site
*	forest mosaic
*	eco-units
*	forest components (organisms)
	organs
	tissues
	cells
	sub-cellular levels

lanced abstraction. In silviculture e.g. different social classes among trees can be identified. Every social class is then considered to be a compartment, e.g. a set of specific forest components (trees in this case). Another example of a useful compartment could be coarse woody debris on the forest floor, or a population of myccorhiza.

In this paper different compartments of trees are distinguished according to the developmental stages the trees are going through, after *Hallé* et al. (1978). *Potential trees* are trees in a stage in which the final size and expansion has not yet been reached (trees with growth potential). Tree development during this stage may be interrupted by premature death or suppression. When the tree has reached its final expansion into the canopy or at a lower level, often by reiteration, it is called a *tree of the present*. Finally it becomes a degrading *tree of the past* (*Hallé* et al., 1978).

Eco-units

At the next integration level eco-units are distinguished: an interposition between forest components and forest mosaic as a distinct hierarchical level. A forest eco-unit is the smallest category of an ecosystem, of which the limits and lifespan have been defined by *Oldeman* (in prep.): every surface on which at one moment in time, a vegetation development has begun, of which the architecture, ecophysiological functioning and species composition are ordained by one set of trees until the end. The subsystems of eco-units are forest components; the supersystem that is built up by eco-units is indicated as a forest mosaic. Eco-units are explained in terms of their components (subsystems) according to structural criteria. Eco-unit development depends on the interaction between all of its components; not only its tree components. But it is convenient to start to explain an eco-unit by the trees that form the skeleton of the eco-unit. Once this is known, the eco-unit can also be explained in terms of other eco-unit components, such as mamals, birds, fungi or nematodes.

The state of an eco-unit, e.g. the interior organisation of an eco-unit, is described in terms of eco-unit size (small, medium and large) and by the architecture and size of its tree components. Eco-unit development is treated as a subprocess in succession. Eco-units come into existence (*innovation phase*), grow up and organise themselves (*aggradation phase*), remain organised during an extended period of time (*biostatic phase*) and become finally disorganised (*degradation phase*). Developmental phases have been defined in many different ways in literature. In this paper we will follow the *Bormann and Likens* (1979) concept, in which a steady state shifting mosaic takes the place of biostasis as meant above. This biostasis implies the breaking up of the original stand (large eco-unit) into a mosaic of smaller patches (small eco-units), due to natural mortality of large trees over time. When they die they leave a gap in which a young eco-unit grows up.

The presence of trees in different developmental stages is symptomatic for the development of that eco-unit. In its innovation phase an eco-unit contains new trees in the seedling stage, next to surviving saplings and root and stump suckers. In the aggradation phase all these trees, except for some small species and shrubs, are competing and have further growth potential. The biostatic phase is structured by layers, determined exclusively by trees of the present. In the biostatic phase potential trees survive in a suppressed state or die prematurely as ordained by layer disposition. The degradation phase is characterised by the death and decay of trees of the present. If these trees do not die at the same time, that eco-unit splits up in smaller ones corresponding to the volumes of the trees or tree groups that have successively disappeared. In this way the event that caused the start of the development of an eco-unit is considered too: the zero event in small sized eco-units e.g. is a chablis (*Hallé* et al., 1978) or the death and decay of large standing trees forming canopy gaps in different ways. Two important processes lie at the basis of eco-unit development: fragmentation and fusion. *Fragmentation* is a diagnostic symptom of a degradation phase, which may be either abrupt or very prolonged. When fragmentation of a large sized eco-unit proceeds, the innovation phase of smaller forest eco-units follows. The early aggradation phase then can be extremely heterogenious, whereas the later aggradation phases, through the process of fusion, are characterised by seeming homogeneity. *Fusion* is the formation of larger eco-units by converging development of neighbouring smaller ones.

Forest mosaic

At the highest level the forest mosaic is dealt with, which can be considered as a mosaic of different eco-units as subsystems with a different size or in a different developmental phase or both. Site conditions form the supersystem for this level: macroclimatic regulation e.g. occurs at the forest mosaic level, whereas biotic regulation usually is predominant at the eco-unit level. No single small eco-unit can be thought of without considering its adjacent units and its place in the forest mosaic. If the forest is built up entirely of very small single-tree-eco-units, perhaps a mixed stand model is a more useful and more practical concept than a model of a mosaic built by eco-units. In any case this is so as long as research questions do not concern very small organisms but are centered upon trees. But in many other situations eco-unit models describe the size and limits of the ecosystem and its subsystems that have to explain it, in a very comprehensive way. It should be noted, however, that the identification of the spatial limits of eco-units still is a major problem in ecosystem architecture analysis. Small sized eco-units may show fusion and form a mosaic that can barely be distinguished from a large, even aged eco-unit without extensive measuring, such as increment core analysis. Although in many old-growth stands the trees in the canopy appear to be even-aged, *Franklin and Waring* (1980) reported that the age class distribution of Douglas-fir trees was often relatively wide.

Note that the 'classical' phases of stand development as e.g. described by *Lei-*

bundgut (1982) and *Mayer* (1984), do not make a sharp distinction between forest mosaics and eco-units. The commonly used classification of natural forests in the Pacific Northwest in second growth stands, mature stands and old-growth stands refers to the forest mosaic level rather than to the eco-unit level. It is possible that a stand is built up by one single eco-unit, but this seems to be rather exceptional in natural forests.

In this study forest structure is analysed in detail by graphical methods derived from those used by *Hallé* et al., (1978) in the Tropics, which are especially adapted to heterogenious forests, using vertical diagrams to describe stand structures. They give a clear diagnosis of what the forest really looks like. In Europe such methods have been applied successfully for more than a century now for both managed and unmanaged forest stands (*Knuchel*, 1944; *Leibundgut*, 1959; *Mayer*, 1984). Most remnants of natural forests in Europe have been analysed this way, beautifully illustrating the development patterns observed in these dif-

Table 2: Survey of fundamental research in natural Douglas-fir forest ecosystems over the past 15 years.

Stand structure and composition	*Floristics and classification:* Franklin and Dyrness (1973); Dyrness et al. (1974); Franklin (1979); Hawk (1979); Otto (1984). *Structure and dynamics:* Long (1973); Juday (1976); Zobel et al. (1976); Hawk et al. (1978); Means (1981); Franklin et al.(1981); Franklin and Waring (1980); Franklin and Hemstrom (1981); Hermstrom and Franklin (1981); Stewart (1986).
Production ecology	*Biomass distribution and production budgets:* Fredriksen (1972); Denison et al. (1972); Overton et al. (1973); Grier and Running (1974); Turner (1975); Fredriksen (1976); Grier and Logan (1977); Weber (1977); Waring et al. (1978); Fogel and Hunt (1979); Turner (1981); Gholz (1982); Santantonio and Hermann (1985). *Nutrient cycling:* Dice (1970); Abee and Lavender (1972); Miller et al. (1976); Sollins et al. (1980); Sollins (1982). *Foliage mass and organic matter:* Grier and Waring (1974); Long and Turner (1975); Turner and Long (1975); Gholz et al. (1976); Fogel and Cromack (1977); Gholz (1982); Massman (1982).
Forest components	*Snags and forest floor:* Grier and McColl (1971); Trappe and Maser (1977); Cline et al. (1980); Maser and Trappe (1984). *Mosses and epiphytes:* Pike et al. (1972); Pike et al. (1975); Pike et al. (1977); Carroll et al. (1980); Binkley and Graham (1981) *Invertebrates:* Mispagel and Rose (1978); Voegtlin (1982); Deyrup (1985) *Wildlife and avifauna:* Anderson (1970); Balda (1975); Wiens and Nussbaum (1975); Mannan (1977); Forsman et al. (1977); Black and Taber (1977); Meslow (1978); Maser et al. (1979); McClelland et al. (1979); Forsman (1980); Bowman and Harris (1980); Mannan et al. (1980); Meslow et al. (1981).

ferent forest communities (*Leibundgut*, 1978 and 1982; *Mayer*, 1976 and 1984; *Zukrigl*, 1970; *Hillgarter*, 1971; *Koop*, 1981; *Winckel*, 1980; *Vyskot*, 1978; *Pintaric*, 1978; *Pruca*, 1985). A good example in the U.S.A. is the work of *Oosterhuis* et al. (1982) who used vertical diagrams in a similar way to analyse the structure of deciduous forest stands in southwest Virginia. In the Pacific Northwest extensive work has been done by *Franklin* and his group on the spatial distribution of stems, snags and logs in more than 60 reference stands throughout the area (*Hawk* et al., 1978). In natural Douglas-fir forest ecosystems a great amount of fundamental research has been done (Table 2). A detailed description of the vertical structure of these forest communities has not been made so far.

2.1 Vertical diagram method

Recording the structure of forest stands by making pictures is virtually impossible in the old growth stands in the Pacific Northwest due to the height and massiveness of the dominant trees. Canopy heights often reach nearly 85 meters (*Harris*, 1984; *Waring and Franklin*, 1979). On the other hand making pictures of edges of clearcut areas, especially when combined with some tree height measurements, will quickly give a first impression of the forest structure. This can be done if the clearcut was established no longer than 2 or 3 years ago so that the trees have not yet responded too much to the sudden change in microclimate. Within forest stands a reliable picture of the stand structure can only result from accurate measurements of stump positions, tree heights and crown widths and by recording the measurements on scale drawings.

The study of stand structures with vertical diagrams is in many ways very similar to the work of a histologist studying particular cells and tissues of an organism under a microscope, but on a different scale. Note that the selection of the transect plot locations is not a random process. Being a structural approach and because structures by definition are characterized by non-random deviations from averages, it is essentially non-statistical. It would not make any sense for a histologist to start making sections randomly, nor for that matter in a systematic grid pattern, and the same is true for a forest structure analist. *Rollet* (1974) clearly demonstrated the weak points of statistical methods in forest structure research.

It is very essential to this approach to carefully select the transect plots and restrict their location to those 'forest-tissues' from which one wants to obtain detailed information. If aerial photographs or stem maps are available a preliminary survey can take place from behind the desk, but in most cases a field survey is necessary. If one is completely unfamiliar with the area or with the forest community it may be a good idea to first run a line-transect through the stand and measure only those trees whose crown projection areas intersect with the line. This brings up the second similarity with microscope work, namely the question of section thickness: too thick a section will give a non-transparant image, whereas too thin a section will not yield an optimal amount of informa-

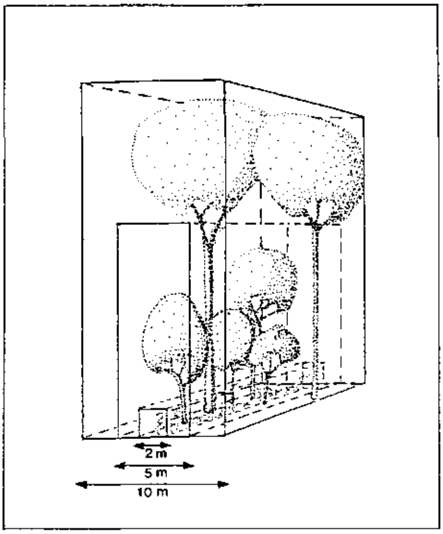


Fig. 1. Nesting of different sized transect plots: to analyse the overstory usually a 10 m wide and 100 m long strip is used. To examine the shrub layer, the strip width should be chosen narrower: usually between 1/3 and 2/3 of the height of its major components. Simultaneously the herb layer can be analysed, e.g. in a 2 m wide transect. Depending on the amount of information one wants to obtain, the transect size can be refined and adjusted accordingly. (after *Koop*, 1981).

tion, and will e.g. leave holes in the diagrams. The section thickness depends on the size of the trees in the specific forest community under study. As a general rule of thumb the transect width should be somewhere between 1/3 and 2/3 of the height of the dominant species (*Oldeman*, 1974). For coniferous forests, however, a better measure seems to be a width of 1 to 2 times the crown diameter of the dominant trees (*Mulder and De Waart*, 1985), because conifers are much more slender in relation to their heights than hardwood species. For most forest types in the Pacific Northwest a transect width of 10 to 15 meter will do; in young stands 5 meter usually is sufficient. If one wants to examine the structure of the shrub layer or of the ground vegetation, one has to reduce the width of the section accordingly, but the same general rules apply. A very elegant way to do this is to 'nest' these different sized transect plots in one another (Fig. 1; *Koop*, 1981).

After the selection of the plot location one starts with running a line through the stand e.g. 50 or 100 m long, marked with flagging tape or poles. The slope is measured at 10 meter intervals. If necessary a slope correction is made: e.g. 10 meter on the horizontal plane (the scale paper) will be somewhat longer along the slope in the forest. Perpendicular to the baseline 10 meter squares are laid out and the plot is conveyed to milimeter or inch paper on scale. All stump positions of the trees inside the plot are mapped and the trees are numbered.

Diameters on breast height are measured. Crown projection areas on the horizontal plane are estimated as folows: beginning from the stem one proceeds towards the periphery of the crown looking upward until one reaches the very end of it. The distance of this point to the stem is measured. When the crowns are regular in shape this is to be done in at least 4 directions (N, E, S, and W). Irregular crowns are measured on more points. Many times a few limbs stretch out far beyond the average crown circumference. These too have to be measured. The crown projection shapes are drawn on the stem map. Dead stumps and logs are included. After this the newly constructed crown projection map is checked in the field. Often one is surprised to see how well the crown shapes fit. *Oldeman* (pers. comm.) made a rapid check of the accuracy of this naked-eye estimate in Finland by performing a parallel series of observations with a Cajanus tube. This is an instrument designed for perpendicular branch tip observation. The accuracy of both methods was comparable, as judged from the resulting crown maps. If the crown shapes do not fit entirely, some adjustments have to be made.

The following measurements of every tree in the plot were made: topheight, height of crown base and height of typical branch systems below the actual canopy, the height where the crown is widest and where irregularities appear in the crown, forks in the stem, etc. A sketch is drawn of the shape of the tree seen in side view. This is always done from the same direction, necessarily drawn perpendicularly to the baseline, in order to avoid showing the wrong face of the tree in the drawing. Tree species and number are recorded along with some observations on the trees general state of health, its social position, fire scars, etc. In fact everything worth mentioning should be included in the field notes.

Behind the drawing table these sketches are worked out on scale and are put in place with the help of the crown projection map, beginning with the trees closest to the front line and proceeding from left to right. This is also the procedure when reading vertical diagrams. The side view and the crown projection map correspond to transversal and radial sections in microscopy. A final check is made in the forest to see if no information has been ommitted and then the document is ready for further analysis. In addition to the drawings a number of graphs and tables are constructed to summarize stand data.

With this vertical diagram method a stand and its major components is recorded at one particular moment in its development. To analyse development patterns, the same stand should be recorded with regular intervals over an extended period of time. Often this is not possible. To overcome this problem, a chronosequence of ages can be established by selecting different stands of various ages at comparable sites with a similar developmental history.

This method, with its shortcomings and merits, was used in the present study. A limitation to this approach was the lack of natural Douglas-fir stands in all age classes: major disturbances, linked with the regeneration of Douglas-fir forests, apparently have occurred at large intervals. The result is that only certain age classes (50-80 years old; 100-200 years old; over 400 years old) are present.

2.2 Accuracy of the measurements

Of all trees in the sample plots, usually 100 × 10 m large, the position of the centre of the stump was measured with an accuracy of plus or minus 20 cm. Crown radius was measured in at least 4 directions with an accuracy of 0.5 m. For very tall trees the accuracy of the crown radius will be in the order of plus or minus 1 m. Tree height, crown base, forks and epicormic branches along the stem were measured with a Suunto tree height measuring device using the percent-scale. This had the advantage of not having to use fixed distances, but instead more flexibility was possible in the measurement position to the tree that was being measured. Slope corrections were made and the actual heights thus calculated, are accurate within a range of plus or minus 1 m (except for the very tall trees over 80 m: their accuracy will be in the order of plus or minus 2.5 m). Crown base is defined as the height of the first whorl with more than two green branches, from which, pointed upwards, the closed crown extends.

Individual tree volumes for Douglas-fir, western hemlock and western red cedar were calculated from volume tables of *USDA-Forest Service* (1955) and *Mc Ardle* (1961), using diameter at breast height (d.b.h.) and tree height as input variables (after converting them to inches and feet respectively). Different tables were used for young and old stands. Calculated mean values of various stand parameters are based on 0.1 ha plots, unless mentioned otherwise. Number of stems/ha refer to all trees with d.b.h. over 5 cm.

Most trees in the plots were bored at breast height for age determination and for analysis of basal area increment. The cores were temporarily stored in flexible plastic drinking straws and were glued on strips of cardboard later on. Small trees were bored right through the centre of the stem; trees thicker than 60 cm were bored as far as possible with a 30 cm increment core, and the radial distance to the tree core, if missing, was estimated. By analysing diameter growth during the early years of tree development on stumps of nearby clearcut areas, the number of annual rings missing was estimated. Note that ages in this report are established from cores at breast height. Strictly speaking trees with widely different ages belong to different eco-units. However, when age differences are three years or less, trees are considered to belong to the same eco-unit: they may well have started their development in the same year, but there may have been a difference of a few years in reaching breast height, or the innovation phase may have covered several years of colonisation by the trees.

2.3 Transect location

Research sites were restricted to the *Tsuga heterophylla* zone in Washington and Oregon (Fig. 2). The plots were sampled on sites where soil moisture conditions ranged from moist to wet. Preferably level sites were selected, or otherwise sites whose slopes were less than 50%. In some cases reference stands established

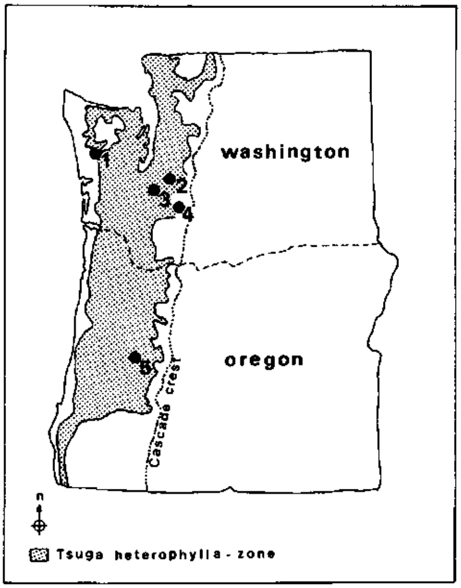


Fig. 2. Research plot locations: 1) Humptulips, Olympic Peninsula (WA); 2) Carbon River, northwestern corner of Mount Rainier National Park (WA); 3) Hugo Peak, C.L. Pack Experimental Forest near Eatonville, La Grande (WA); 4) Ohanapecosh, southeastern part of Mount Rainier National Park (WA); 5) Reference stand 27, H.J. Andrews Experimental Forest (OR).

by *Hawk* et al. (1978) were used. The actual location of the transect plots within each stand was carefully selected after a field survey. In the reference stands case, they were selected after examining the existing stem maps combined with a field survey. Because the focus of this study was on Douglas-fir as a component of natural Douglas-fir forests, the location of the plots in the older stands was such that a maximum number of Douglas-fir trees were situated within the transect strip. For the younger stands a representative plot was selected, not necessarily containing a maximum number of Douglas fir trees, because in these stands there were always enough Douglas-fir trees.

Note that for the old-growth stands the figures in this paper represent the upper limit of what actually can be found in natural Douglas-fir forests. Conversion into one hectare stand parameter values, extrapolated from 0.1 ha plots with a more than average number of Douglas-fir trees, will be somewhat overestimated, and is unrealistic anyway because of the fact that such homogenious hectares do not exist in nature. Basal area and total standing volume e.g. can have extremely high values. However, they are representative of patches within these forests. As such, they are very characteristic of the mosaic pattern of these forests.

3. Results

3.1 Transect descriptions

In this paragraph an analysis is made of the structure of the stands, using
- the vertical diagrams and crown projection maps;
- the distribution of various parameters, including
  - number of trees/ha and volume/ha for the major species;
  - diameter distribution and crown length percentages of Douglas fir, calculated as percentage of the number of Douglas fir trees in each sample;
  - the spatial distribution of basal area over the transect.

The stands are arranged in increasing age order. Note that in the description a distinction is made between strata and layers. The term layer is restricted exclusively to a set of fully grown 'trees of the present'. The vegetation types refer to *Dyrness* et al. (1974) and *Franklin and Dyrness* (1973).

The synecological classification of *Dyrness* et al. (1974) is based on shifts in species dominance rather than on differences in species composition. Only a few species show restricted ecologic amplitudes and these are generally limited to extreme habitats (e.g. *Holodiscus discolor* and *Oxalis oregana* on dry and very wet sites respectively). On modal sites high-fidelity species are rare or lacking. Classification of units on modal sites thus generally is based upon shifts in dominance or relative abundance. *Polystichum munitum* and *Gaultheria shallon* e.g. are present in almost every forest community. But they are characteristic for wet and dry sites respectively when showing great abundance and a high cover. In the *Tsuga heterophylla* zone indifferent species of widespread occurence include *Berberis nervosa, Vaccinium parvifolium, Achlys triphylla, Linnaea borealis* and *Acer circinatum*. Forest communities occupying the extremes of the moisture gradient are the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* association at wet sites (Tshe/Pomu-Oxor), and the *Pseudotsuga menziesii/Holodiscus discolor* association at dry sites (Psme/Hodi). Of the more commonly occurring communities situated on modal sites, the *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa* association is considered to be the climatic climax (*Dyrness* et al., 1974).

HUMPTULIPS:	young mixed stand, 50 years old (Fig. 3)
location:	East Humptulips road, SE 1/4-SW 1/4, section 2, Township 20 N, region 10 W (WA).
altitude:	150 m
exposition:	none
inclination:	none

vegetation type:	*Tsuga heterophylla/Polystichum munitum-Oxalis oregana* association
plot size:	100 × 20 m (0.20 ha)
species:	Douglas-fir, western hemlock (*Tsuga heterophylla*) and red alder (*Alnus rubra*).

Tree components

Douglas-fir is 45-55 year old, 20-45 m tall, has paraboloid crowns, which vary considerably in size (e.g. nrs 25 and 36). The crown base is often asymmetrical and many trees have a few live branches below the actual canopy (e.g. tree nrs 1 and 57). Note that many trees have a fork in the stem at 20 m height: presumably the result of the 1955 freeze (pers. comm. *Oliver*). Western hemlock is 5-40 m tall. Suppressed western hemlock trees have typical short and wide crowns (e.g. nrs.4, 17, 88); codominant western hemlock trees have long and regular crowns (e.g. nrs 55, 97)

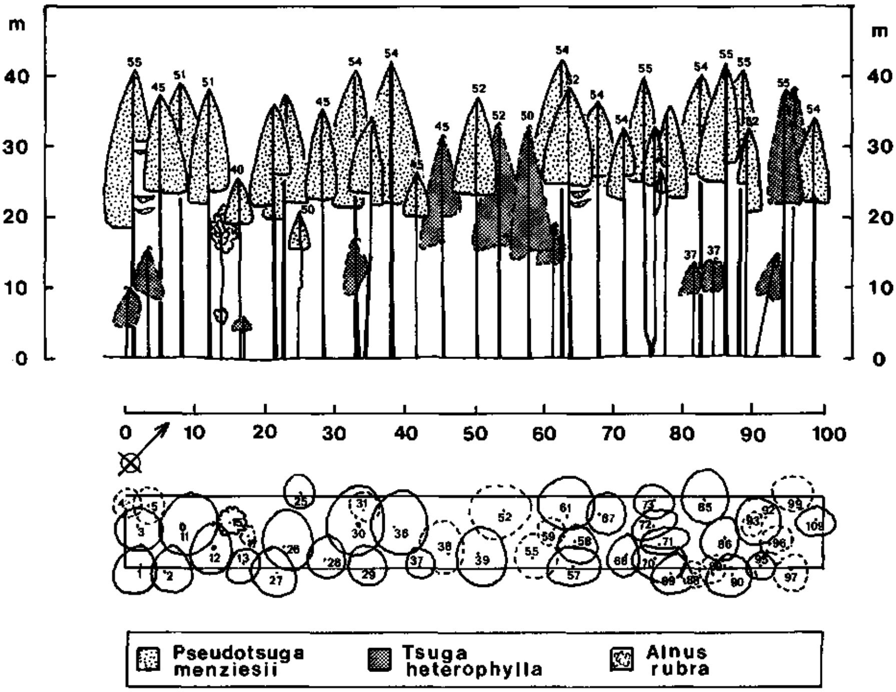


Fig. 3. Vertical diagram and crown projection map of the Humptulips plot. Tree numbers are written on the crown projection map; tree ages are indicated above the treetops.

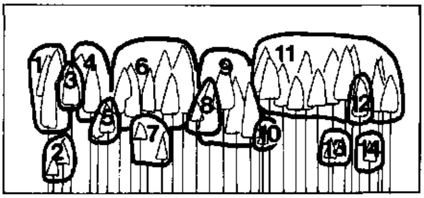


Fig. 4. Eco-units in the Humptulips plot (numbers refer to the different eco-units that are distinguished on the basis of groups of trees of similar age).

Eco-units (Fig. 4)

The first impression is that of an even-aged stand that consists of one large eco-unit. The process of fusion makes it difficult to distinguish between eco-units on the basis of structural criteria alone. On the basis of tree age, however, on the 0.2 ha plot 14 different eco-units can be distinguished. This corresponds with approximately 70 different eco-units/ha. All eco-units are in the aggradation phase of development. Unit size is small (1-4 trees) to intermediate (e.g. eco-units nrs. 6, 9 and 11).

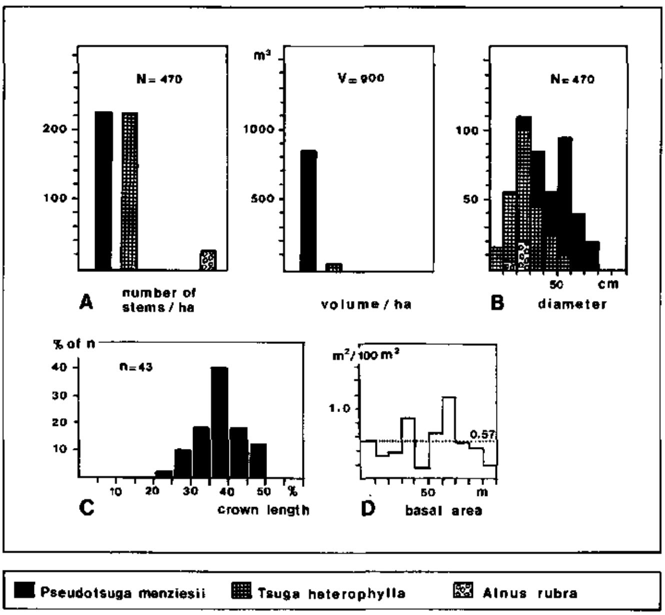


Fig. 5. A) Distribution of the number of stems and volume over the different species. B) Diameter distribution. C) Distribution of relative crown lengths of Douglas-fir; D) Distribution of basal area along the transect.

Stand structure

Stratification: upper stratum, mainly consisting of Douglas-fir and a few western hemlock trees (nrs 97, 99), commences at 25 m and extends to a height of 45 m; the crowns of a lower stratum of western hemlock, together with a few suppressed Douglas-fir and red alder commence at 10 m and extend to a height of 28 m. The trees in this lower stratum are often somewhat younger than those in the upper stratum (e.g. nrs. 13, 37, 88, 89).

Canopy closure: few small gaps, 1 mean crown diameter large.

Understory: because of the closed canopy the understory vegetation is poorly developed: few scattered individuals of *Polystichum munitum*, *Oplopanax horridum* and *Blechnum spicant* and small patches of *Oxalis oregana* and mosses (*Eurhynchium oreganum*, *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, *Dicranum* sp).

Fig. 5: total of 470 stems/ha is equally distributed over Douglas-fir and western hemlock, but Douglas-fir is mainly responsible for total standing volume of 900 m^3/ha. Diameters show an almost normal distribution with Douglas-fir in the higher diameter classes and western hemlock in the lower diameter classes, but there is a considerable overlap between these two species. Crown lengths of Douglas-fir vary between 20-50% of top height and have a normal distribution. The spatial distribution of the basal area is quite uniform with a stand mean value of 57 m^2/ha.

HUGO PEAK:	mature stand, 160 years old (Fig. 6)
elevation:	430-460 m
exposition:	east
inclination:	12%
vegetation type:	seral unit of the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* association
plot size:	two parts, the second part is located 100 m northeast of the first part, to exclude a section disturbed by a recent clearcut.
species:	Douglas-fir, western hemlock and western red cedar (*Thuja plicata*).

Hugo Peak is part of the C.L. Pack Experimental Forest of The University of Washington, located near La Grande (Eatonville), WA. Hugo Peak is a 600 m high hilltop, overlooking the foothills of the western Cascades, located 25 miles west of Mount Rainier. The area is from vulcanic origin and the higher elevations are generally characterized by colluvium and residual soils formed from andersite. Rainfall averages of approximately 1100 mm per year; mean annual temperature is 9.5 degrees C.

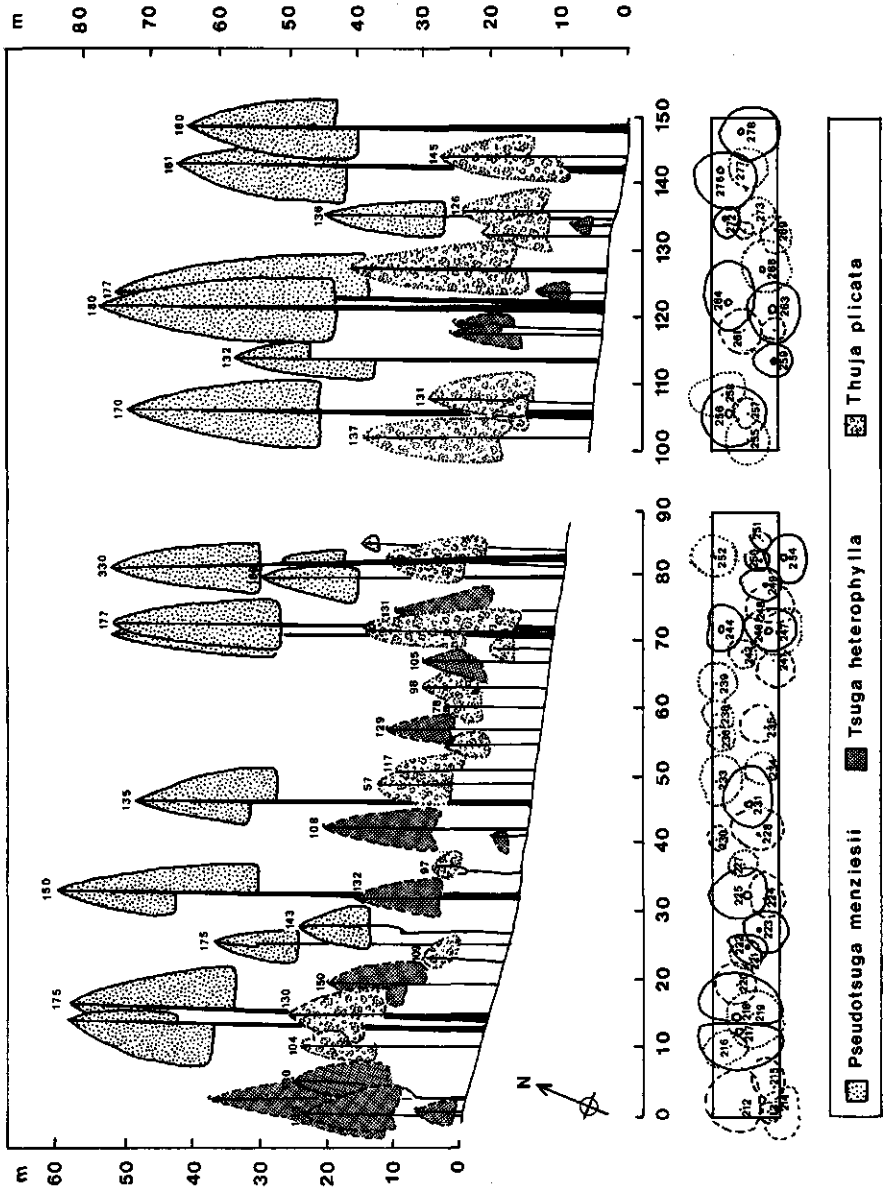


Fig. 6. Vertical diagram and crown projection map of the Hugo Peak plot.

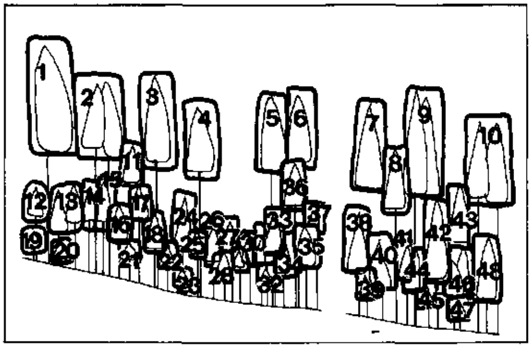


Fig. 7. Eco-units in the Hugo Peak plot.

Tree components

Douglas-fir is 30-75 m tall and 131-180 year old. Tree number 254 is 330 years old: a fire-scarred remnant of the previous generation. Note that the size of this older tree is not much different from the others. Tree crowns in general are long. Western hemlock is 5-25 m tall and has long uniform crowns. Western red cedar is 5-35 m tall and has an average age of 130 years. Most crowns are long, but a number of western red cedar trees have a short and suppresed crown (nrs. 221, 240, 242, 257).

Eco-units (Fig. 7)

Almost every single Douglas-fir tree forms an eco-unit, in a late aggradation phase of development (nrs. 1–11, 36 and 43), surrounded by western hemlock and western red cedar units in an early aggradation phase (nrs. 12–48). These eco-units with shade tolerant species are almost as numerous as there are trees. Hugo Peak thus is a mosaic of very small eco-units; or in other words: an individually mixed, very heterogenious stand.

Stand structure

Stratification: three strata: the upper Douglas-fir stratum has its crown base at 40 m and tree heights of 75 m. Canopy closure in this stratum is relatively low. A middle stratum consisting of a limited number of suppressed Douglas-fir and a few western hemlock (nr. 212 e.g.) and western red cedar (nr. 268) trees with a crown base at 20-30 m and tree heights of 40 m. A well developed lower stratum of western red cedar, western hemlock and two suppressed and damaged Douglas-fir trees (nrs. 223 and 251), with tree heights of 35 m and a mean crown base at 10 m.

Canopy closure: gaps two mean crown diameters large.

Understory vegetation: moderately developed and patchy. *Polystichum muni-*

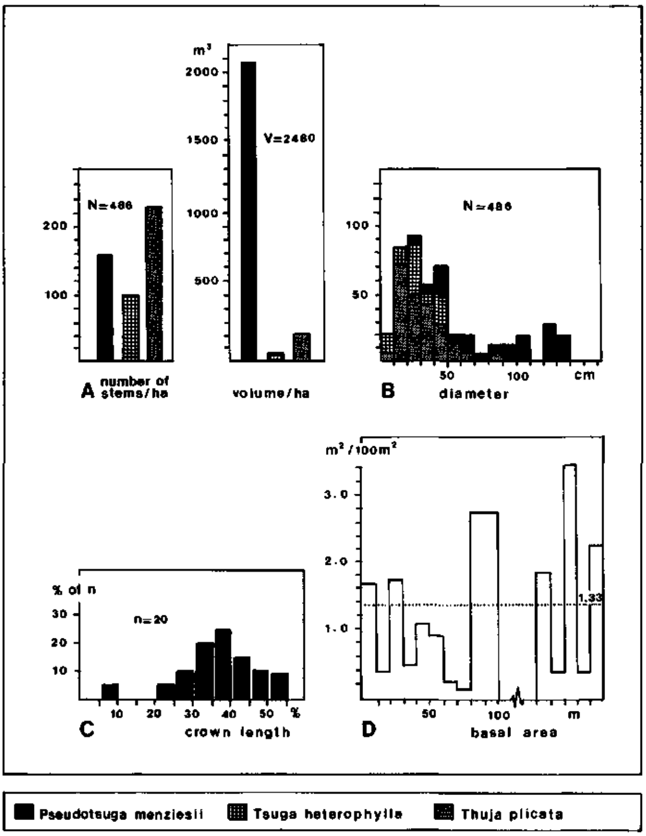


Fig. 8. Distribution of various stand parameters of the Hugo Peak plot: A) number of stems and volume; B) diameter distribution over the different species; C) distribution of relative crown length of Douglas-fir; D) spatial distribution of basal area over the transect.

tum dominates, but present also are *Vaccinium parvifolium, Linnaea borealis, Trillium ovatum* and *Galium trifolium.*

Fig. 8: 47% of the total of 486 stems/ha is western red cedar; 30% is Douglas-fir and 23% is western hemlock. Douglas-fir however is responsible for 88% of the total volume of 2480 m^3/ha. Diameter distribution is wide for Douglas-fir with only few trees in each diameter class, and also quite wide for western red cedar with many trees in the lower classes. Crown length percentages for Douglas-fir show a wide range from 5-55% with relatively many trees in the higher classes. Basal area is distributed very heterogeniously over the transect with a stand mean value of 133 m^2/ha.

OHANAPECOSH: mature stand, 250 years old (Fig. 9)

location:	south-eastern part of Mount Rainier National Park (WA)
altitude:	670 m
exposition:	west
inclination:	12%
vegetation type:	*Tsuga heterophylla/Polystichum munitum* association
plot size:	125 × 10 m (0.125 ha), at the base of a steep slope.
species:	Douglas-fir, western hemlock and pacific silver fir (*Abies amabilis*).

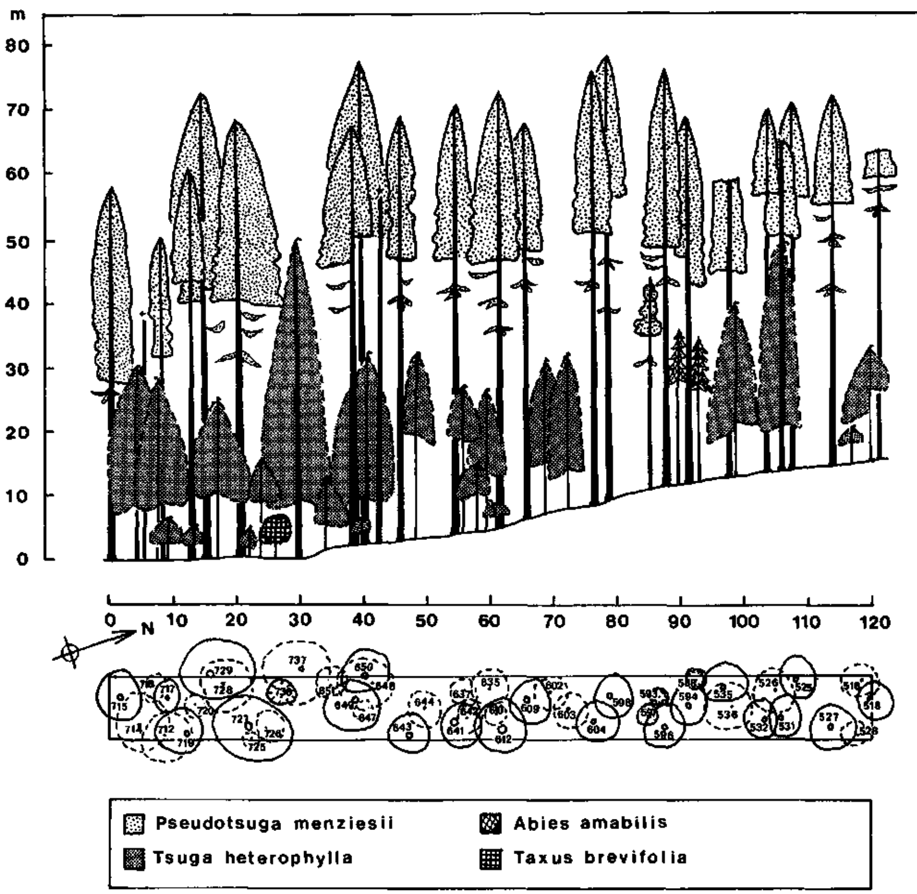


Fig. 9. Vertical diagram and crown projection map of the Ohanapecosh plot.

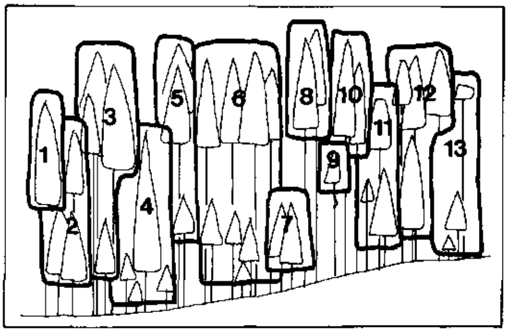


Fig. 10. Eco-units in the Ohanapecosh plot.

Tree components

Douglas-fir is 50-70 m tall, has long narrow crowns and usually has a number of epicormic branches below the actual canopy. Note that the trees on the right side of the transect are smaller than on the left. Western hemlock is 5-50 m tall, with most trees about 25 m tall. Western hemlock trees have long crowns.

Eco-units (Fig. 10)

Aggradation units (nrs. 1, 2, 4, 7) and biostatic units (nrs. 3, 5, 6, 8, 10, 12) are small sized; degrading units usually are single-tree-units (nrs. 9, 11 and 13). It seems quite likely that most Douglas-fir eco-units during earlier aggradation phases of stand development merged into one large eco-unit by the process of fusion. They now seem to have reached a phase in which fragmentation becomes predominant.

Stand structure

Stratification: three strata can be distinguished: the upper stratum of Douglas-fir with their crown base at 40 m and a height of 60-75 m. This stratum is rather open and heterogenious: both dominant trees (nrs.729, 650, 598), codominant trees (the majority) and intermediate trees (nrs.717, 535, 518) are present, of which the latter often have their top broken out. Major gaps in the upper stratum are already filled up by western hemlock (e.g. nr. 737, 526). The middle stratum is formed by western hemlock and a few rare pacific silver firs (*Abies amabilis*), in which the trees have a mean crown base at 10 m and a topheight of 30 m. Note that the density in this stratum is higher on the left side of the transect. The lower stratum consists mainly of suppressed western hemlock trees, with typical short flattened crowns (nrs. 718, 725, 647, 610, 528).

Canopy closure: moderate. Gaps 3 times the mean crown diameter are present. Western hemlock has already started to fill up some of these gaps. Huge

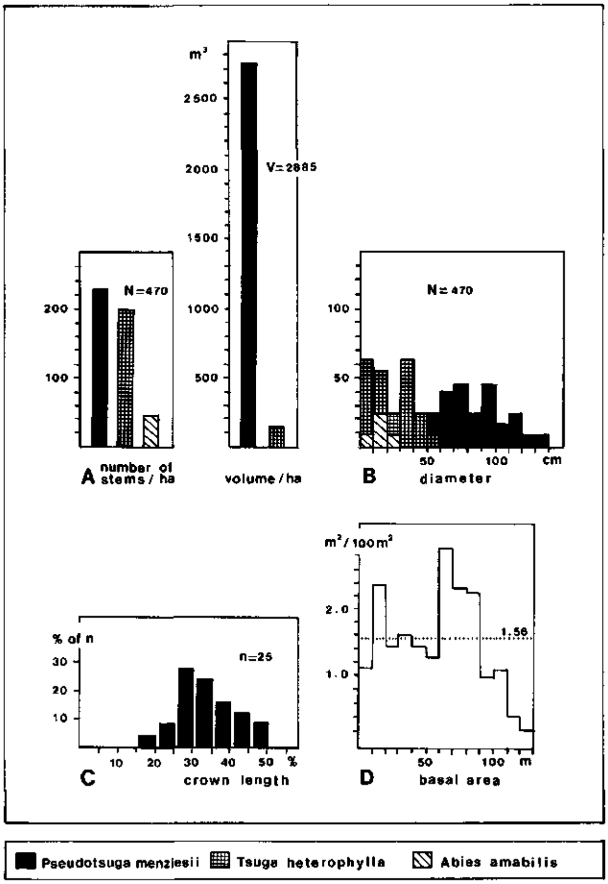


Fig. 11. Distribution of various stand parameters of the Ohanapecosh plot: A) number of stems and volume; B) diameter distribution over the different species; C) distribution of relative crown length of Douglas-fir; D) spatial distribution of basal area over the transect.

dead wood boles (snags) are visible close to tree nrs. 712 and 643.

Understory vegetation is moderately developed, with low shrub cover (*Acer circinatum, Berberis nervosa, Vaccinium parvifolium)* and a well developed herb layer: *Polystichum munitum, Linnaea borealis, Chimaphilla umbellata, Achlys triphylla, Tiarella unifoliata.*

Fig. 11: 50% of the total number of 470 trees/ha is Douglas-fir; 42% is western hemlock and 8% is other conifers. Of a total standing volume of 2885 m^3/ha 95% is Douglas-fir. There is a wide range in diameter distribution. The two major species, Douglas-fir and western hemlock, hardly overlap. Relative crown lengths of Douglas-fir have a normal distribution that is skewed towards the higher values (up to 50%). The basal area is not distributed uniformly over the transect. Stand mean basal area is 156 m^2/ha, which is very high.

REFERENCE STAND 27: old-growth stand, 400 years old (Fig. 12, 13 and 14).

location:	H.J. Andrews Experimental Forest (OR)
titude:	870 m
exposition:	none
inclination:	none
vegetation type:	*Tsuga heterophylla/Abies amabilis/Rhododendron macrophyllum/Linnaea borealis* association
plot size:	100 × 10 m (0.1 ha)
reference plot:	Fig. 15
species:	Douglas-fir, western hemlock, western red cedar and pacific jew (*Taxus brevifolia*).

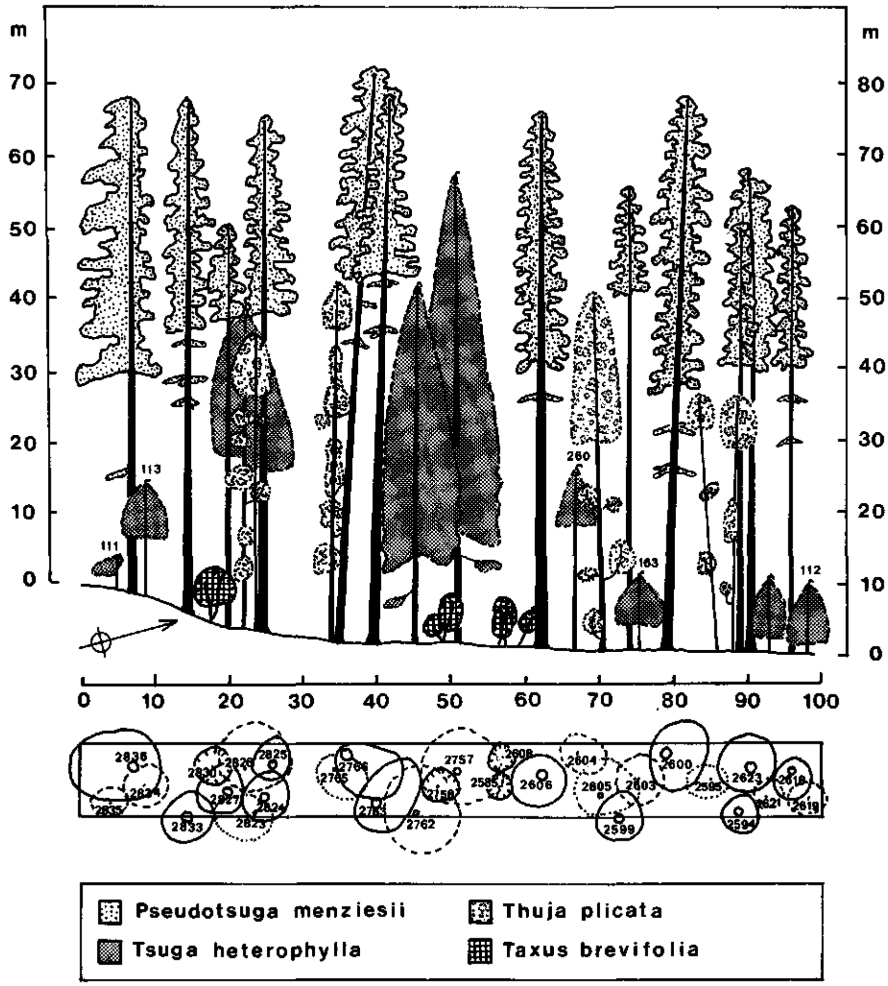


Fig. 12. Vertical diagram and crown projection map of Reference stand 27.

Fig. 13. View in the interior of the 400 year-old Reference stand 27 of the H.J. Andrews Experimental Forest (OR). The stand is open, well stratified and very heterogenious. The large tree with the rough bark in the middle of the picture is a gigant Douglas-fir; the large tree next to it with the finer bark is a western hemlock.

Fig. 14. Forest floor of a 400 year-old Douglas-fir stand. The understory vegetation is patchy with typical species such as Oxalis oregana, Polystichum munitum and Tsuga heterophylla (saplings). A number of logs is visible in various degrees of decomposition, covered with a blanket of moss.

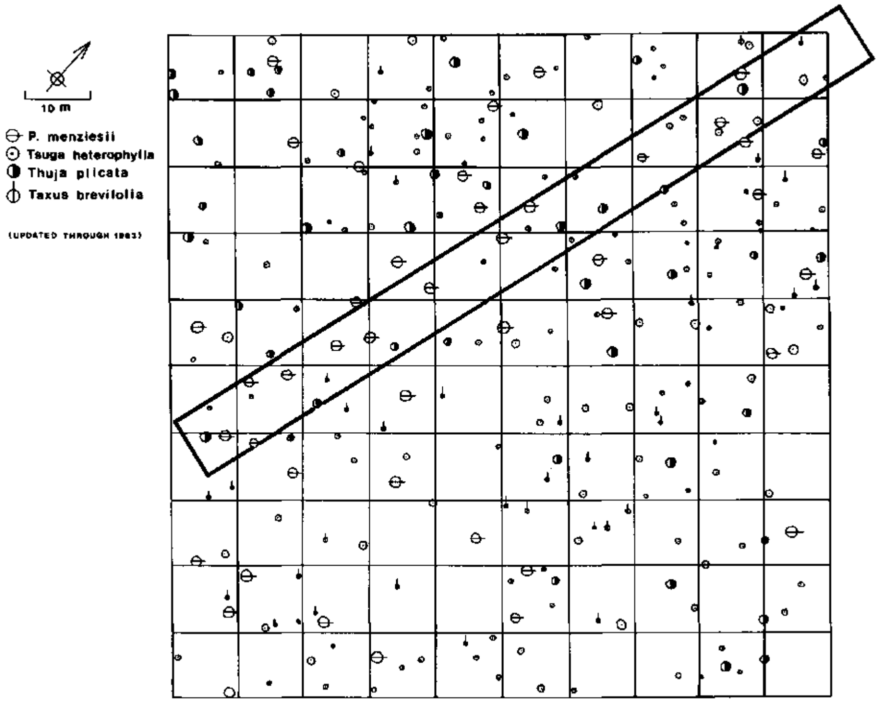


Fig. 15. Stump positions of all trees and the location of the transect plot within the 1 ha Reference stand 27 (Courtesy Forestry Sciences Laboratory, Corvallis).

Tree components

Douglas-fir is 60-80 m tall. The trees have long crowns and usually tree tops are not damaged. Most trees have epicormic branch systems below the actual canopy. Western hemlock is 5-65 m tall and ranges in age from 111 to 260 years in the lower strata (nrs. 2835 and 2604 respectively), whereas western hemlock tree nr. 2757 is likely to be as old as the overstory Douglas-fir. Western red cedar is 35-50 m tall, but their crowns are very much reduced and they do not show great vitality. Characteristic are the many reiterations along the stem of all western red cedar trees.

Eco-units (Fig. 16)

Biostatic eco-units are small sized and single-tree units (nrs. 1, 3, 5, 7, 9). Eco-unit nr. 4 and 10 are in a degradation phase; unit nr. 6 is in a late aggradation phase, passing on to a biostatic phase; and unit nr. 2, 8 and 11 may be classified as biostatic units, that are fragmented and have a complex structure and perhaps should be split into a number of different eco-units.

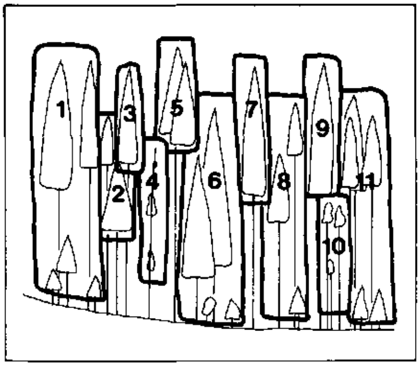


Fig. 16. Eco-units in the Reference stand 27 plot.

Stand structure

Stratification: three layers and two strata can be distinguished: the upper layer of Douglas-fir reaches from 40 to 80 m. One western hemlock tree with an extremely long crown (nr. 2757) belongs to this layer. Closure in this layer is still relatively high in spite of the recent blow-down of two Douglas-fir trees. The middle layer consists of senescent western red cedar trees, about 45 m tall, and is characterised by a low density. The lower layer consists of Taxus brevifolia, 5 m tall. The upper stratum consists of only a few western hemlock trees with their crown base at 15 m and their topheight at 50 m. Hence the closure is low in this stratum. The lower stratum consists of small groups of western hemlock, up to 15 m tall, and is also not very dense.

Understory vegetation: moderately developed shrub layer, with dominant species: *Acer circinatum, Rhododendron macrophyllum, Vaccinium parvifolium* and *Berberis nervosa*. The herb layer is well developed with common species such as *Linnaea borealis, Viola sempervirens, Cornus canadensis, Chimaphilla umbellata, Tiarella unifoliata* and *Rubus* sp.

Fig. 17: the total of 370 stems/ha is almost equally distributed over Douglas-fir, western hemlock, western red cedar and the other conifers. Douglas-fir however is responsible for 75% of the total standing volume of 3670 m^3/ha. Diameter distribution is wide for all three major species, with Douglas-fir occupying the higher classes; western red cedar the middle classes and western hemlock and the other conifers the lower diameter classes. The spatial distribution of basal area is neither uniform, nor extremely heterogenious. The relatively low values at 50-60 m and 70-80 m may have resulted from the recent blow down of two large Douglas-fir trees. Stand mean value of basal area is 193 m^2/ha.

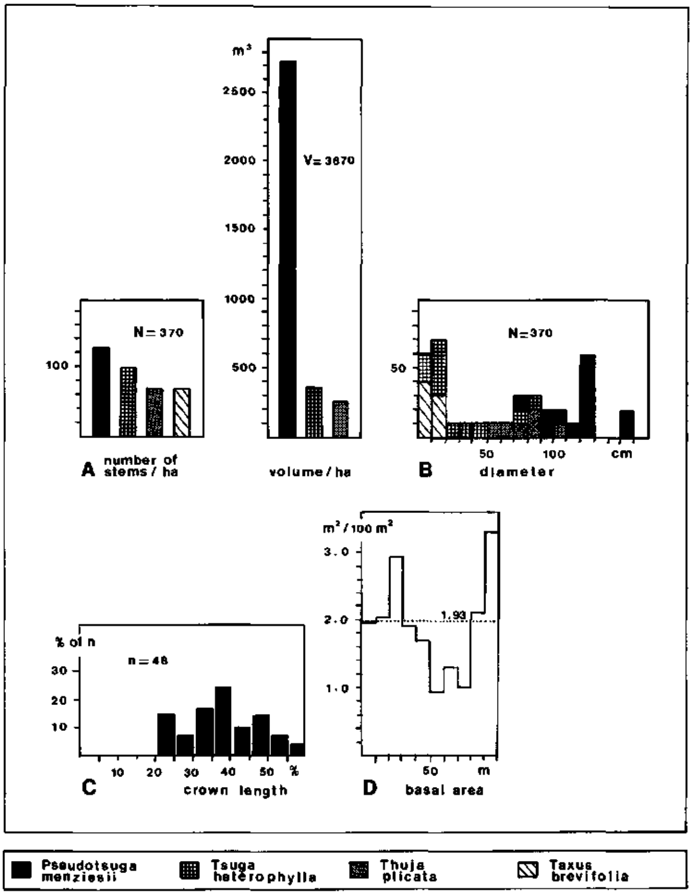


Fig. 17. Distribution of various stand parameters of the Reference stand 27 plot: A) number of stems and total standing volume; B) diameter distribution over the different species; C) distribution of relative crown length of Douglas-fir (pooled data from 4 old-growth stands); D) spatial distribution of basal area over the transect.

CARBON RIVER STAND: super old-growth stand, 1000 years old (Fig. 18).

location:	NW-corner of Mount Rainier National Park (WA)
altitude:	600 m
exposition:	none
inclination:	none
vegetation type:	*Tsuga heterophylla/Oplopanax horridum* association
plot size:	130 × 10 m (0.13 ha)
species:	Douglas-fir, western hemlock, western red cedar.

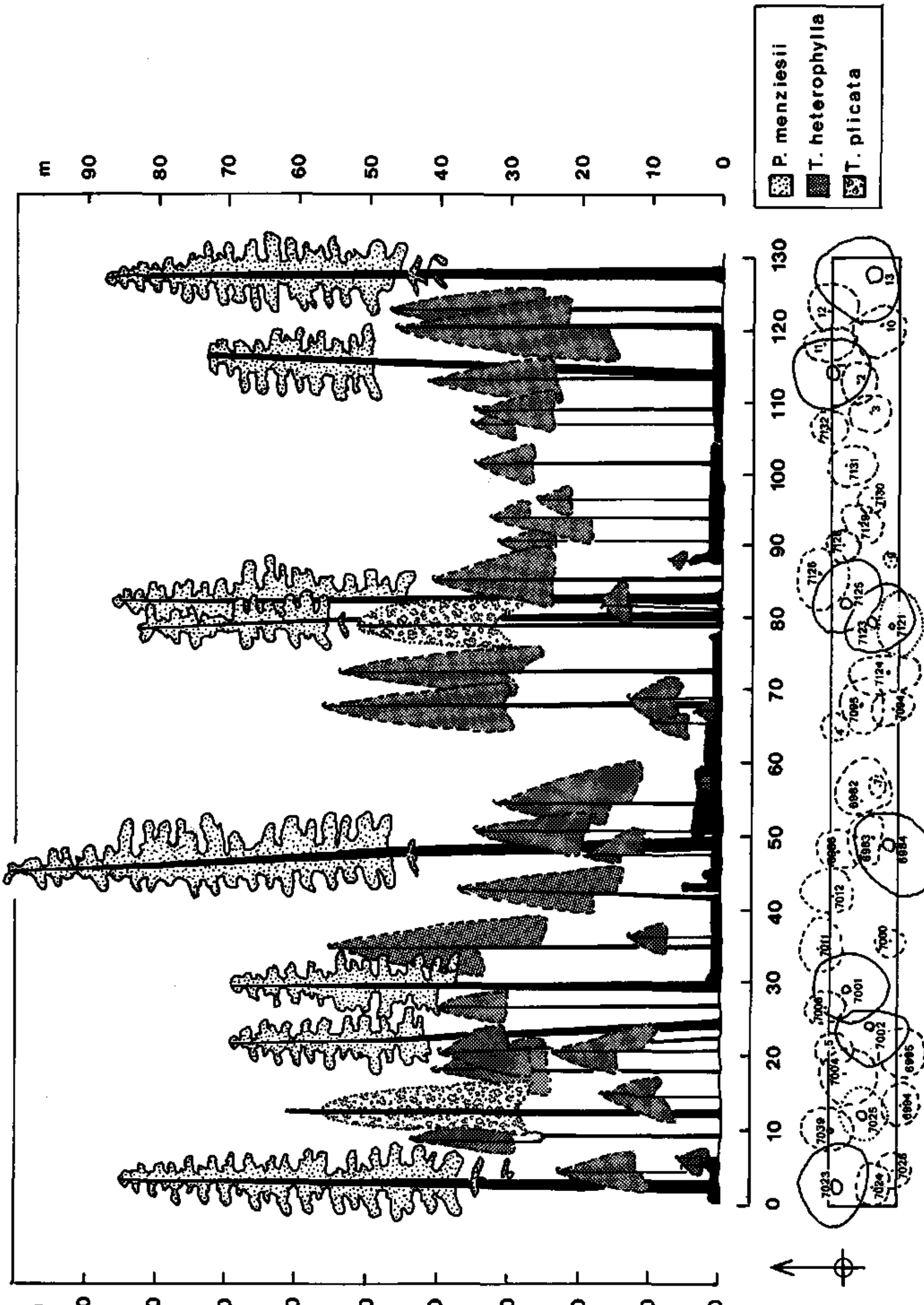


Fig. 18. Vertical diagram and crown projection map of the Carbon river plot.

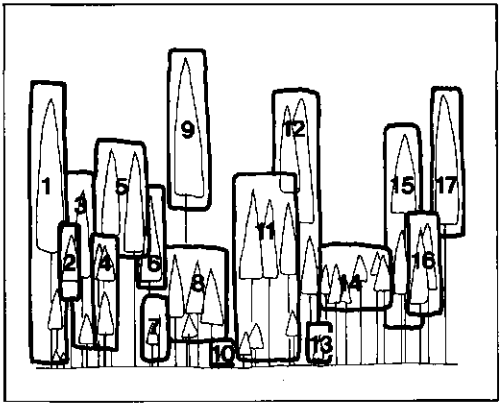


Fig. 19. Eco-units in the Carbon river plot.

Tree components

Douglas-fir is 70-104 m tall. Tree nr. 6984 is perhaps one of the tallest living Douglas-fir trees in the world. In spite of their high age the few Douglas-fir trees that are found in this stand still have relatively long crowns and do not show signs of senescence. Western hemlock is 5-60 m tall. Note that a number of western hemlock trees that are not suppressed, have relatively short crowns, which is rather uncommon for western hemlock (nrs. 7129, 7131, 7132, 2, 3). Western red cedar is maximally 55 m tall. There are only a few western red cedar trees.

Eco-units (Fig. 19).

Six small and single-tree units are the fragments of a large Douglas-fir eco-unit that may have formed the upper canopy centuries ago (nrs. 1, 5, 9, 12, 15 and 17). Eco-units 2, 3 and 4 occupy a gap that was formed by the death of a large Douglas-fir tree. One may as well distinguish two more eco-units in this gap (western hemlock units). Unfortunately no trees were bored in this plot. Eco-units 6, 11 and 16 are in a late aggradation phase; units 8 and 14 in an earlier aggradation phase; and units 7, 10 and 13 represent a very early aggradation phase. The Carbon river plot beautifully illustrates the ongoing fragmentation process of the biostatic units, which results in a highly diversified mosaic structure, and in which western hemlock gradually takes the place of Douglas-fir (Fig. 20).

Stand structure

Stratification: two layers and 3 strata can be distinguished: the upper layer of Douglas-fir, with a low density. Nrs. 7001 and 7002 form a transition to a layer of western hemlock and western red cedar, with a mean crown base at

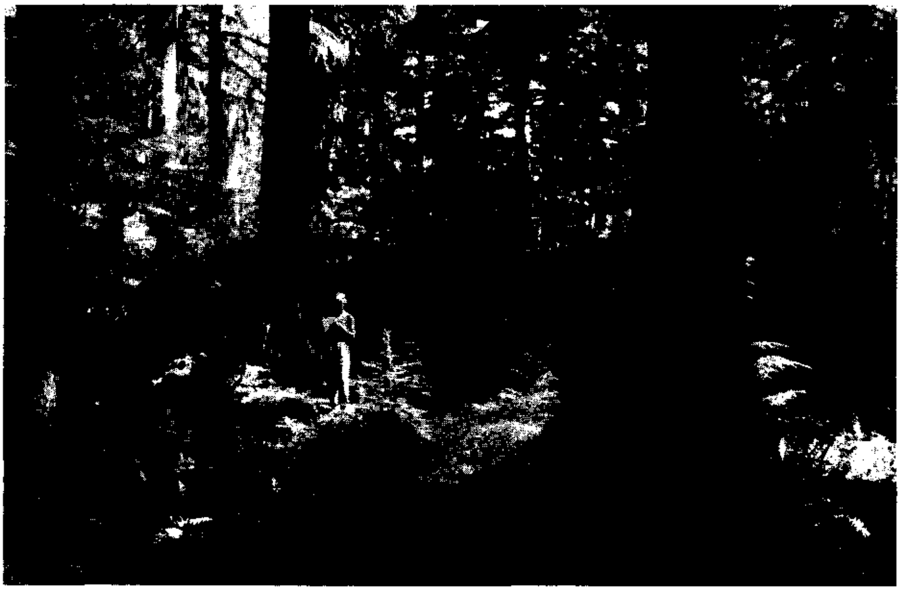


Fig. 20. Thousand year-old Carbon river stand in Mount Rainier National Park (WA). The majority of the trees are western hemlocks, of which several are visible. Note the lush undergrowth of ferns, mosses and wersten hemlock saplings, which cover the many logs in various stages of decay.

30 m and a topheight of 55 m. The upper stratum of western hemlock ranges from 25-45 m; the midle stratum of western hemlock ranges from 10-25 m and the lowest western hemlock stratum ranges from 1-10 m. The distinction between the various strata is somewhat superficial here, because there is a gradual transition between the strata and some overlap. It perhaps is better to speak of western hemlock trees of all sizes from 1-55 m tall, distributed all over the transect. Note that western hemlock regenerates abundantly on nurse logs. This reference stand contains one of the largest accumulations of logs ever recorded: 418 tons/ha, covering 23% of a 1 ha plot area (*Franklin* et al., 1981).

Canopy closure: the upper canopy is open, but a second, lower canopy has been formed, in which gaps twice the mean crown diameter are present. Understory vegetation: well developed, with typical species like western hemlock (seedlings and saplings), *Vaccinium parvifolium, Linnaea borealis, Polystichum munitum, Achlys triphylla, Vancouveria hexandra, Oxalis oregana, Oplopanax horridum, Blechnum spicant* and a dense blanket of mosses, of which *Hylocomium splendens, Rhytidiadelphus triquetrus* and *Eurhynchium oreganum* are most common.

Fig. 21: western hemlock outnumbers Douglas-fir by far: of the total of 314 trees/ha 76% is western hemlock and only 20% is Douglas-fir. Of a total of 4330 m^3/ha 75% is Douglas-fir; 14% is western hemlock and 11% is western red cedar.

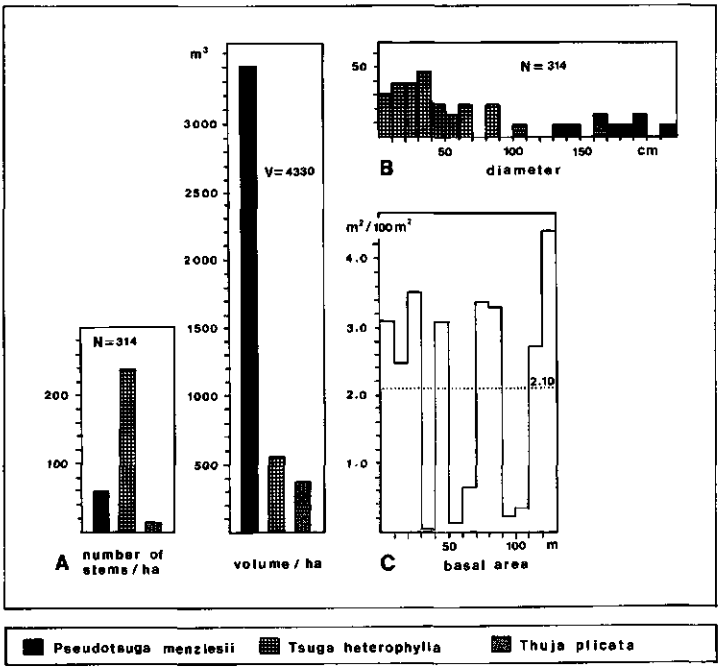
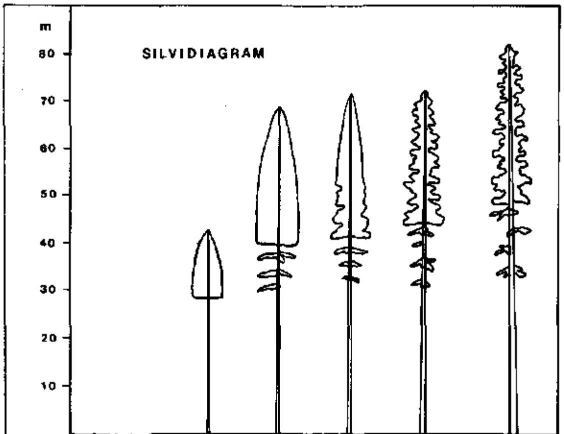


Fig. 21. Distribution of various stand parameters of the Carbon river plot: A) number of stems and total standing volume; B) diameter distribution over the different species; C) spatial distribution of basal area over the transect.

Diameter distribution is extremely wide, with Douglas-fir forming a distinct group at the higher diameter classes; western hemlock confined to the lower diameter classes and western red cedar somewhere in between. The basal area distribution is extremely heterogenious, indicative of patchiness, with a stand mean value of 210 m^2/ha.

3.2 Individual tree development

The characteristics of an 'average' dominant Douglas-fir tree in chronosequencial order are presented in the form of a silvidiagram (Fig. 22). This is a graphical representation of the architecture of an individual tree (usually a stand mean tree) during its life cycle. A list of tree size data and data concerning ecological interactions with other forest components is usually included. To construct such a silvidiagram for each stand the mean tree height, d.b.h., volume, crown base, crown length and crown width was calculated for the 100 tallest trees/ha, and the crown shape of a representative tree was used for illustration. Ecological interactions with other forest components were not included in the silvidiagram of Fig. 22.



tree age	y	50	150	250	400	1000
tree height	m	43	70	71	71	82
diameter	cm	65	120	107	129	176
tree volume	m³	4.6	22.8	18.3	26.5	55.6
crown base	m	28	40	40	43	49
crown width	m	7.7	8.0	8.2	8.2	9.9
crown length	%	43	45	37	43	38

Fig. 22. Silvidiagram of individual tree development on relatively good sites. The characteristics of a stand mean dominant tree are presented here.

The general architecture of the trees is characterised by Massart's model (*Hallé* et al., 1978). Trees in young stands have uniform crowns with a paraboloid shape and relative crown lengths of approximately 40%. The crown of mature trees is uniform in the upper parts, but becomes increasingly more irregular in the lower parts: a few epicormic branches are present below the actual canopy. The large, deep, irregular old-growth Douglas-fir crown is characterized by a total lack of uniformity. Its shape is highly individualistic due to reiteration processes (Fig. 23). According to *Franklin* et al. (1981) they resemble a bottle brush with many missing bristles. In the lower two-thirds of the crown there often are gaps of many meters on one side of the tree. Epicormic branches prevail and it is difficult to describe where the actual crown stops and epicormic branches along the stem begin. Fan-shaped epicormic branch systems are very typical. The upper part of some old-growth trees have a more regular shape, with more numerous branches resembling those of younger trees. Very often the entire tree-top is broken out. In some cases replacement-reiteration of a lateral branch can be observed.

3.3 Eco-unit and forest mosaic development

The Humptulips, Hugo Peak and Carbon river plots belong to the *Tsuga heterophylla/Polystichum munitum-Oxalis oregana* association and occupy good

Fig. 23. Typical crown of a 400 year-old Douglas-fir tree. Its shape is very irregular, open and consists almost entirely of fan-shaped epicormic branch systems.

sites. The Ohanapecosh stand and Reference stand 27 occupy relatively moist, modal sites and thus can also be considered to be characteristic of relatively good sites. Unfortunately, these 5 stands represent an elevation range of 150-870 m. This means that complex temperature factors might complicate a general pattern of forest development. In the ideal situation for research the plots would all belong to the same forest association and would be located within a narrower elevation range. This was not possible because such a range of stands could not be found.

50 years old – second growth stand:	Humptulips
150 years old – mature stand:	Hugo Peak
250 years old – mature stand:	Ohanapecosh
400 years old – old growth stand:	Reference stand 27
1000 years old – super old growth stand:	Carbon River

The following general pattern of stand development in chronosequencial order can be deduced from the descriptions of paragraph 3.1:

In second growth stands the structure of the forest seems to be quite uniform: there is only a single stratum; the forest canopy is very dense and closed and understory vegetation is only sparsely developed. Although there may be a large number of eco-units due to a heterogenious situation during the innovation phase of stand development, the overall picture at the age of 50 is one of uniformity, for which the process of fusion is largely responsible. The individual trees show considerable differentiation in total height, crown length, crown shape and tree volume, and can easily be grouped together in different compartments (social classes; *Leibundgut*, 1958). Uniformity is apparent, but in reality there is a lot of variation and differentiation in natural second growth stands.

Mature stands are characterised by a greater stratification of the canopy: the forest canopy is more open, and an upper stratum can be clearly distinguished from a middle stratum. Small groups of western hemlock form a lower stratum. Differences in size and shape of the overstory Douglas-fir trees become more pronounced (Hugo Peak). The Ohanapecosh stand is typical for the point of transition between mature stands and old-growth stands: the canopy is more heterogenious, and a lower stratum of western hemlock is well developed. Many eco-units are built up of trees which have attained their maximum size and reiteration will be the predominant growth activity from then onwards. The Douglas-fir trees still have paraboloid-shaped crowns, but the distinction between the lower whorls and epicormic branches along the stem becomes less pronounced.

An example of a typical old-growth stand is given by Reference stand 27: an open multi-layered forest canopy, fragmented into many different eco-units, of which the biostatic ones are built up of truly impressive Douglas-fir trees with highly individualistic crown shapes and epicormic branches all along their massive trunks. A second layer is built up of fully grown, long-crowned western hemlocks and western red cedars. Two to three strata of western hemlock trees in various sizes and ages can be found, waiting for an opportunity to penetrate the canopy. And below that, often a sparsely developed third layer of *Taxus brevifolia* is present. In some eco-units a shrub layer is well developed, including species like *Rhododendron macrophyllum, Acer circinatum* and *Cornus nutallii.* Standing dead trees, snags and rotten stubs are common. On the forest floor numerous logs in various states of decay are present, often covered by a dense blanket of mosses. The patchy ground vegetation consists of ferns, huckleberries and western hemlock saplings. The forest structure is a mosaic of different eco-units; is very heterogenious; and offers an unique habitat to a number of rare organisms (*Franklin* et al., 1981).

A super old-growth Douglas-fir stand is examplified by the 1000 year-old Carbon River stand. Fragmentation of the biostatic eco-units has proceeded

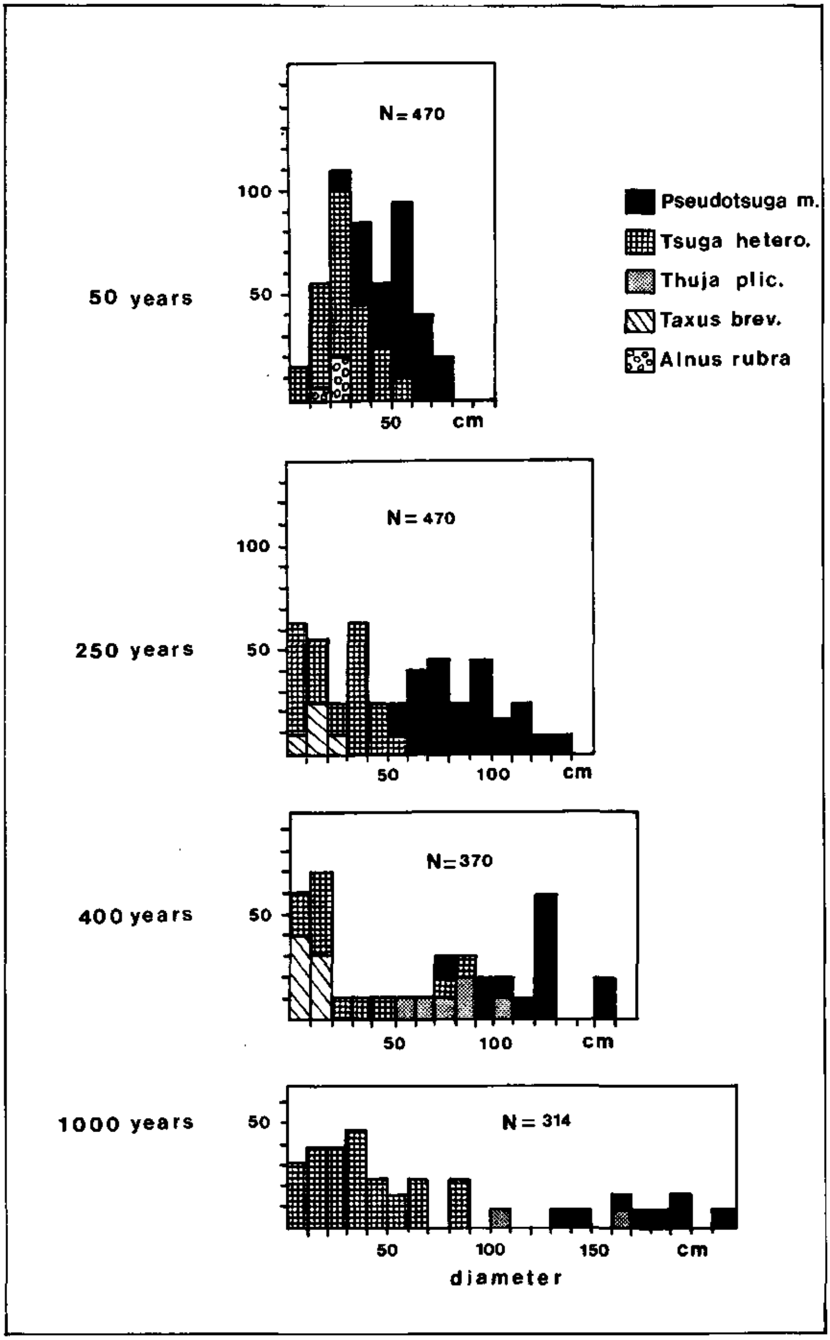


Fig. 24. The diameter distribution becomes increasingly wider with age and its shape changes, due to the differentiation and stratification of the forest canopy and the continuous initiation and development of eco-units with shade tolerant species.

Table 3: Summary of stand data

plots:	Humptulips	Hugo Peak	Ohanapecosh	R.S.27	Carbon River
N/ha	470	490	410	370	310
N (Psme)/ha	225	160	160	130	60
% (Psme)	48	33	47	35	20
B.A. (m^2)	57	133	156	193	210
V (m^3)	900	2500	2900	3700	4300

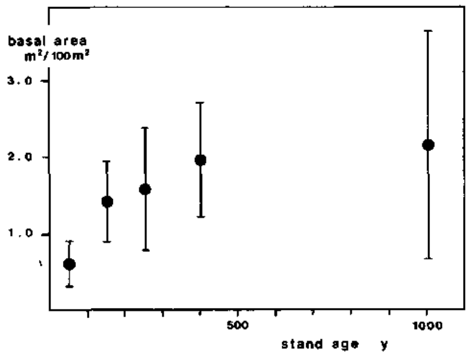


Fig. 25. The basal area increases with age, and its spatial distribution becomes more and more heterogenious, as the process of fragmentation proceeds.

to the extent that only a few large Douglas-fir trees are still present, but they are very tall and very impressive. The forest consists mainly of a mosaic of western hemlock and western red cedar eco-units. Both species form a canopy layer somewhat beneath the scattered Douglas-fir trees. Below this layer there is a continuum of hemlock regeneration in all sizes and ages, so that no distinct strata can be distinguished. The forest structure is very diverse. The amount of dead wood, both standing and down on the forest floor is very large.

This general pattern of eco-unit and forest mosaic development can also be expressed quantitatively.

With increasing age the diameter distribution becomes increasingly wider due to the greater diversification of the canopy and as a result of the continuous innovation and development of eco-units built up of shade tolerant species (Fig. 24). The spatial distribution of basal area becomes increasingly more heterogenious, as patchiness increases (Fig. 25). Stand mean values for basal area and total standing volume keep on increasing. The number of Douglas-fir trees gradually declines both absolutely and relatively, whereas the more shade-tolerant species become more numerous (Table 3). Mean diameter and mean volume of the dominant trees keep on increasing with age (Fig. 26).

In Fig. 27 the general pattern of Douglas-fir forest development in the absence

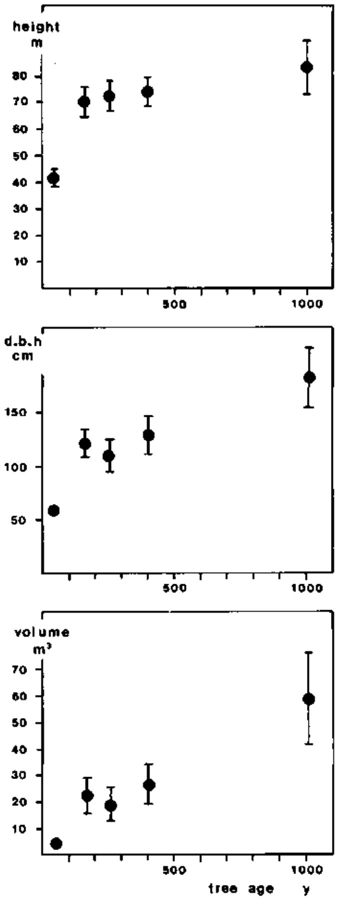


Fig. 26. Mean values for tree height, d.b.h and volume of the 100 tallest trees per ha for stands at different ages. Note the regular increase for both d.b.h and volume and the regularly increasing uncertainty interval, pointing to fragmentation, causing mean values to become less and less relevant for a stand.

of major disturbances, on relatively good and on relatively poor sites within the Tsuga heterophylla zone is summarized schematically. Also forest development on very poor (marginal) sites is hypothesized: it is suggested that on marginal sites second growth stands will hardly reach maturity and degradation will start very soon. Although some observations in Douglas fir stands on exotic sites in Europe point in this direction, this is still scarcely more than speculation in an area of research that needs more attention.

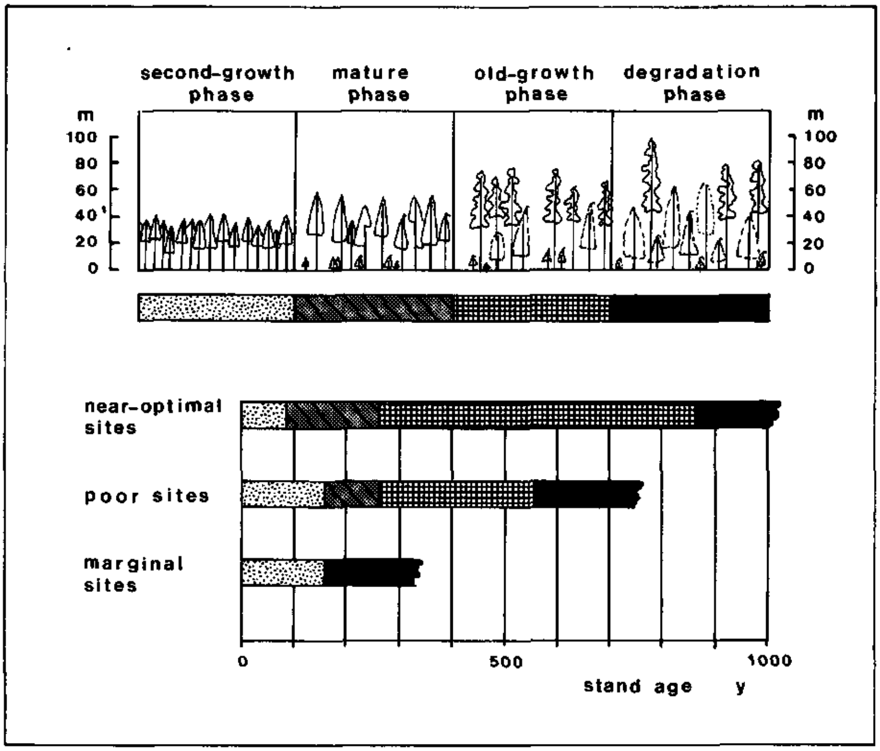


Fig. 27. Summary of the general pattern of forest development within the Tsuga heterophylla zone, in the absence of major disturbances, for relatively good sites and for relatively poor sites. Forest development on marginal sites is hypothesized, after data from the Netherlands. The transition between the different development phases is a gradual one. Note that on good sites the old-growth phase continues for a long time (many centuries), whereas on relatively poor sites this phase will sooner develop into a degradation phase. On marginal sites the old-growth phase may be very short and abrupt or may not be present at all.

4. Discussion and conclusions

A detailed analysis of stand and tree structure with vertical diagrams can be useful to identify development phases in coniferous forests dominated by Douglas-fir in the Pacific Northwest. The use of vertical diagrams has the advantage that the spatial coherence of forest components becomes visible and that the information is presented in such a way that it is both illustrative and transferable. Some aspects become obvious which would have otherwise remained obscure: e.g. the 1955-freeze in the Humptulips plot, the size and shape of gaps in the canopy, or patterns in tree mortality and regeneration. The results of this study indicate that natural Douglas-fir forests are very heterogenious and diversified: great variation can be found between indiviual trees; between eco-units and on the level of the forest mosaic.

Trees vary so much in age, size, shape and growth potential that they can easily be grouped together into different compartments of social classes, each with its own typical distribution pattern of various tree and stand parameters. Distinguishing different social classes can be useful when analysing the structure of second growth stands and of mature stands. In old-growth stands every single tree is so unique and completely different from its neighbours, that it is of no use to distinguish different tree compartments.

Douglas-fir is commonly believed to be a secondary pioneer species, that regenerates and establishes itself after extensive forest fires in the form of large, even-aged stands. However, this study indicates that in natural Douglas-fir forests eco-units in general are very small and heterogeniously distributed, so that it is more realistic to think of Douglas-fir stands in terms of a mosaic of eco-units rather than of one large, even-aged unit. The further stand development proceeds, the more heterogenious the stands and their components will become. With increasing age Douglas-fir stands go successively through a second growth phase, a mature phase and an old-growth phase. The transition between the various phases is a gradual one: the old-growth phase may extend over many centuries before its biostatic eco-units gradually degradate by the process of fragmentation. According to *Franklin* et al. (1981) the stratification and diversity of old-growth canopies are responsible for an important micro-climatic buffer, by which old-growth stands provide a habitat for several unique plant and animal communities. Many species of epiphytic plants (mosses and lichens), invertebrates and insects are housed in old-growth canopies as well as several rare vertebrates like the northern spotted owl, northern flying squirrel and red tree vole (*Franklin* et al., 1981). Thus biostatic and degrading eco-units of Douglas-fir forests not only are very valuable from the viewpoint of nature conservation

(*Harris*, 1984), but also for the functioning of a well-balanced ecosystem (*Maser and Trappe*, 1984).

In comparison with old-growth stands, second growth stands are characterised by relative uniformity. Note that this is only relative: in fact the structure of young stands is often very diverse and heterogenious. This may be partially due to the heterogeneity of the situation after the zero-event, with dead wood irregularly spread over the surface, irregular seed dispersal, micro-relief and competing understory vegetation (cf. *Koop* (1981), for German broadleaved 'Urwald').

This leads to the question whether plantations of Douglas-fir, which are established all over the world in the form of even-aged monocultures, can provide all silvicultural requirements for optimal tree development. The present results indicate that a mixture of small-sized eco-units, which consist of only a limited number of trees, is a much more natural setting to grow Douglas-fir trees. This may be one of the reasons that strip cutting systems and selection cutting systems used in Douglas-fir silviculture in Europe are so successfull. When the individual trees are exposed to a variable set of growth conditions in different eco-units, only certain trees will reach dominance and a relatively large proportion of trees will play a subordinate role in stand development. This leads to a very diversified situation, in which the growth potential of the trees is being utilised in a more nature-conform way, compared with the artificially simplified growth conditions in even-aged plantations. This certainly will affect tree growth, and, most likely, the other forest components as well: some of these organisms might depend on a more natural and diversified silvicultural system. Many of the ecological interactions between the various forest components are poorly understood, but there is growing evidence that a diversified forest structure is a necessity for a number of organisms, which play an important role in the decomposition of organic matter (*Maser and Trappe*, 1984; *Grier and McColl*, 1971; *Trappe and Maser*, 1977; *Fogel and Cromack*, 1977; *Mispagel and Rose*, 1978), in nutrient cycling (*Miller* et al., 1976; *Pike* et al., 1972; *Fogel and Hunt*, 1979; *Maser* et al., 1979) and in seed dispersal (*Balda*, 1975; *Bowman and Harris*, 1980).

Not only old-growth Douglas-fir stands, but also second-growth stands provide excellent 'field-laboratories' for baseline studies. This has relevance for Douglas-fir silviculture and plantation management. Because many second-growth stands are being harvested in western Washington and western Oregon, it should be a matter of concern to policy makers to preserve sufficient areas of unmanaged second-growth stands as natural research areas, including different sites, different genotypes and stands with different developmental histories. European foresters have become very aware of the values unmanaged forests can provide for basic research, perhaps because there are so few examples of virgin forests left in Europe.

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