

Analysis and modelling of interspecies competition
during forest secondary succession

by

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THESIS ABSTRACT

The Coastal forest of southwestern British Columbia is examined at three levels of interpretation: the Biogeoclimatic Subzone level, the plot level, and the single tree level. These levels correspond to the three major strata of the population: the geographic range, the community, and the individual. The data base consists of 40 years of observations on 730 Permanent Sample Plots describing over 70,000 trees.

The highest level of interpretation, the Biogeoclimatic Subzone level, covers several thousand square kilometers of extremely varied topography and climate. The total study area is subdivided into five main low elevation Biogeoclimatic Subzones. The age structure of each subzone is analysed on an average span of 80 years and forest-type succession dynamics is described. The very nature of forest succession from one type to another, with a finite number of possible forest-types over the time horizon, seems admirably suited for a finite-state Markov process. However, the Markov models cannot fit adequately the observations at the subzone level because transition probabilities are not entirely time-homogeneous and because there is a wide range of communities and origins of perturbation within a subzone.

The sample plot offers an intermediate level of interpretation and is considered sufficiently homogeneous to represent larger units of forest. The entire forest can be described by the agglomeration of the fundamental units. The growth of a given species is likely to be different in a pure forest than in a mixed one, and between different

types of mixed forests. Tree species constitute the pool of biotic variables with the highest biomass and are estimated to have a high biotic impact on each other's growth.

Each Biogeoclimatic Subzone is divided into several plot-types which represent fundamental units of forest composition. The growth of any given species shows, indeed, significant variation from one plot-type to another. The trends in succession at the plot type level coincide closely with those observed at the Biogeoclimatic Subzone level. Thus it is hypothesized that succession at the subzone level is a consequence of variation in species growth rate between plot types, due to site conditions and competition.

At the lowest stratum of the population, the growth, mortality, and regeneration of a single tree are investigated. The growth rate of a tree is dependent on its past history, on the climatic and geographic components characterizing a Biogeoclimatic Subzone, and on the other trees growing in its immediate neighborhood. These variables have a very significant effect on whether a tree lives or dies in any time period. The analysis indicates that recently dead stems appear to have a history of sub-standard growth when compared with the population. Moreover, the immediate neighborhood of dead stems corresponds to a specific composition and structure of the vegetation.

On the other hand, new stems show large interspecies differences in their preference for forest composition and structure of their immediate surroundings. The habitat composition and structure leading to the mortality of a stem of one species may constitute a good habitat for the

regeneration of a stem of another species. This is viewed as a mechanism which gives rise to plot type succession, which in turn leads to forest-type succession. The levels of the individual, of the community, and of the geographic range display consistent population dynamics. Succession appears to be explained by simple mechanisms involving competition for light and space; it is not necessary to postulate more complex synergistic or antagonistic mechanisms of species interaction.

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GENERAL INTRODUCTION

Succession appears to be a central concept in both animal and plant ecology. In its broadest sense, succession can be defined as a repeatable sequence of dominant species in an ecosystem. This concept is, however, perceived with a different flavor according to the scale at which the ecosystem is observed. On a very small scale, large areas of vegetation can appear to be rather homogeneous, while on a large scale the heterogeneity of the communities and the variability among individuals become obvious.

The problem is then to evaluate how perspectives about the forces acting during secondary succession change with the level of interpretation. The coastal forest of southwestern British Columbia is large enough to offer observations from a very small to a very large scale. The general hypothesis of this study is that, although the perception of succession might be quite different at the scale of the Biogeoclimatic Subzone, at the scale of the forest stand, and at the scale of the individual tree, each level of interpretation must be consistent with the others. Furthermore, there must be some underlying mechanism responsible for the population dynamics observed at each level.

The Biogeoclimatic Subzone level is studied in Chapter I, the plot level, in Chapter II, and the individual tree level, in Chapter III.

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CHAPTER I

A Markov model
of forest-type succession after disturbance
in Coastal British Columbia.

ABSTRACT

Succession models were built for five Biogeoclimatic Subzones of the coastal forest of British Columbia from a data bank of 730 plots. Each plot was characterized by a forest-type every five years and probabilities of moving from one type to another over the next five years were calculated. The models tested the hypothesis that the future state of the forest, given past and present states, is not fixed, but is determined by a set of transition probabilities based only on the present state of the forest.

P. menziesii stand-types showed a very slow decrease in the Dry Douglas-fir Subzone to the advantage of T. plicata, this decrease being faster in the wet subzone where T. heterophylla stand-types succeeded after 100 years; this succession occurred after 50 years in the Dry Western Hemlock Subzone. In the wet part of this subzone, T. heterophylla stand-types always stayed prominent with minor succession possibly occurring from P. sitchensis stand-types to A. amabilis. In the Fog Subzone, T. plicata stand-types were more abundant soon after disturbance, but T. heterophylla stand-types would progressively take over.

The models did not adequately replicate the observations and failed to produce realistic long-term predictions. Transition probabilities were not entirely time-homogeneous and the models were too general in relation to the diversity of communities, types of disturbance, and patterns of invasion. Using this type of data, it is concluded that forest succession is not a Markov process.

RÉSUMÉ

On a construit des modèles de succession pour cinq sous-zones biogéoclimatiques de la forêt côtière de Colombie Britannique à partir d'une banque de données de 730 placettes. Le type forestier de chaque placette a été déterminé à tous les cinq ans et les probabilités de transition d'un type à un autre durant les prochaines cinq années ont été calculées. Les modèles ont testé l'hypothèse selon laquelle l'état futur de la forêt, connaissant ses états passé et présent, n'est pas figé, mais plutôt déterminé par un ensemble de probabilités de transition basées seulement sur l'état actuel de la forêt.

Le type forestier P. menziesii a diminué très lentement dans la sous-zone sèche du sapin de Douglas au profit de T. plicata et plus rapidement dans la sous-zone humide où le type T. heterophylla lui succède après 100 ans; cette même succession se produit également dans la sous-zone sèche de la prûche de l'ouest après 50 ans. Dans la partie humide de cette sous-zone, le type forestier T. heterophylla est demeuré prééminent tandis qu'une succession mineure pouvait se produire du type P. sitchensis au type A. amabilis. Dans la bande brumeuse de la zone, le type T. plicata était le plus abondant immédiatement après perturbation mais le type T. heterophylla pourrait lui succéder.

Les modèles n'ont pas reproduit fidèlement les observations et n'ont pu produire de prédictions réalistes à long terme. Les probabilités de transition ne furent pas rigoureusement constantes et les modèles furent trop imprécis quant à la variété des communautés, des types de perturbation et d'invasion des espèces. On a conclu que la succession forestière n'est pas Markovienne, selon les observations analysées.

INTRODUCTION

There exists no precise theory to predict the response of disturbed ecological systems. Yet very large ecosystems subjected to natural and man-made disturbances are routinely exploited and a better understanding of their biotic responses is required. The Pacific Coastal Mesothermal Forest (Krajina 1969) of British Columbia (Canada) has been exploited for over a century and recently collated data permit the study of succession after disturbance for a time range covering the forest rotation.

Raup (1967) pointed out that most forests have a constant history of fires, disease, insect pests, and windfalls. Cooper (1913) showed how Abies balsamea (L.) Mill. was preponderant soon after windfall and was then out-competed by Betula papyrifera Marsh., although this species never became abundant due to low germination performance. Henry and Swan (1974) reconstructed forest succession for 300 years and found that disturbance was more important in creating compositional changes than was autogenic succession. Morris (1963) and Holling et al. (1975) showed that the spruce budworm can cause up to 100% mortality in stands over hundreds of hectares. Kilgore (1973) and Viereck (1973) found that wildfires were a key factor in the generation of new successions and in the control of species composition. Flaccus (1959) studied the revegetation and the succession of species on 29 landslides in the White Mountains of New Hampshire and showed the gradual replacement of pioneer species by transitory species by age 70. Recently Horn (1976) has studied the effect of different patterns of devastation on succession, Slatyer and Connell (1976) have documented the patterns of colonization after

perturbation, and Shugart et al. (1973) have looked at the feedback effect of disturbance on pioneer species.

Man is the major biotic agent affecting the forest (Kimmins 1972). Bartos (1973) has shown how fire and cutting cause the aspen (Populus tremuloides Michx.) community to revert to early successional stages. Likens et al. (1970) have made a detailed study on the effects of clear-cutting and herbicides on soil nutrient contents and cycling. They showed that clearcutting can produce high nutrient losses from soils before the rate of nutrient utilization by early successional species reaches the rate of supply. Cole and Gessel (1968) and Gessel et al. (1973) studied the impact of clearcutting and even-age management on forest productivity and mineral cycling. They found a 54 to 60% increase in the amount of water in the soil after clearcutting. There is abundant literature on other examples of human disturbance to the forest.

Early stages of succession including mosses, liverworts, annuals and short-lived perennials, shrubs and tree seedlings were studied by Mueller-Dombois (1965), Kellman (1969), and Dyrness (1973). The present data set did not provide observations on understory vegetation and its inclusion in the models was not possible. In his study covering all vegetation strata, Kellman (1969) found that no prediction could be made as to floristic organization at different stages of succession because of the highly stochastic process of propagule dispersal in minor vegetation. For the purpose of predicting later stages of forest succession, it appears to be safer to wait until after the apparently haphazard stage of early competition among minor vegetation and tree saplings.

The purpose of this paper is to provide a synthesis of the succession dynamics of the coastal forest of southwestern British Columbia after disturbance, at the scale of the Biogeoclimatic Subzone. As a first approach a small-scale analysis is judged necessary to encompass the general behaviour of this large ecosystem ($1.3 \times 10^5 \text{ km}^2$). The time horizon (the period of time over which modelling is applied) required to perceive the dynamics of the system must be kept rather short, by necessity, since the cutting rotation is assumed to be sixty to eighty years. Under these conditions, an adequate model of succession should be general, synthetic and dynamic; general, due to the size and variability of the study area and because details are useless at this level of interpretation; synthetic, because integration over several levels of response is necessary; dynamic, because growth processes of a community generate constant changes in environmental conditions and because forecasting techniques rely on an orderly flow of events from one time period to the next.

DATA SAMPLING

The data base

The data for this study were collected by MacMillan Bloedel Limited, Forestry Division, on their Tree Farms and Tree Farm Licences in coastal British Columbia. Some of the oldest plots were established by Powell River Company and by the British Columbia Forest Service. The plots are part of the Company's Permanent Sample Plot and Spacing Assessment Plot programs. They are located mainly in the Powell River region, on a few

islands of the Johnstone Strait, and at many locations on Vancouver Island and on the Queen Charlotte Islands. The plots are grouped in clusters of variable size in the different Biogeoclimatic Zones (Packee 1974). The position of the clusters on Vancouver Island and the adjacent mainland, and on the Queen Charlotte Islands are shown (Figures 1 and 2).

Study area

The study area is classified into four Biogeoclimatic Zones: Coastal Douglas-fir, Coastal Western Hemlock, Subalpine Mountain Hemlock, and Alpine. The study plots are restricted to the first two zones, the lower elevation zones ($\leq 1000\text{m.}$), each of which is further divided into a dry and a wet subzone (Krajina 1965, 1969; Packee 1974, 1976). Packee (1974) also recognizes a Fog Western Hemlock / Sitka Spruce Subzone at low elevation along the west coast of Vancouver Island and on the Queen Charlotte Islands, within the Western Hemlock Zone. The main climatic parameters forming the basis for classification of these five subzones are listed in Table 1. The distribution of major tree species in each subzone appears in Figure 3.

Description of the data

The Forestry Division of MacMillan Bloedel Limited has established the Permanent Sample Plot program as a complement to its inventory system to assess timber production, forest rotation, and annual allowable cut, and the Spacing Assessment Plot program as a tool for experimenting with stocking, thinning, fertilization, and planting. The plots are rectangular or square, and vary from 0.04 to 0.8 hectares in area. They are grouped in clusters of 2 to 10 plots, in several management blocks in

FIGURE 1

Location of the sample plots of Vancouver Island and the adjacent islands and mainland. The Biogeoclimatic Subzones after Packee (1974) are indicated by the map texture. The size of the cluster marker indicates the approximate number of plots per cluster. The subzones without any sample plots have not been included.

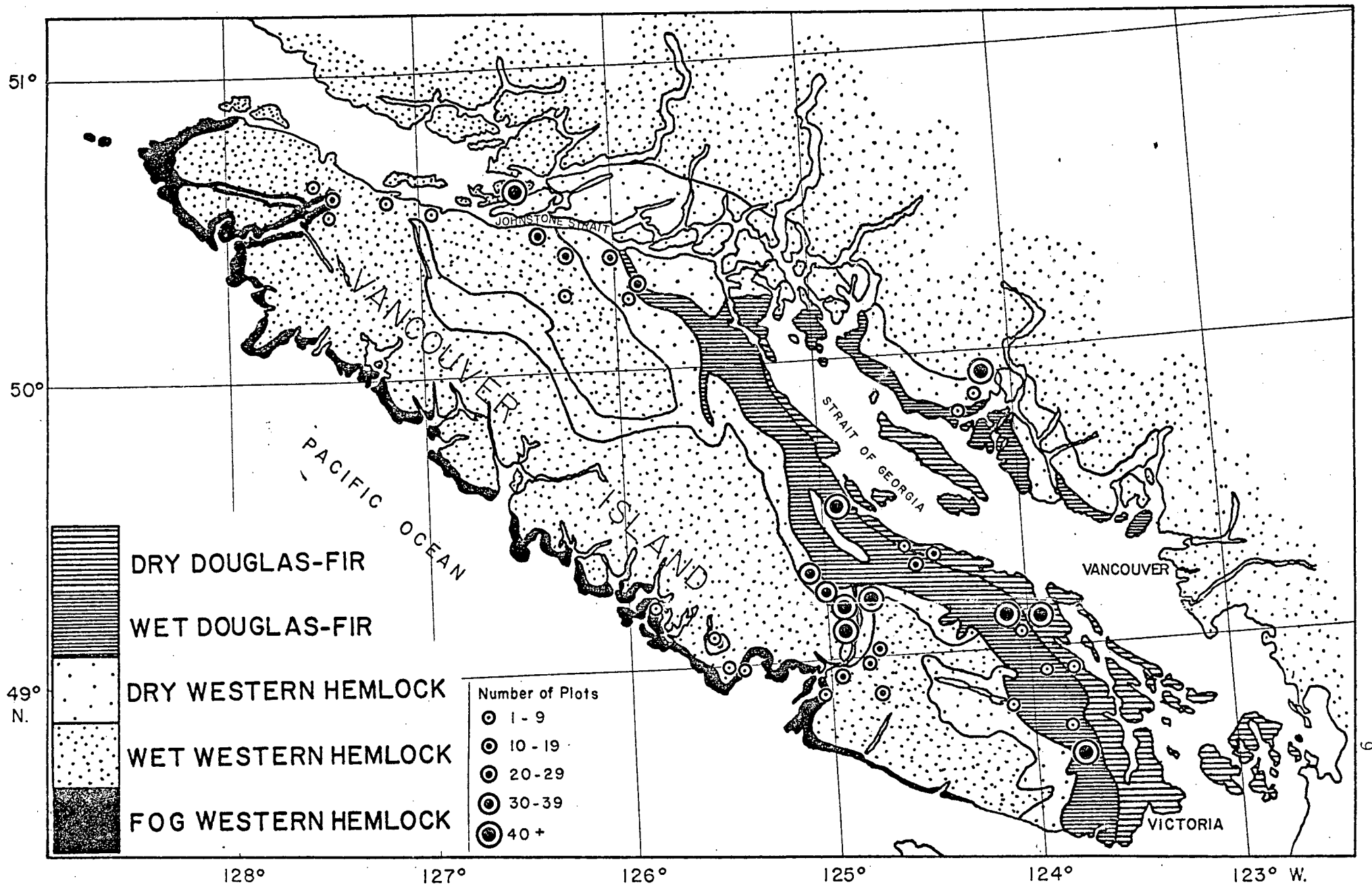
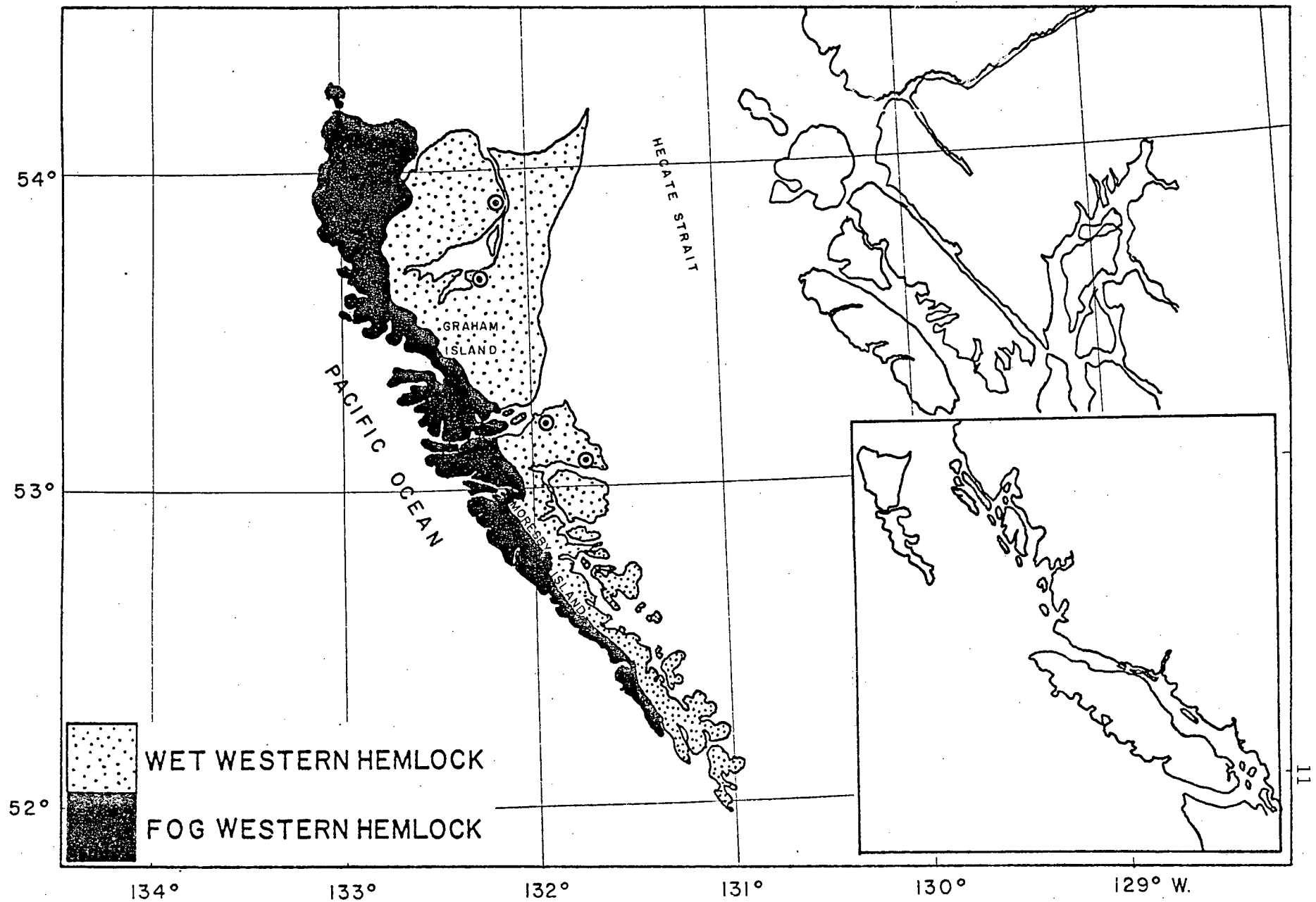


FIGURE 2

Location of the sample plots on the Queen Charlotte Islands. The Biogeoclimatic Subzones after Packee (personnal communication) are indicated by the map texture. The size of the cluster marker indicates the approximate number of plots per cluster. The subzones without any sample plots have not been included.

The insert shows the relative position of Vancouver Island and the Queen Charlotte Islands.



BIOGEOCLIMATIC ZONE	Coastal Douglas-fir		Coastal Western Hemlock		
BIOGEOCLIMATIC SUBZONE	Dry	Wet	Dry	Wet	Fog
PRECIPITATION (cm)					
Annual Total	66-102	102-152	165-280	280-665	<165
Moist. Deficit ¹	13.4	9.3	6.2	2.7	0.4
DRIEST MONTH	1.5-4.8		3-16.5		
WETTEST MONTH	12.7-26.4		28-117		
ANNUAL SNOWFALL	25-107		13-750		
SNOW IN % OF ANN. PREC.	4-10		1-38		
climate (KOPPEN) ²	CSB (+DRIEST CFB)		CFB (+MILDEST DFB)		
temperature (°C)					
MEAN ANNUAL	9-11		5-9		
ANNUAL RANGE (MEAN MONTHLY)	12-18		9-21		
MEAN JANUARY	1-4		-4 TO 5		
MEAN JULY	16-19		13-18		
NUMBER OF FROST-FREE DAYS	150-250		120-250		
elevation (M)					
WINDWARD	0-150		0-900		0-150
LEEWARD	0-450		450-1050		-

TABLE 1

The main climatic parameters which are used to classify the Biogeoclimatic Zones (Krajina 1965, 1969, Packee 1974). The Fog Western Hemlock / Sitka Spruce subzone is after Packee (1974). Knowledge of the climax species is also needed to correctly assess the zone and the subzone.

¹ Mean Annual Moisture Deficit with 200 mm of soil water storage capacity (Packee 1976).

² Koppen's classification can be found in Strahler (1969).

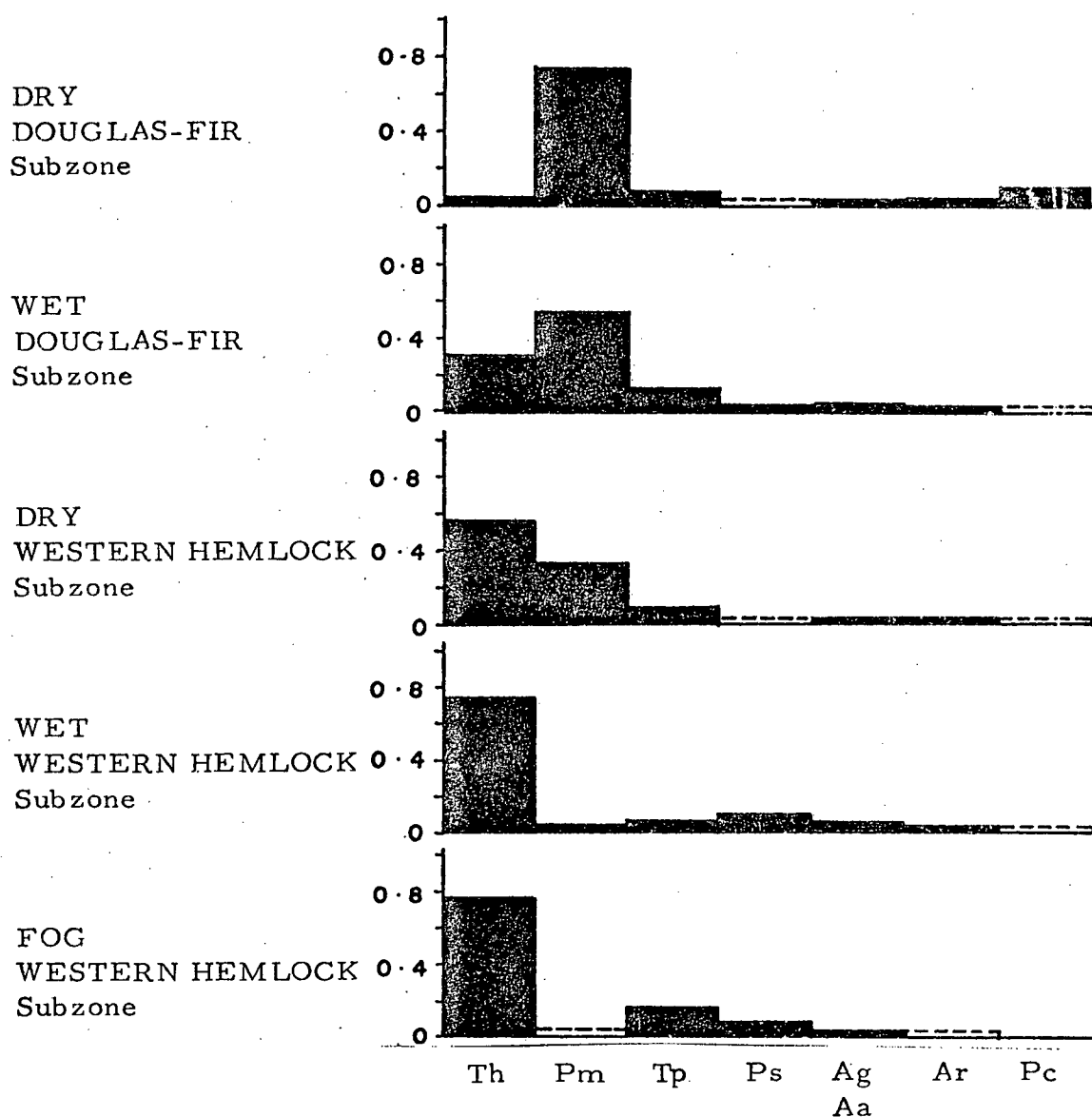


FIGURE 3

Frequency distribution of the seven most abundant tree species in each Biogeoclimatic Subzone based on immature plot data. The subset of unthinned plots only was used in the computation. Species marked in a dashed line have a frequency of less than 0.01. Th: T. heterophylla, Pm: P. menziesii, Tp: T. plicata, Ps: P. sitchensis, Ag: A. grandis, Aa: A. amabilis, Ar: A. rubra, Pc: P. contorta.

each Biogeoclimatic Subzone (except in the Alpine and Subalpine Zones). The total forest area managed by the Company is approximately 1.4×10^6 hectares. The program was started during the 1930's, and oldest plots have yielded observations over a period of more than 40 years. Plots are remeasured at five-year intervals. An initial pool of 730 natural regeneration plots, with over 70,000 trees, was available for this study.

1) Tree parameters

The following variables are taken or measured for each tree at least 4 cm in DBH (Diameter at Breast Height, 1.4 m from ground level): tree number, species name, DBH, stem and butt characteristics, tree defects, crown class, and pathological factors. Breast height is marked on the tree and DBH is measured with a diameter tape to the nearest 0.25 cm. In addition, the age and the height are measured on enough trees to assess the plot age and height. These trees are chosen randomly in each of the canopy strata: dominant, co-dominant, intermediate, and suppressed.

2) Plot parameters

The slope angle, slope aspect, position on slope, and plot area are determined. The following are calculated from the tree data: forest-type, plot cover, site height, site age, site index (for Pseudotsuga menziesii (Mirb.) Franco¹, and Tsuga heterophylla (Raf.) Sarg.). The Biogeoclimatic Zone is assessed, based on the climax species and plot location. For each tree species, the number of stems and basal area are calculated on a per plot and per hectare basis, for each DBH class. Between measurements

¹ English species names are given in Appendix A.

population parameters such as ingrowth (realized regeneration), mortality, and thinning are calculated on a five year basis. All changes in tree size and basal area, and the rates of change are also computed. The distribution of sample plots is shown in Table 2.

Assessment of the data

Since large bodies of data similar to this one are increasingly available, it is important to carefully assess their merits and limitations for ecological studies. The main advantages of this data assemblage are:

1. The availability of a data set rich with the expertise of several thousand man-days is invaluable to the ecologist. It allows him to focus on theoretical ideas and on analytical aspects rather than on time-consuming data acquisition.
2. The large sample size, the long range of observations and the uniformity in the field procedures assure a high level of statistical reliability for most parameters.
3. The geographic area sampled is on a Biogeoclimatic Region level - the Pacific Coastal Mesothermal Forest (Krajina 1969). This allows elaboration of generalities pertinent to the whole region, and also concentration on between-zone variation.
4. The data were obtained from MacMillan Bloedel Limited in a form prepared for computer analysis, already verified and edited.

BIOGEOCLIMATIC ZONE	Coastal Douglas-fir		Coastal Western Hemlock			
BIOGEOCLIMATIC SUBZONE	Dry	Wet	Dry	Wet	Fog	TOTAL
% Total Area ¹	5.5	9.0	13.0	40.0	2.2	69.7 ²
ALL PLOTS						
Number of Plots	100	198	157	255	20	730
% of Total	14	27	21	35	3	100
Sampling Period	1955-71	1946-73	1935-72	1932-72	1967-72	-
Sampling Range (years)	16	27	37	40	5	-
UNTHINNED PLOTS						
Number of Plots	71	167	142	248	19	647
% of Total	11	26	22	38	3	100
Number of trees	4070	12964	10076	21774	1154	50038
Average number of trees per plot	57	77	70	87	60	-

TABLE 2

Distribution of the sample plots per Biogeoclimatic Subzone. The complete sample consists of 730 plots, some of which have been thinned for experimental purposes. Some analyses use the complete sample, and others use the subsample of 647 unthinned plots.

¹ After Packee (1976).

² The Mountain Hemlock, Alpine, and Urbane Biogeoclimatic Zones cover the remaining 30.3% area.

There are however some noteworthy limitations in using inventory-type data for ecological analysis:

1. Some parameters such as height and age are not systematically measured for each tree, but only for a random subset of the plot. As a consequence, species with a low frequency are sometimes not measured and a significant age variation in this case could suggest artificial patterns of succession.
2. Environmental variables (micro-climate, pedology, fauna, etc.) are usually lacking from inventory sampling, and their absence makes it impossible to relate the forest structure to environmental variation between plots. (This kind of information is, however, being incorporated progressively into the sampling procedures of MacMillan Bloedel Limited.)
3. Understory flora is not recorded. This seems to be the most serious lack in the data set since it is widely recognized that understory vegetation is a better indicator of site potential than early seral tree composition.

METHODS

The analysis of succession

Various studies on succession in relation to disturbance were mentioned earlier. Several other studies on forest succession are published and some authors have reviewed the matter. Harbo (1972), in his thesis, reviewed at length the pre-1970 work on succession. Shugart et al. (1973)

used a set of differential equations based on stand dynamics to model large forest areas. Their approach takes advantage of the concept of rate of change and gives some insight into management. Vitousek and Reiners (1975) analysed the nutrient retention towards climax in relation to the importance of each nutrient to plant growth. They developed and refined the concept of biomass accumulation (Rodin and Bazilevitch 1967; Odum 1969) and they discussed other nutrient cycling studies. Whittaker (1953, 1957, 1970), Odum (1969, 1971), and Drury and Nisbet (1971, 1973) have discussed successional patterns quite thoroughly.

Four elements are essential to a complete definition of succession.

(1) Succession is a property of a system. None of the elements of the system considered separately can give a valid picture of succession. (2) Succession consists of a change in the net rate of increase of species. As Horn (1974) pointed out, this is the condition without which one could not perceive succession. (3) The controls over succession are either extrinsic to the system: fire, flooding, climatic changes etc., or intrinsic: competition, predation etc. Finally, (4) there is a certain convergence of the system towards a relatively steady state, the so-called climax, where species composition seems to change over a much longer time scale than in earlier stages of succession.

The Markov approach to succession

From the essential characteristics of succession emerges the general concept of transition of the forest from one "state" to another. Two conditions bound the choice of states: their number must be finite and they must describe the conditions of the forest at any time. For the

study of large regions, Shugart et al. (1973) used a finite number of cover-states or forest-types. Waggoner and Stephens (1970) and Stephens and Waggoner (1970) classified the forest into five types "according to which of the five classes had the most stems on the tract". Once the forest-types are identified, repeated observations at regular time intervals on several sampling plots show transitions from one type to another during the course of succession.

MacArthur (1958, 1961) suggested that succession could be viewed as a plant-by-plant replacement process amenable to the Markovian approach. This approach views state transitions as a probabilistic phenomenon, where the future of any site is not fixed, but is determined by a set of probabilities of moving to another state over time. Anderson (1966), Olson and Cristofolini (1966), and Horn (1974, 1975a, 1975b, 1976) have all used this method in their studies of succession. Recently Horn (1975b) and Noble and Slatyer (1976) have reviewed this approach for plant succession. Mathematical treatments of the Markov process are found in Bharucha-Reid (1960), Kemeny and Snell (1960), and Hillier and Lieberman (1967).

As Waggoner and Stephens (1970) point out, sets of extensive observations in time and space necessary for the verification of the transition probabilities are rare. However the data for this study seem suitable for the task. Due to the absence of data on understory flora, a forest-type classification was used and each plot was characterized on the basis of the tree species with the largest number of stems and, alternatively, with the largest basal area. This was done for each measurement

on a five-year interval basis and the stand-type (a stand of a given forest-type) frequencies were plotted across stand age, for each Biogeoclimatic Subzone in terms of stems and basal area.

The sampling period varies for each Biogeoclimatic Subzone and the maximum is 40 years (Table 2). Since young and old stands were sampled, data were plotted across stand age to show variations in stand-type frequency as a function of stand age rather than as a function of an arbitrary time scale such as calendar year. This permits the reconstruction of a long-lived ecosystem from observations of plots of different age measured over the same period of time.

However, this approach has one implication that complicates the extraction of transitions from the data. Consider two adjacent forest stands 25 and 70 years of age respectively, observed at five-year intervals for 40 years. If a transition is observed within any of the two stands, this is recorded. Additionally the last observation of the youngest stand, taken at age 65, can be merged with the first observation of the oldest stand, taken at 70, as an implied transition. Historically, most work on forest succession in North America is based on implied transitions (Drury and Nisbet 1973). Ecologists have measured forests of different ages and have assumed that the oldest ones represented the state towards which the young forests were progressing. This approach has been proven adequate in older forests of Europe and in short-lived ecosystems.

When hundreds of stands of different ages are pooled together, the total age span is increased, but implied transitions cannot be determined. Therefore, some transitions are bound to be missing from a transition

matrix generated from the observed transitions alone. However, prior biological knowledge of the system and published work can contribute to produce prior estimates of the transitions. A subset of the observed transitions can then be used to modify the prior estimates through the use of Bayes' rule (see Thompson and Vertinsky 1975) and to yield the final transition probability matrix. If E is the prior estimates matrix, and O the observed matrix, the function f such that $f[E, O] = T$, the final transition matrix, is simply: $f[E, O] = (E(i, j) - O(i, j)) / (E \text{ total}(i) - O \text{ total}(i))$ for all i 's and j 's, where i and j represent rows and columns respectively. The same weight is given to the observations and to the estimates by setting each column total of the estimates equal to the column total of the observations. Therefore, this simply makes the transition matrices a little more likely to succeed in modelling the data. Figure 4 gives an example of the calculation for the transitions in stems in the Dry Western Hemlock Subzone. Matrices are documented in Appendix B.

From the ecological viewpoint, the meaning of a transition probability matrix is as follows. All observations of a given forest-type, the P. menziesii type for instance, represent plots which may belong to different communities on the basis of their understory vegetation, and which may have different origins depending on the source of perturbation. Some of these plots may have the potential to remain the P. menziesii type, while others might progressively become the Thuja plicata Donn or the T. heterophylla type for instance. Therefore, all the possibilities are implicit within the transition matrix and the observed and assumed possibilities are included in the matrix in terms of probabilities.

O MATRIX Observations						E MATRIX Estimates				
<u>P. menziesii</u>	100	1	0	0	0	98	1	0	0	0
<u>A. rubra</u>	0	5	0	0	0	0	5	0	0	0
<u>T. heterophylla</u>	4	0	129	0	0	6	0	129	1	0
<u>T. plicata</u>	2	0	3	2	0	2	0	3	1	0
<u>A. grandis</u>	0	0	0	0	3	0	0	0	0	3
TOTAL	106	6	132	2	3	106	6	132	2	3

T MATRIX Transitions					
<u>P. menziesii</u>	933	167	0	0	0
<u>A. rubra</u>	0	833	0	0	0
<u>T. heterophylla</u>	48	0	977	200	0
<u>T. plicata</u>	19	0	23	800	0
<u>A. grandis</u>	0	0	0	0	1000
TOTAL	1000	1000	1000	1000	1000

FIGURE 4

Transition probability matrix evaluation. The estimated matrix (E) is modified by the observed matrix (O) to produce the final transition probability matrix (T) using Bayes' rule. The transitions are expressed from the column stand-type at time t , to the row stand-type at time $t+1$. Probabilities have been multiplied by 1,000 for presentation in the table. The column stand-types are the same as the row stand-types.

This makes the Markov process very powerful and very general.

Once the transition probability matrix of a system is determined, the Markov process allows the computation of the steady-state of the system, if it exists. In other words, if forest succession is to reach a state of climax where there is virtually no change in forest-types over a long period of time, this state can be predicted. This assumes, of course, that the system is truly Markovian.

The underlying assumptions to the Markov process

The coastal forest succession could be treated as a finite state Markov process if it shows the following four properties (Hillier and Lieberman 1967) :

(1) The system can take only a finite number of states. Classifying each sample plot into forest-types gives a theoretical maximum number of 24 states over the entire study area. A maximum of eight forest-types were found in any Biogeoclimatic Subzone.

(2) The transition probabilities of the system must be the same for each time interval, i.e. they must be time-homogenous. This was tested by comparing the probability matrices from five-year period to five-year period for the time horizon considered in each Biogeoclimatic Subzone. The number of five-year time periods is 8 for the Dry Douglas-fir Subzone, 16 for the Wet Douglas-fir Subzone, 18 for the Dry Western Hemlock Subzone, 15 for the Wet Western Hemlock Subzone, and 5 for the Fog Western Hemlock Subzone. An adapted chi-square statistic for Markov matrices (Billingsley 1961) was used to test the similarity of the transitions for all the time periods, for each subzone, in terms of stems

and basal area. The expected matrix was computed from a weighted average of the complete sample. Two matrices out of 16 in the Wet Douglas-fir Subzone were significantly different ($p = 0.01$) from the expected matrix, 2 out of 18 in the Dry Western Hemlock Subzone, 1 out of 15 in the Wet Western Hemlock Subzone, and none in the two remaining subzones. So time-homogeneity is not rigorous in 3 subzones out of 5, although the departures from homogeneity are small.

(3) The system must have the Markovian property. A system is said to have the Markovian property if the conditional probability of any future state, given any past and present state, depends only on the present state of the system. This is an hypothesis that will be tested. If a model based on the Markov process fits the observations well, it suggests that the system might be Markovian; if the model does not fit the observations, it is very likely that the system is simply not Markovian.

(4) A set of initial probabilities for all states must exist. The probabilities of the forest to be in any state is theoretically unknown at the origin of the observations. However the frequency distribution can be taken as representative of the probabilities. Table 3 gives the initial frequencies of each stand-type for all the Biogeoclimatic Subzones.

RESULTS AND DISCUSSION

The Markov simulation

Simulation runs were made from the transition matrices and the

	DOUGLAS-FIR		WESTERN HEMLOCK		
	Dry	Wet	Dry	Wet	Fog
<hr/>					
STEMS					
<u>Pseudotsuga menziesii</u>	92	78	65	0	0
<u>Tsuga heterophylla</u>	0	8	26	67	33
<u>Thuja plicata</u>	0	9	0	8	67
<u>Alnus rubra</u>	4	5	9	4	0
<u>Picea sitchensis</u>	0	0	0	21	0
<u>Pinus contorta</u>	4	0	0	0	0
<u>Abies grandis</u>	0	0	0	0	0
<u>Abies amabilis</u>	0	0	0	0	0
TOTAL	100	100	100	100	100
BASAL AREA					
<u>Pseudotsuga menziesii</u>	92	77	68	0	0
<u>Tsuga heterophylla</u>	0	18	28	75	33
<u>Thuja plicata</u>	0	0	0	0	67
<u>Alnus rubra</u>	4	5	4	0	0
<u>Picea sitchensis</u>	0	0	0	25	0
<u>Pinus contorta</u>	4	0	0	0	0
<u>Abies grandis</u>	0	0	0	0	0
<u>Abies amabilis</u>	0	0	0	0	0
TOTAL	100	100	100	100	100

TABLE 3

Initial stand-type frequencies for each Biogeoclimatic Subzone in percentage. The stand-type is defined as the species with the absolute maximum number of stems or absolute maximum basal area.

results compared with the observations. The Markovian nature of the simulation has two important features. First, the whole system of stand-types is simulated simultaneously and the rate of change of frequency in each stand-type is dependent on all other stand-type behaviour. Secondly, the frequencies change asymptotically to a steady-state. The Markovian process emphasises the interrelationships between species rather than their frequency distribution. Figure 5 (A to J) shows the simulated frequency curves and the observed data points in number of stems and in basal area alternatively for each subzone. A two-tailed Kolmogorov-Smirnov statistic (K-S test) was used to test the goodness of fit between observations and predictions. Most frequency curves were found to fit the data well ($p = 0.05$), with some exceptions that will be discussed for each subzone.

Dry Douglas-fir Subzone

Although some observations fall off the predicted curve of P. menziesii, none of the curves are rejected by the K-S test. The probability of P. menziesii stems dominating the stand is very high in young stands (0.92) and declines slowly with stand age to reach 0.61 at age 75 (Figure 5 A). Alnus rubra Bong. and Pinus contorta Dougl. each have a probability of 0.04 in young stands and A. rubra decreases to 0.02 while P. contorta increases to 0.16 by age 75. T. plicata does not dominate any stand at early stages but increases progressively to 0.21 by age 75.

There are two major differences in this pattern when the probabilities are calculated in terms of dominance by basal area (Figure 5 B) rather than by number of stems. The probability for P. menziesii does not decrease as fast: 0.92 at age 35 and 0.72 at age 75. This means

FIGURE 5

Markovian simulation of succession. The results are presented alternatively in number of stems and in basal area for each subzone:

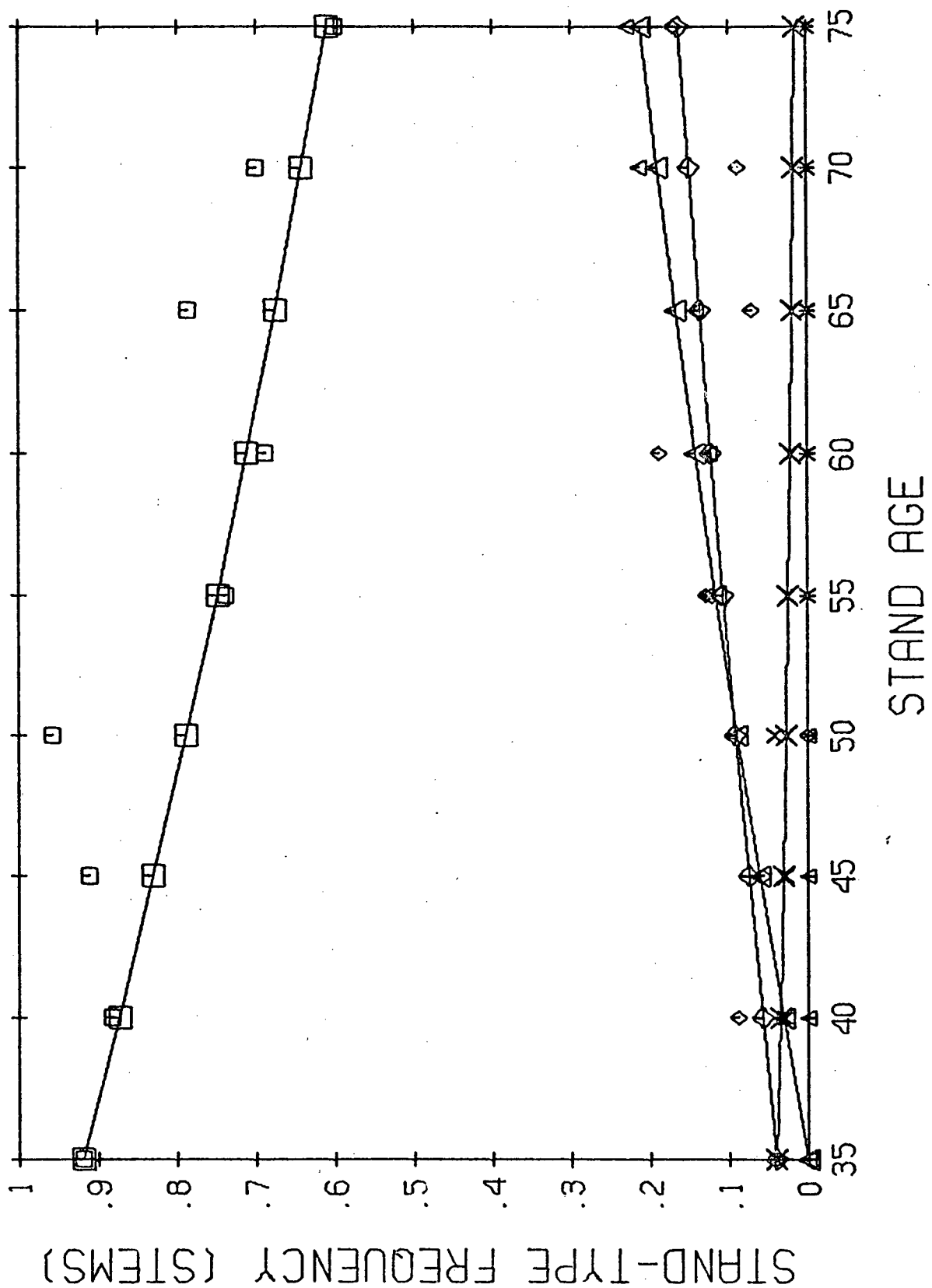
- A Dry Douglas-fir Subzone (stems)
- B Dry Douglas-fir Subzone (basal area)
- C Wet Douglas-fir Subzone (stems)
- D Wet Douglas-fir Subzone (basal area)
- E Dry Western Hemlock Subzone (stems)
- F Dry Western Hemlock Subzone (basal area)
- G Wet Western Hemlock Subzone (stems)
- H Wet Western Hemlock Subzone (basal area)
- I Ecg Western Hemlock Subzone (stems)
- J Ecg Western Hemlock Subzone (basal area)

Each graph shows the observed data points with the following symbols, and the simulated curves with identical larger symbols:

- P. menziesii □
- T. heterophylla ○
- T. plicata △
- A. rubra ×
- P. sitchensis ↑
- A. macrophyllum ×
- P. contorta ◇
- A. grandis
(in the Wet Douglas-fir Subzone) +
- A. amabilis
(in the Wet Western Hemlock Subzone) ... +

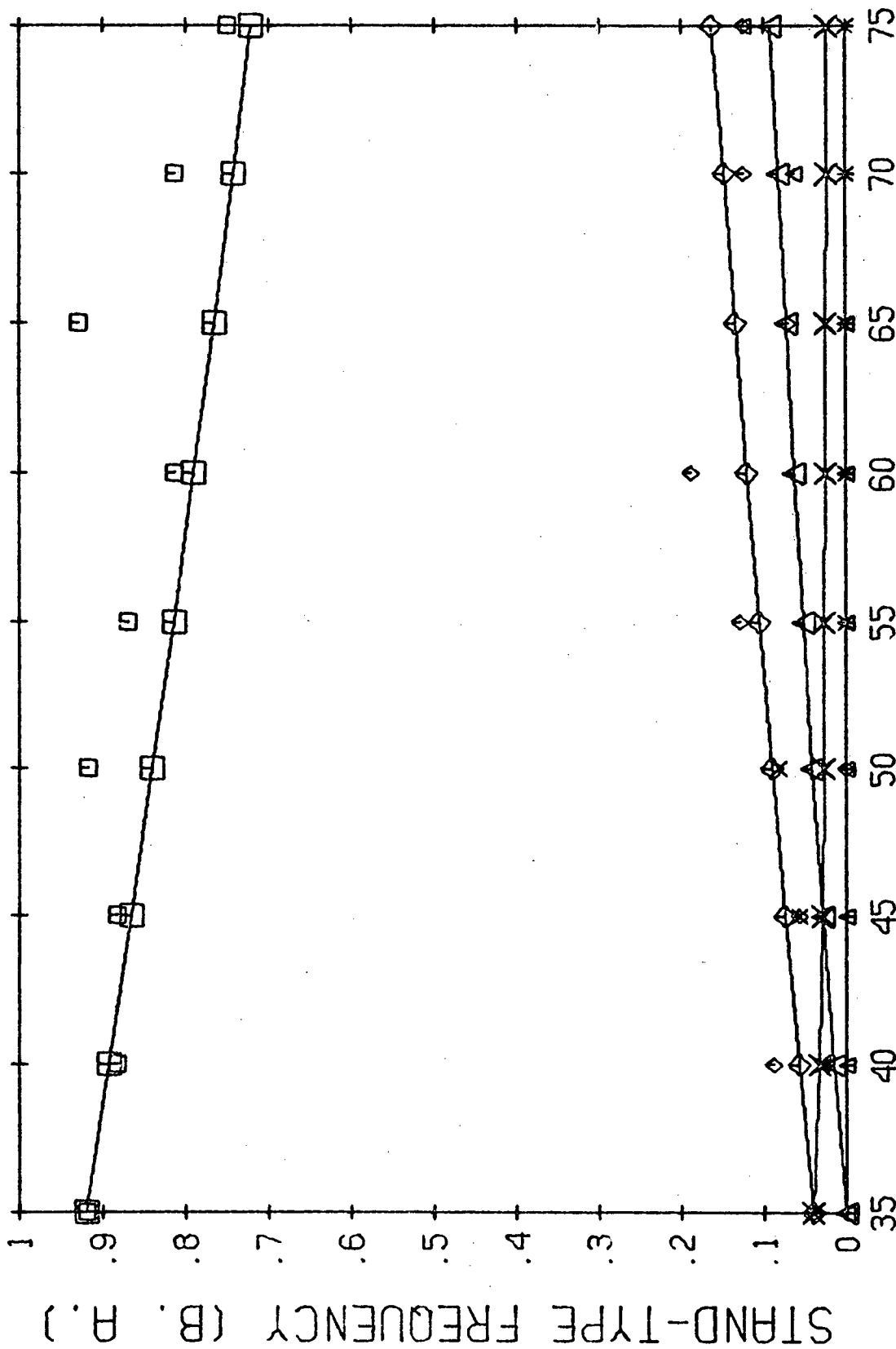
DRY DOUGLAS-FIR

(MARKOV SIMULATION)



DRY DOUGLAS-FIR

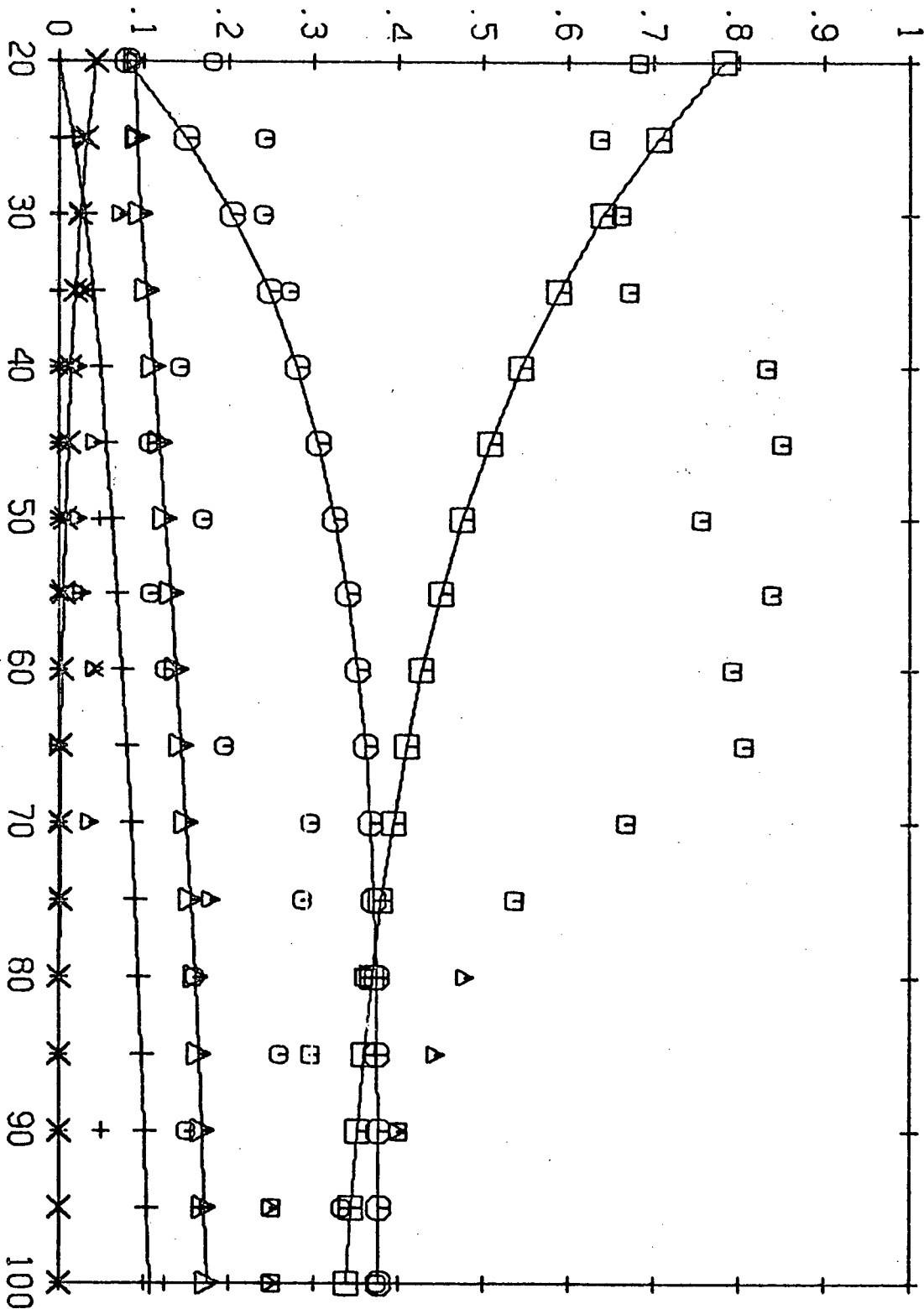
(MARKOV SIMULATION)



WET DOUGLAS-FIR

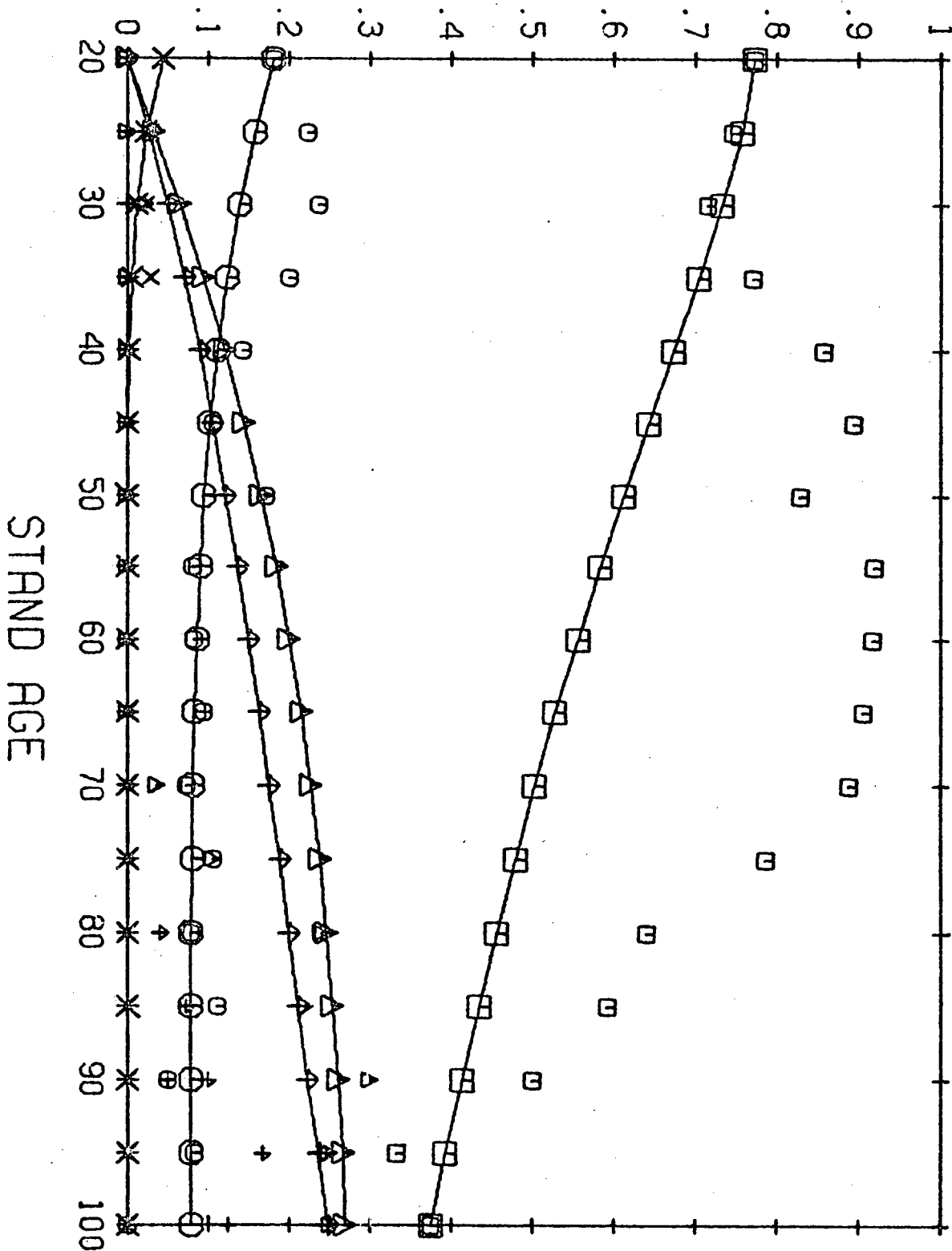
(MARKOV SIMULATION)

STAND-TYPE FREQUENCY (STEMS)



WET DOUGLAS-FIR (MARKOV SIMULATION)

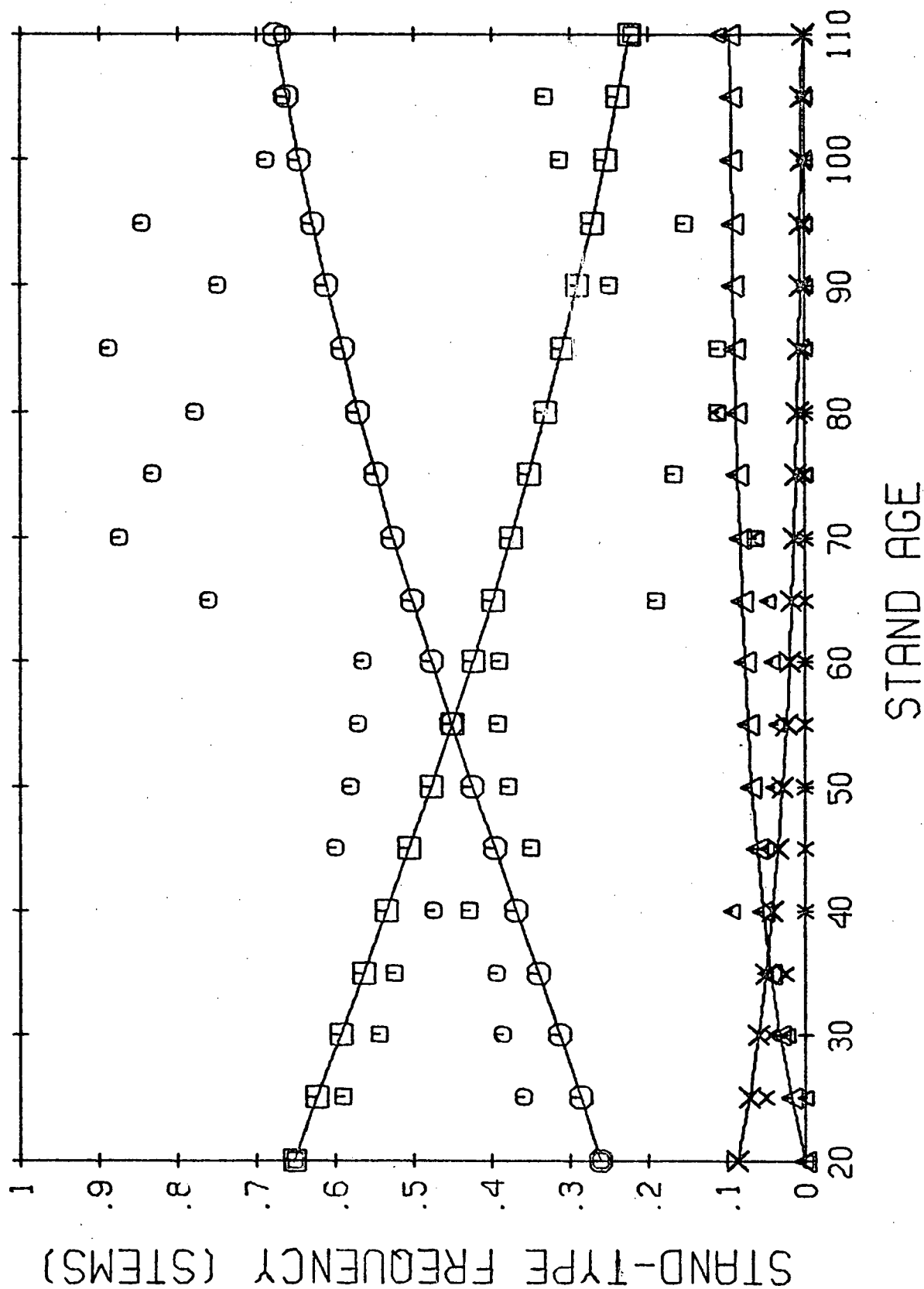
STAND-TYPE FREQUENCY (B. A.)



D

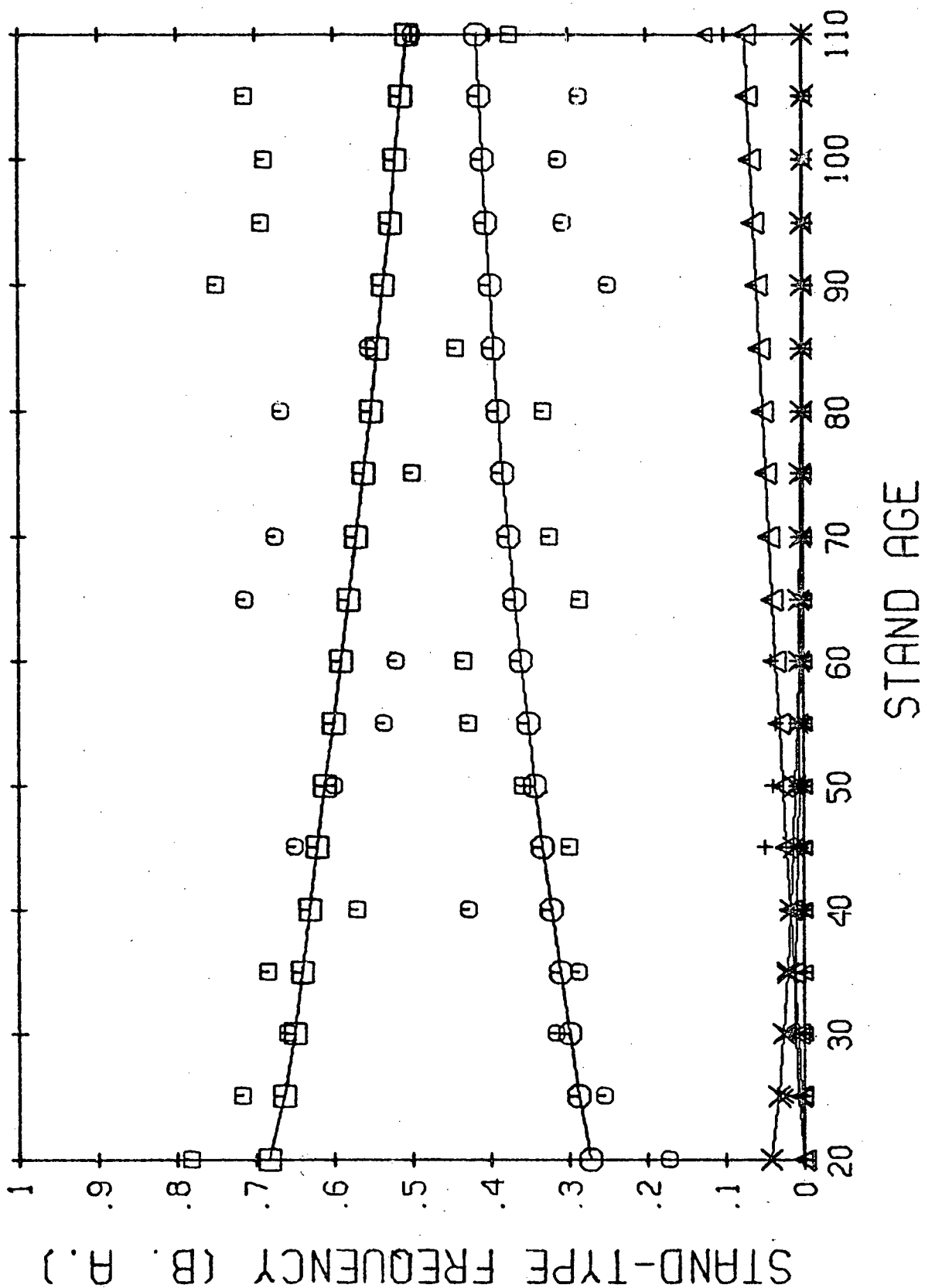
DRY WESTERN HEMLOCK

(MARKOV SIMULATION)

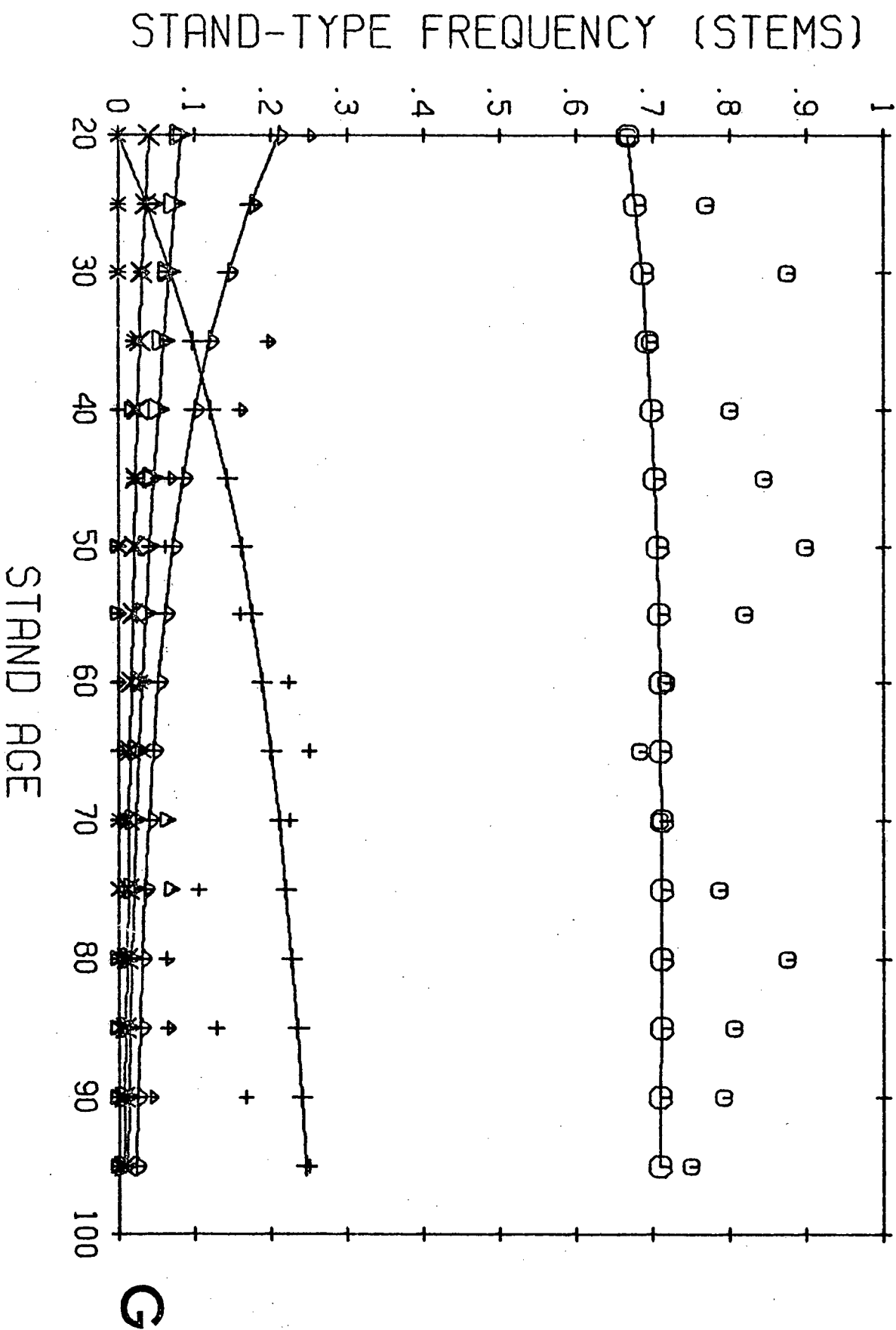


DRY WESTERN HEMLOCK

(MARKOV SIMULATION)

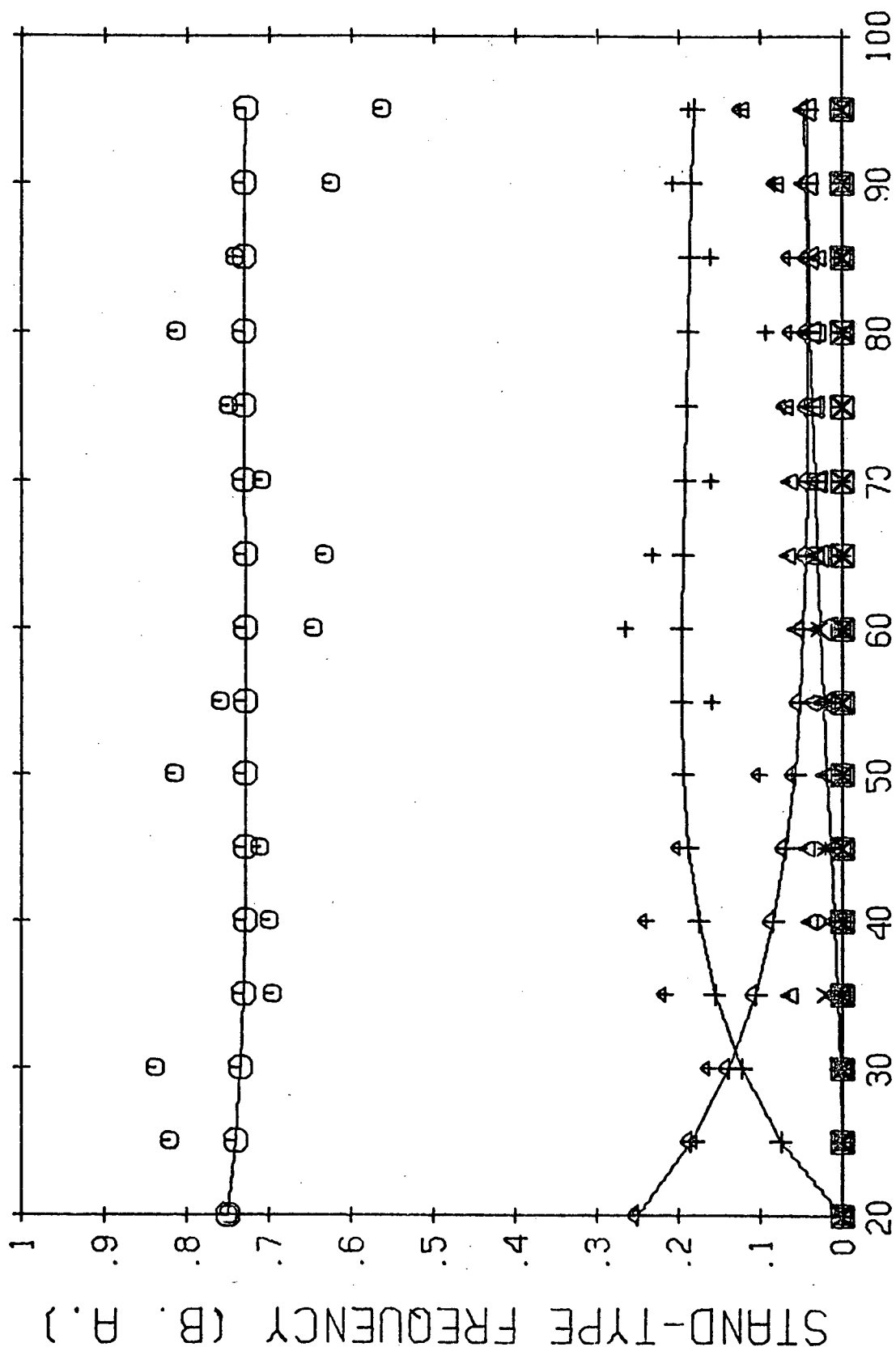


WET WESTERN HEMLOCK (MARKOV SIMULATION)



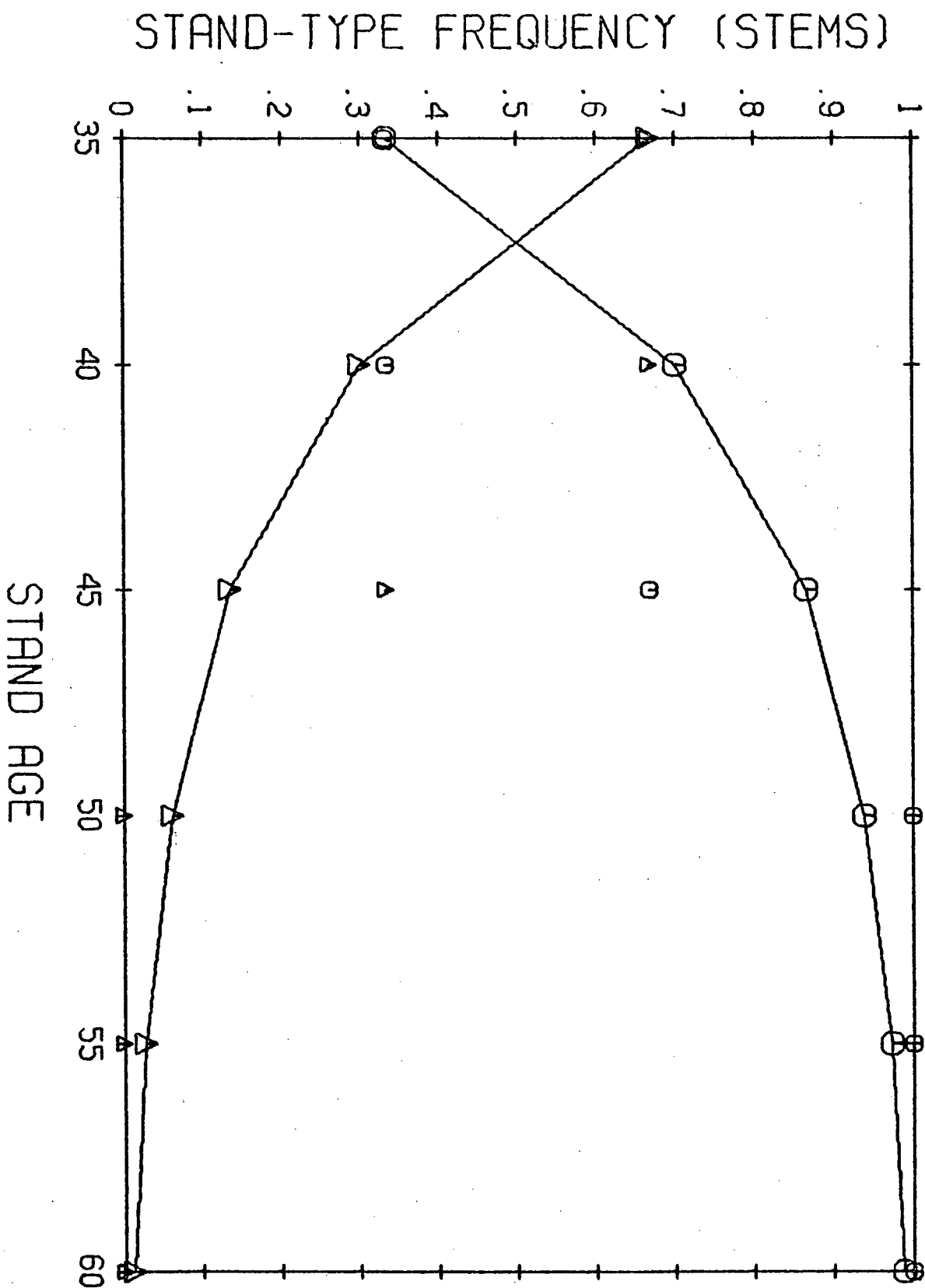
WET WESTERN HEMLOCK

(MARKOV SIMULATION)



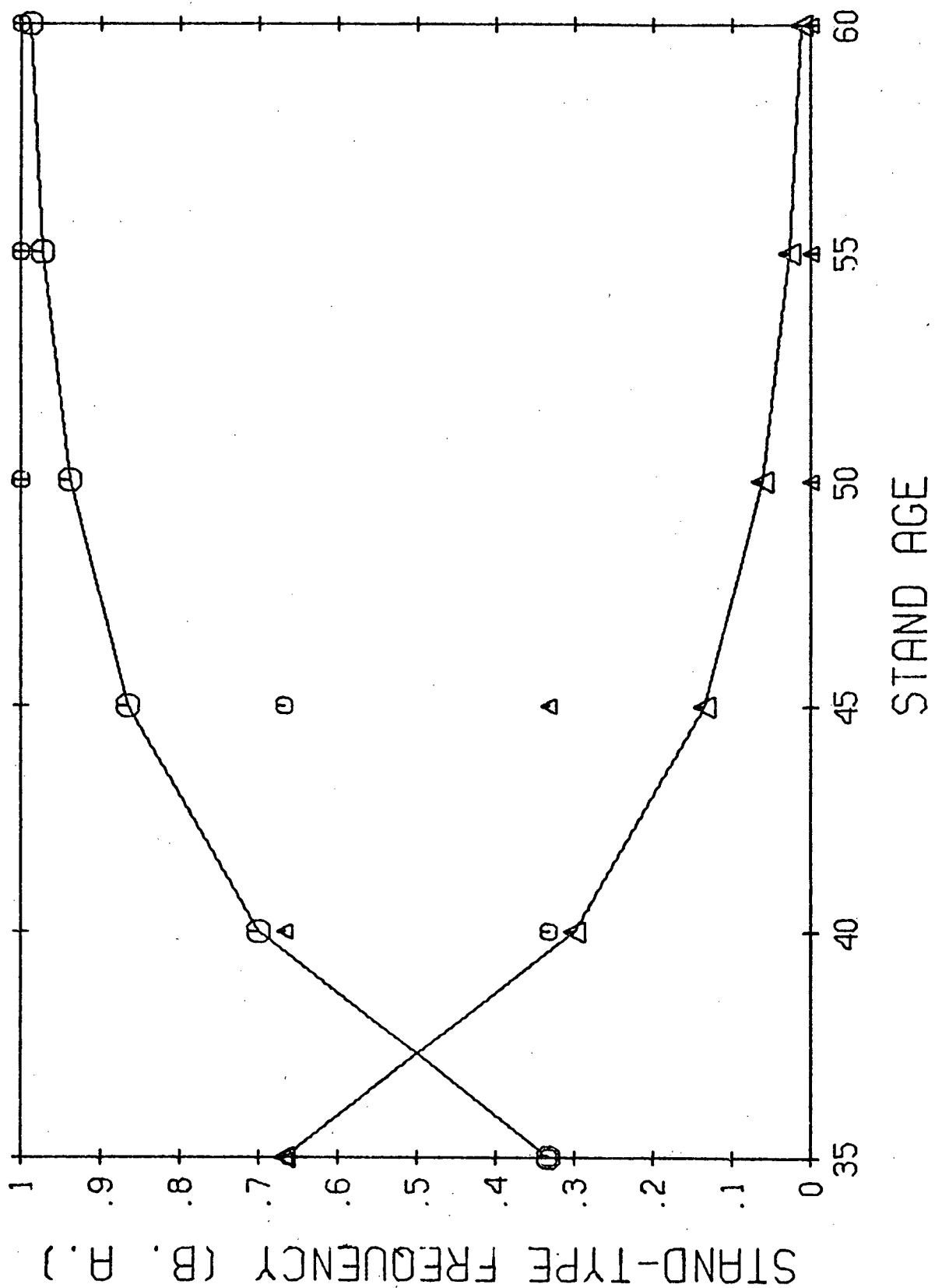
FOG WESTERN HEMLOCK

(MARKOV SIMULATION)



FOG WESTERN HEMLOCK

(MARKOV SIMULATION)



that there are 11% more P. menziesii stand-types that dominate in terms of basal area than in terms of stems at age 75. At this stand age, T. plicata shows, to the contrary, a lower stand-type frequency in terms of basal area (0.09) than in number of stems (0.21). Therefore, even though T. plicata is increasing its number of stems due to its ability to regenerate in the shade, P. menziesii displays a better basal area growth rate per stem. A. rubra shows the same kind of behaviour in both units of measurement; its frequency of dominance is 0.04 at age 35 and 0.02 at age 75. Packee (personal communication) believes that A. rubra can dominate more commonly on certain sites, and he argues that lack of sufficient sampling on those sites might explain the low observed frequencies. No other tree species in this subzone have been found able to dominate the stands either in number of stems or basal area.

Krajina (1969) points out that P. menziesii is shade tolerant in this subzone, except on hygric edatopes. As the subzone in general is xeric to mesic, it leaves little room for hygric species to dominate the wettest sites, and this is the role that T. plicata plays. Its increase in frequency with stand age might be attributed to its ability to reproduce in the shade on both wet and dry sites. Packee (1976) reports that T. plicata is commonly found on relatively dry sites, often in association with Arbutus menziesii Pursh, but only in the Dry Douglas-fir Subzone. P. contorta has a chance to dominate on the most xeric sites and Krajina (1969) mentions that it would be overtaken by shade tolerant T. plicata at about 50 years in terms of stems. Packee (1974) classifies P. menziesii and T. plicata as major climax species, A. rubra as a minor seral species, and P. contorta as a major seral species. The results of

the model seem to contradict his classification of P. menziesii. Although this species is dominant in more than 90% of the stands after disturbance, the proportion of P. menziesii stand-types decreases steadily thereafter. P. menziesii should be classified, on this basis, as a pioneer.

Long-term projections based on the model show T. plicata and P. contorta to become climax species (Table 4). This is likely to cast serious doubts on the validity of the model. Indeed, it is argued that the decrease of P. menziesii, and the consequential increase of T. plicata and P. contorta, is an artefact generated by a higher species diversity in the oldest plots (above 55 years in the Douglas-fir Zone) originating mainly from natural disturbances: wind, fire, insects, disease (Packee, personal communication). The younger plots are nearly pure P. menziesii. Therefore, the model is based on biased data and cannot be used for predictions of the steady state. In the light of this bias, Packee's (1974) classification mentioned earlier appears to be exact. Packee also mentions that Abies grandis (Dougl.) Lindl. can be a major climax species on suitable soils, but this species did not dominate any of the stands. The lack of A. grandis plots in this data set might be due to the past sampling procedures of the Company, which did not focus on this species (Packee, personal communication).

Wet Douglas-fir Subzone

Three species curves failed the K-S test of fit in this subzone: P. menziesii, T. plicata, and Acer macrophyllum Pursh. The latter did not fit well because it usually does not constitute a forest-type in this area (with two exceptions in the original data), and was not included in

	DOUGLAS-FIR		WESTERN HEMLOCK		
	Dry	Wet	Dry	Wet	Fog
<hr/>					
EXPECTED TIME:	400	430	400	1000	100
<u>Pseudotsuga menziesii</u>	2	30	0	0	0
<u>Tsuga heterophylla</u>	0	35	90	33	100
<u>Thuja plicata</u>	58	22	10	0	0
<u>Alnus rubra</u>	0	0	0	0	0
<u>Picea sitchensis</u>	0	0	0	0	0
<u>Pinus contorta</u>	40	0	0	0	0
<u>Abies grandis</u>	0	13	0	0	0
<u>Abies amabilis</u>	0	0	0	67	0

TABLE 4

Expected time of theoretical steady-state and probability distribution of stand-types for each subzone at time of steady-state in terms of stems.

the graphs. Here P. menziesii dominates clearly and decreases steadily with stand age from a probability of 0.78 at 20 years to 0.34 at 100 years (Figure 5 C). Again, the decrease is smaller in basal area (Figure 5 D). T. heterophylla has a probability of 0.08 at age 20, and slightly overtakes P. menziesii at age 100 with a level of 0.38. However P. menziesii is still well ahead of T. heterophylla in basal area. Krajina (1969) stresses that P. menziesii achieves a higher forest production here than in the dry subzone while T. heterophylla grows rather poorly. The discrepancy between the predictions and the observations for P. menziesii, between age 45 and 75 (Figures 5 C and D), has a twofold explanation. The oldest plots were first measured in the 1930's and were located as a function of road accessibility, i.e. in valley bottoms, where higher moisture content favored T. plicata over P. menziesii. Thus the observations show an abrupt decline for P. menziesii after about age 70. This is compounded by the bias mentioned earlier whereby the higher species diversity of the oldest plots produces an artificial decrease of P. menziesii at older ages. The Markov model reflects this decrease by converging asymptotically towards a steady-state, starting from a high frequency at early stand age. This results in a smooth and steady decline corresponding closely to the observations in the early and late stages, but departing greatly in the middle stages.

T. plicata increases its dominance in stems with stand age and even at a faster rate in basal area. This suggests a better moisture availability and a higher soil nutrient content than in the dry subzone, and a better uptake by T. plicata than by T. heterophylla. According to

Krajina (1969), T. plicata needs richer soils than T. heterophylla, and the oligotrophic edatopes required for T. heterophylla are very rare in this subzone. Packee (1976) attributes the lower frequency of T. plicata to moisture deficit. The simulation failed to replicate the three peaks observed at age 80, 85, and 90 on the graph in stems for T. plicata. It is noteworthy that Picea sitchensis (Bong.) Carr. never appears to dominate in stems in any stand, yet its basal area dominance increases steadily with time, seemingly taking advantage of the moisture. The absence of dominance in the stem model agrees with Krajina's (1969) remark that P. sitchensis is very rare in this subzone. Its presence in the basal area model agrees on the other hand with Phelps' (1973) contention that P. sitchensis may dominate on sites where the soils are well drained, fairly rich in nutrients, and continuously moist. As far as number of stems goes, Packee (1974) does not mention P. sitchensis either as a seral or as a climax species. A. grandis increases its frequency of stem dominance from nil at age 20 to 0.08 by age 100, but has no chance to dominate in basal area in this area, within the studied time horizon. Krajina (1969) showed that eutrophic conditions are necessary for A. grandis to attain a good growth, while Packee (1976) argues that soil moisture is a more important factor. As in the dry subzone, A. rubra may dominate in few young stands, but not in older ones.

Packee's (1974) classification for this subzone is: P. menziesii and T. plicata are major climax species, A. grandis is an edaphic major climax species, T. heterophylla is a minor climax species, and A. rubra is a major seral species. The results agree qualitatively with that,

with the exception of T. heterophylla which tends to become a major climax species on moist sites of older stands. Kellman (1969), working in an area mid-way between the Wet Douglas-fir Subzone and the Dry Western Hemlock Subzone, found species frequency similar to these at age 13, 42, and 100, with an expected T. plicata - T. heterophylla climax. However, due to the bias in the data, it is likely that P. menziesii does not decrease as much as shown here, and consequently T. plicata and T. heterophylla would both have a lower frequency at higher ages; this makes the use of the model for extrapolation unsafe. The theoretical steady-state in stems would be reached in this subzone at about 430 years of age (see Table 4), if the forest were truly Markovian.

Dry Western Hemlock Subzone

No curve was rejected by the K-S test in this subzone, although the curves for P. menziesii and T. heterophylla do not visually seem to fit the observations: the test is not very robust. There is a remarkable shift from a high frequency (0.66) of P. menziesii and low frequency of T. heterophylla (0.26) at age 20 to 0.22 for P. menziesii and 0.68 for T. heterophylla at age 10 (Figure 5 E). This shift also occurs in basal area, although much more slowly (Figure 5 F). Discrepancies between observations and predictions of frequencies of T. heterophylla and P. menziesii are likely caused by an oversampling in the valley bottoms, 30 and 40 years ago, because of better road accessibility (Packee, personal communication). Valley moisture overemphasized frequency of T. heterophylla plots over P. menziesii plots. Since plots were not sampled before 20 years of age T. heterophylla plots now 50 years or older are overrepresented in the observations. This might slightly exaggerate the upward trend of

T. heterophylla in the older ages, although there is no doubt that T. heterophylla is taking over P. menziesii in terms of stems. Again A. rubra may dominate young stands only, and T. plicata more frequently dominates older stands, with a maximum probability of 0.10. Here P. menziesii can be a major climax species, but edaphically controlled (Packee 1974), or else a major seral species; T. plicata is a major climax species, and A. rubra is again a major seral species.

Graphs show T. heterophylla to become a major climax species, and this agrees with Packee's contention, although present results give more information concerning the definite succession to T. heterophylla. There is a threefold explanation for this shift. (1) The fact that P. menziesii is edaphically controlled and is competitively superior on xeric sites favors its appearance just after disturbance. (2) The seedlings of T. heterophylla are sensitive to heat and their establishment succeeds better in the shade of P. menziesii. Thereafter T. heterophylla is able to continue regenerating in the shade. (3) Unless there are frequent openings in the canopy, the seedling survival of P. menziesii is threatened. Krajina (1969) describes P. menziesii as a definite pioneer species in the subzone, and T. heterophylla as a climatic climax species. There were two isolated observations of A. grandis that were not possible to simulate and were deleted from the graphs. It is expected that the Markovian steady-state will not appear before 400 years, with probability distribution of 0.90 for T. heterophylla and 0.10 for T. plicata (see Table 4). For the same reasons as above, long term extrapolations are certainly unsafe.

West Western Hemlock Subzone

All curves in this subzone fit the observations according to the K-S test. This subzone exhibits very slow changes and no significant differences between the evaluations in number of stems and basal area (Figure 5 G and H). The dominance of T. heterophylla is practically constant within the time horizon at a frequency of about 0.7 while Abies amabilis (Dougl.) Forbes succeeds to an early dominance of P. sitchensis in about 0.20 of the stands. T. plicata may dominate infrequently (0.08) in early ages, but is soon succeeded by A. amabilis. No stand dominated by P. menziesii was found here and Krajina (1969) points out that P. menziesii is indeed strongly outcompeted by T. heterophylla, T. plicata, and A. amabilis. He also stresses that the climax T. heterophylla has its best production here. The frequency of stands dominated by A. amabilis is very low in younger stands. Krajina (1969) states that it is shade requiring in mesic and drier edatopes. Macbean (1941, in Packee 1976) points out that its regeneration is very poor in stands following clearcutting, which is the case in the younger plots. P. sitchensis might be outcompeted by A. amabilis since the former is shade intolerant in dense stands (Krajina 1969), although it will persist on fluvial bottomlands where its growth is best (Packee 1976).

Packee (1974) assigns species as follows: T. heterophylla, A. amabilis, and T. plicata are major climax species, A. rubra is a major seral species, and P. sitchensis an edaphic minor seral species. Since the changes in frequency distribution are so slow, it would theoretically take a very long time (about 1000 years, see Table 4) to reach a steady-state.

Fog Western Hemlock Subzone

T. plicata and T. heterophylla share the dominance of the young stands with a probability of 0.67 and 0.33 respectively in number of stems and also in basal area (Figure 5 I and J). Very soon T. heterophylla succeeds in all the stands, and dominates everywhere. But this subzone has the smallest number of plots (see Table 2) and the shortest period of observations, and the data do not represent well the exact situation. Packee (1974) assigns T. plicata and T. heterophylla as major climax species; the results agree with his classification of T. heterophylla, but show T. plicata to be a pioneer. He also assigns A. amabilis as a major climax species, which was never observed in the few stands of the study area in this subzone. He also classifies P. sitchensis as a major seral species and Phelps (1973) reports that P. sitchensis occurs more frequently in mixture than in pure stands, and that the associated species usually assume dominance, which the results seem to confirm.

It is obvious that there are too few plots in this subzone. Krajina (1969) states that P. sitchensis has its best growth along the ocean in the Wet Coastal Western Hemlock Subzone, which corresponds to Packee's (1974) Fog Western Hemlock / Sitka Spruce Subzone. This is also supported by Phelps (1973) and Packee (1976). The absence of P. sitchensis stand-types is, therefore, very surprising. On the other hand, Packee (1976) reports that this species is usually associated with T. heterophylla which often dominates the stand. Hence the high frequency of T. heterophylla stand-types would reflect the presence of P. sitchensis.

The data and the model show T. plicata strictly as a pioneer and Packee (1974, 1976) states that it is definitely a major climax species.

There are too few plots in the data set to make a better assessment of the situation and the extrapolation to an exclusive T. heterophylla climax is unlikely.

CONCLUSION

Forest succession

The general trends of the succession in each subzone are clear within the period of observations, although the rates of change are exaggerated by a certain bias in the data set. Over the whole study area, only P. menziesii shows a large difference between its abundance in stems and in basal area. Its stand-type frequency is always higher in terms of basal area than in terms of stems. A. rubra always appears as a pioneer which may dominate up to 10 percent of the stands in all but the Fog Western Hemlock Subzone, and is always progressively outcompeted. T. plicata behaves like a pioneer species in the Wet Western Hemlock Subzone, and is slowly succeeded by A. amabilis and T. heterophylla. The data show the same behaviour in the Fog Western Hemlock Subzone, but in this case the behaviour is an artefact since T. plicata is climax in this region. In other subzones, the frequency of T. plicata stand-types increases with stand age.

In the Dry Douglas-fir Subzone, the slow decrease of P. menziesii from a high initial frequency, and the equivalent increase of T. plicata and P. contorta are in fact much smaller in terms of basal area. P. menziesii behaves like an efficient pioneer and maintains its supremacy well over the rotation period. Krajina (1969) notes that P. menziesii is shade

tolerant in the drier climates, which might explain the low frequency of T. plicata and P. contorta stand-types. In the Wet Douglas-fir Subzone on the other hand, P. menziesii appears also as a pioneer, but T. heterophylla overtakes it rapidly. A large proportion of the habitats of this subzone are moist and P. menziesii is shade-intolerant on these edatopes. Yet its basal area is the highest of all species throughout the forest rotation. P. sitchensis and T. plicata show a basal area progressively larger than the basal area of T. heterophylla despite their lower number of stems.

P. menziesii also occurs abundantly at the early stages of succession in the Dry Western Hemlock Subzone but the number of stems of T. heterophylla predominates by age 55. Here again the decrease in basal area of P. menziesii follows its decrease in stems at a much slower pace and its basal area maintains predominance over T. heterophylla. T. plicata increases its frequency up to nearly ten percent of the stands by age 110. In the Wet Western Hemlock Subzone, P. menziesii is never seen to constitute a stand-type. The trends observed for all species in this subzone are similar in terms of stems and basal area. T. heterophylla dominates over the rotation with a constant frequency of about 70 percent. The P. sitchensis stand-type has a higher frequency at early ages, and A. amabilis is more frequent after 40 years. In the Fog Western Hemlock Subzone; the T. plicata stand-type predominates at early stages and is largely overtaken by T. heterophylla after 35 years of age; this is an artifact and T. plicata should remain up to the climax stage.

The Markov model

The Markov model is not satisfactory for any subzone except the Wet Western Hemlock Subzone, which is the one where the fewest changes occur. The model fails to fit the observations and does not produce realistic predictions. It shows what would happen if the forest were Markovian and its long-term predictions are sufficiently unlikely to suggest, for the following reasons, that forest succession is not Markovian: (1) the transition probabilities were not found to be entirely time-homogenous. (2) The model is much too general as far as diversity of communities and origins of perturbation are concerned. A different model would be necessary for each kind of disturbance, each type of community, and each kind of site. (3) The model does not allow species invasion. This could be rectified by making it a multi-step model with as many transition probability matrices as life-history strategies identified within the life of the forest. (4) Even if succession were Markovian over the period of observations, the transition probabilities are unlikely to stay constant after forest maturity. Noble and Slatyer (1976) have pointed out that time homogeneity of transition probabilities is counter-intuitive, at least over long periods of time. This precludes any extrapolation or any prediction of a steady-state if it occurs outside the period of observations.

Using this particular kind of observations, it is concluded that forest succession is not Markovian. The future of a given forest-type cannot be determined solely on the basis of its present state, and its prediction necessitates a sound knowledge of how the forest got there in the first place.

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Analysis and modelling of interspecies competition
during forest secondary succession.

Pierre Bellefleur

CHAPTER II

The analysis of tree growth variation
within different plot types in
Coastal British Columbia.

ABSTRACT

Relative abundance and relative basal area of each major tree species were plotted against stand age and compared with stand-type succession data for five Biogeoclimatic Subzones of British Columbia. Forest heterogeneity within each subzone was broken down by classifying sample plots into statistically defined plot types in which tree composition was assumed to give an image of site conditions and competition regimes. The basal area growth variation of tree species was compared among plot types by analysis of variance and its correlation with stand age and site index was tested. Finally, the site index distribution of each subzone was analysed and correlated with subzone characteristics.

The time series of species relative abundance revealed the same type of species behaviour as the stand-type succession data of the previous chapter but gave more details about less abundant species. Two to seven plot types per subzone were sufficient to classify all plots. Tree species occurring in more than one plot type showed significant differences in their basal area growth which could not be entirely accounted for by stand age and site index. The response of co-occurring species was found to vary between subzones and mean subzone site index was highly correlated with soil moisture deficit. It was concluded that the variation in growth rates due to differences in site conditions and competition regimes is one of the agents generating succession.

RÉSUMÉ

On a tracé l'abondance relative et la surface terrière relative des principales espèces arborescentes en fonction de l'âge des stations et l'on a comparé ces courbes avec les données de succession des stations-types dans cinq sous-zones biogéoclimatiques de Colombie Britannique. L'hétérogénéité de la forêt à l'intérieur des sous-zones a été réduite en classifiant les places-échantillons en places-types où la composition arborescente donnerait une bonne idée des conditions du site et du régime de compétition. La variation dans la croissance en surface terrière des essences arborescentes a été comparée entre les places-types par analyse de variance et sa corrélation avec l'âge des stations et avec l'indice de site fut testée. Enfin, la distribution de l'indice de site de chaque sous-zone fut analysée et corrélée avec les attributs de la sous-zone.

L'évolution de l'abondance relative des espèces a révélé le même genre de comportement que les données sur la succession des stations-types du chapitre précédent, avec plus de détails sur les espèces moins abondantes. De deux à sept places-types par sous-zone furent suffisantes pour classifier toutes les places-échantillons. Les espèces retrouvées dans plus d'une place-type ont montré des différences significatives dans leur croissance en surface terrière inexplicables par seulement l'âge des stations et l'indice de site. La réponse des espèces en coexistence varie entre les sous-zones et l'indice de site moyen est corrélé au manque d'humidité du sol. On a conclu que la variation des taux de croissance due aux différences de conditions du site et des régimes de compétition est l'un des agents qui engendre la succession.

INTRODUCTION

In the previous chapter, secondary succession was analysed at the level of forest stand-types in the Coastal Douglas-fir and the Coastal Western Hemlock zones and subzones of British Columbia. Markov models failed to adequately fit the observations and it was concluded that forest succession was seemingly not Markovian. It appeared that the main reason for the inadequacy of the Markov approach was that it necessitated pooling together plots that belonged to different communities, since understory vegetation was not available to distinguish them. However, variation in tree composition might be suitable to distinguish plots into broad categories. Species occurring in more than one category are likely to respond and to compete differently. These sets of conditions under which competition takes place will be termed "competition regimes".

The objectives of this chapter are: (1) To monitor the composition of each subzone for the rotation period, in terms of relative abundance and relative basal area for each major tree species. (2) To compare these observations with the stand-type succession data mentioned above. (3) To separate each subzone into major competition regimes. (4) To analyse the growth variation of each species among the different competition regimes within each subzone at the level of the forest stand. (5) To test correlation of tree growth with stand age and site index. (6) To analyse site index distribution for each subzone and to test its correlation with subzone characteristics.

Achievement of these objectives should permit to test the following two hypotheses: (1) The growth of a given species is influenced by the

nature and abundance of other species growing in the same stand. (2) The difference in net rate of population growth of different tree populations is sufficient to trigger transition from one plot type to another, and hence to generate succession.

DATA AND METHODS

Heterogeneity within subzones

The data set used for this study is part of the data bank of MacMillan Bloedel Limited, Forestry Division, and was described in the previous chapter. It consists of 730 Permanent Sample Plots and Spacing Assessment Plots, all located within the Coastal Douglas-fir and Coastal Western Hemlock zones of British Columbia.

In the previous chapter, each forest plot was assigned a stand-type, depending on which species had the absolute maximum stem count and basal area. That approach had the advantage of categorizing the whole forest into different states and permitted monitoring and simulation of the succession from one state to another through a finite-state Markov model. However, it concealed a lot of information about species whose abundance was always too low to constitute a stand-type. The relative abundance of each tree species was therefore plotted against stand age to show its dynamics within the various subzones. The species relative abundance (in percentage) was chosen over absolute abundance on the basis of the unequal total number of observations at each five-year measurement. The comparison of these results with stand-type frequency distribution will be discussed later.

The main goal is to find if one can detect whether the growth of a given species is indifferent to species composition in the stand at the same time. Several cases may occur. A subject species may cover a wide range of abundance in the stand, from a unique seedling to absolute predominance. The rest of the stand may in turn be distributed among virtually any number of other species, with varying relative abundance, thus constituting several competition regimes. The difference in rate of growth can be monitored at the level of each individual stem, and at the level of the species. Only the latter case is considered in this chapter.

Each Biogeoclimatic Subzone as defined by Krajina (1969) and Packee (1974, 1976) has a theoretically homogeneous set of geoclimatic conditions. However, various vegetation patterns reveal a mosaic of habitat types within each subzone (Daubenmire 1968, Daubenmire and Daubenmire 1968). Since most species can occur within several vegetation patterns, it is necessary to distinguish typical patterns which might offer completely different situations from the viewpoint of competition. Packee (1976) has reviewed four major vegetation classification schemes which apply to southwestern British Columbia.

Rowe's (1972) classification, based on the previous work of Halliday (1937), is essentially a geographic description of the different forest regions of Canada. Southwestern British Columbia lies entirely within the Coast Forest Region of Subalpine Forest Region, and Rowe (1972) subdivides it into 4 Forest Sections. These Sections are defined quite arbitrarily "from above" (Rowe 1972), i.e. following conspicuous geographical entities, for the purpose of convenience, and represent broad

cover types of rather stable associations. Rowe (1972) mentions that a classification "from below", i.e. based on ecological knowledge of vegetation, would be desirable, but would require information not available on a large scale.

The Society of American Foresters (1954) has described forest types and forest cover types for Canada and the United States. Packee (1976) has identified 16 of these cover types relevant to southwestern British Columbia. The cover types are defined on the basis of present vegetation, regardless of the potential climax. The type name is based on the species which constitutes at least 50% of the stem composition, or, if more than one species predominates, the type is given a binomial or trinomial name. The composition of each type is described without any quantitative assessment.

Franklin and Dyrness (1969, 1973) published an ecological study of the plant communities of Washington and Oregon. Their classification is based on the zone, defined as the area covered by the climatic climax association. The associations found in each zone are described in qualitative terms -- rare, occasional, common, and abundant -- based on the presence of species. Seven of Franklin and Dyrness' (1973) zones occur in southwestern British Columbia (Packee 1976).

Krajina (1969) classified the forests of British Columbia into Biogeoclimatic Zones and Subzones. Packee (1974) followed this classification scheme for the coastal forests in defining detailed boundaries at the level of the subzones for Vancouver Island and the adjacent mainland and islands, and recognized a new subzone within the Coastal Western Hemlock Zone, the Fog Sitka Spruce - Western Hemlock Subzone. Packee (1976)

made some additional modifications to his classification, based on his findings that moisture deficit with 200 mm of soil water storage capacity was a good climatic variable to differentiate zones.

Definition of the classification scheme

For the purpose of this study, the classification scheme must be able to distinguish between vegetation patterns which present different competition regimes, where a competition regime is defined by the number of tree species present in a plot and by the abundance of each species. The measure of abundance should be based on an index as representative as possible of biomass. The assessment should be made on the basis of present vegetation, without reference to the assumed climax, nor to understorey. Finally, the method should be quantitative and objective so that plots could be categorized by computer and groups be statistically described. Since none of the classification schemes mentioned above satisfies all these requirements, a suitable scheme was developed.

Strictly speaking no two plots in a subzone are alike, and each plot can constitute a category of its own. This is useless since it yields as many categories as there are plots. At the other extreme, all the plots can be considered similar since they all belong to the same subzone. Somewhere between these extremes, plots with similar composition should constitute a similar competition regime. It is argued that, from the competition viewpoint, the single most important parameter relevant to any species' growth is the nature and abundance of competitors, assuming that environmental attributes are homogeneous within the plot boundaries. If the maximum number of major potential tree species is 8 for instance,

this gives 255 potential species combinations. In practice however, since certain combinations of species are biologically impossible, it was found that a maximum of 7 groups was sufficient to conveniently subdivide each subzone, provided less abundant species were grouped together.

The obvious choice of a measure of abundance is total volume per species, but since the data set lacks tree height information for certain species, the next best choice is basal area. For each plot, basal area was calculated for every species at each five-year measurement on a per hectare basis. Species occurring in all observations, with a basal area representing at least 5% of the total of each observation are referred to as "major species" and were included in the name of the plot type. Species with smaller basal area and which do not occur in all observations are referred to as "minor species". The presence of minor species was indicated in the name of the plot type by a plus sign (+) in suffix. For all species occurring in a number of plot types within one subzone, one-way analysis of variance was used to detect variation in growth variables among plot types. The variables analysed belong to two groups: age attributes and basal area attributes. The first group consists of the mean age of the plots and the mean site index for P. menziesii and T. heterophylla. The second group contains the mean five-year basal area increment and the mean basal area of the subject species, the mean ratio of the two previous variables, the mean total basal area (all tree species), and the mean ratio of basal area increment over total basal area. The site index distribution was further analysed at the subzone level.

RESULTS AND DISCUSSION

Dynamics of forest stands

The changes in mean species relative abundance against stand age are presented in Figures 6 A to J. Results are shown as stem count percentages and basal area percentages. As expected, these graphs are very similar to the graphs of the stand-type frequencies presented in the previous chapter (Figure 5). Stand-type was defined as the species with the maximum number of stems (or basal area) in a stand. Therefore the previous set of graphs (Figure 5) showed the proportion of stands of each type at each five-year measurement and this set shows the proportion of stems of each species at each measurement. Obviously if 90% of the stems are P. menziesii at age 35 for instance, chances are that a high proportion of the stands will be of the type P. menziesii. However species representing a low proportion of the subzone total stems in the species relative abundance graph might never constitute a stand-type, and would never appear in the stand-type graphs. A brief description of the species behaviour is given for each zone, and the relation to growth variation will be discussed later.

Douglas-fir Zone

The Dry Douglas-fir Subzone is dominated by P. menziesii, but T. plicata increases significantly after 70 years (Figures 6 A and B), although this trend is exaggerated for reasons explained in the previous chapter. A. rubra appears as a pioneer and nearly vanishes at approximately 60 years, while P. contorta and T. heterophylla seem to be

FIGURE 6

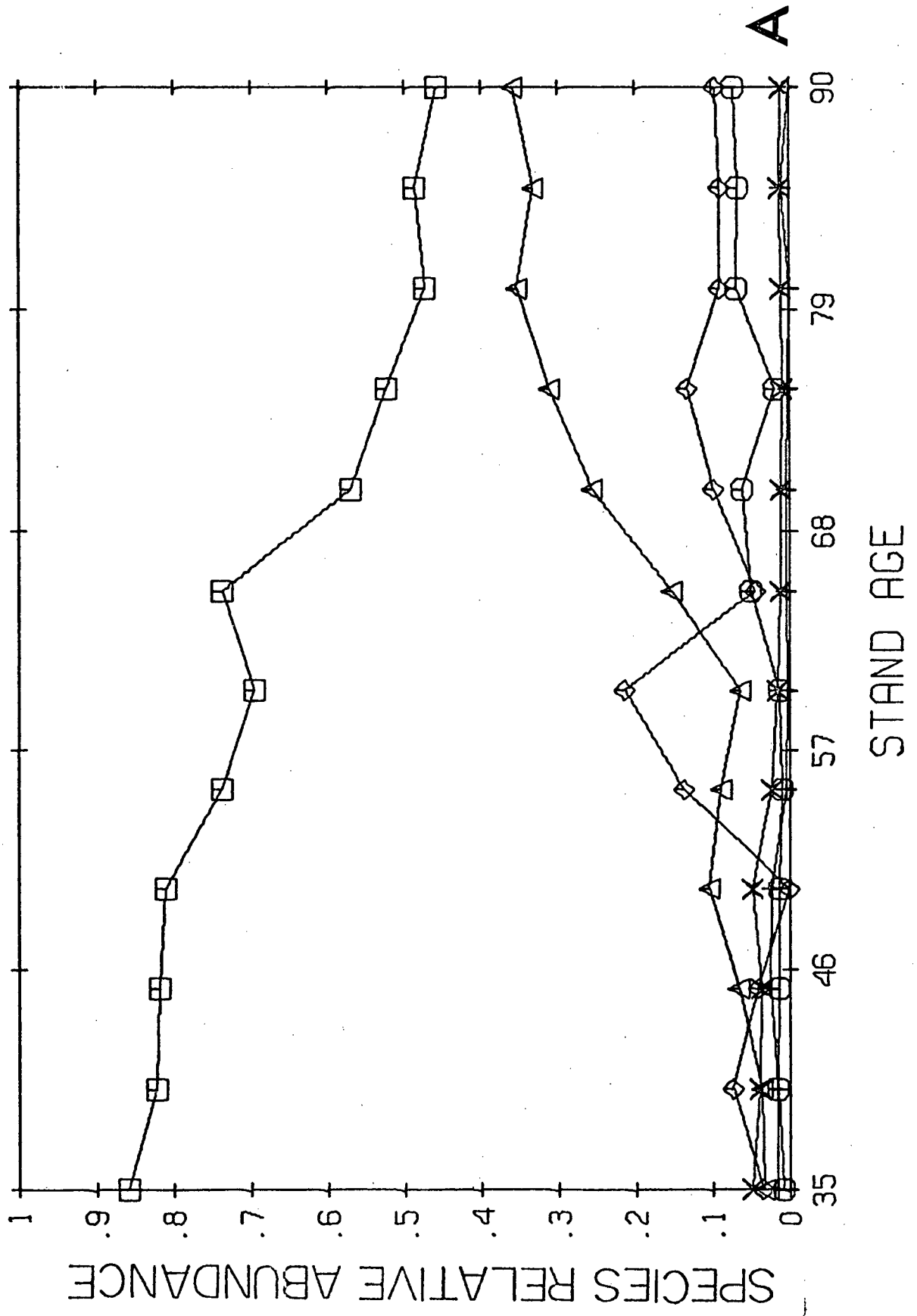
Mean species abundance at five-year measurements. The results are presented alternatively in number of stems and in basal area for each subzone:

- A Dry Douglas-fir Subzone (stems)
- B Dry Douglas-fir Subzone (basal area)
- C Wet Douglas-fir Subzone (stems)
- D Wet Douglas-fir Subzone (basal area)
- E Dry Western Hemlock Subzone (stems)
- F Dry Western Hemlock Subzone (basal area)
- G Wet Western Hemlock Subzone (stems)
- H Wet Western Hemlock Subzone (basal area)
- I Fog Western Hemlock Subzone (stems)
- J Fog Western Hemlock Subzone (basal area)

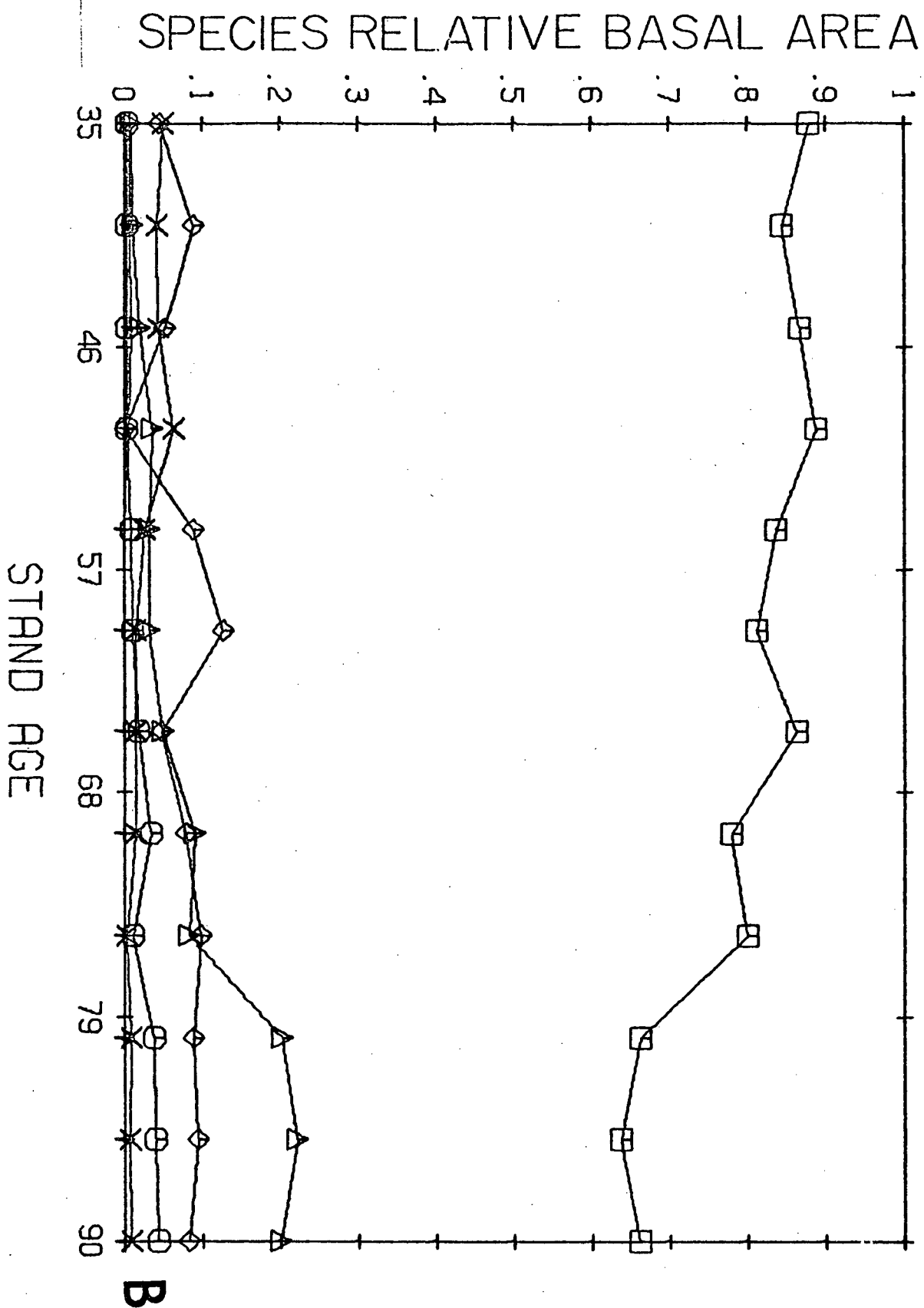
The symbols used for each species are:

<u>P. menziesii</u>□
<u>T. heterophylla</u>○
<u>T. plicata</u>△
<u>A. rubra</u>x
<u>P. sitchensis</u>↑
<u>A. macrophyllum</u>x
<u>P. contorta</u>◇
<u>A. grandis</u>	
(in the Wet Douglas-fir Subzone)+
<u>A. amabilis</u>	
(in the Wet Western Hemlock Subzone)+

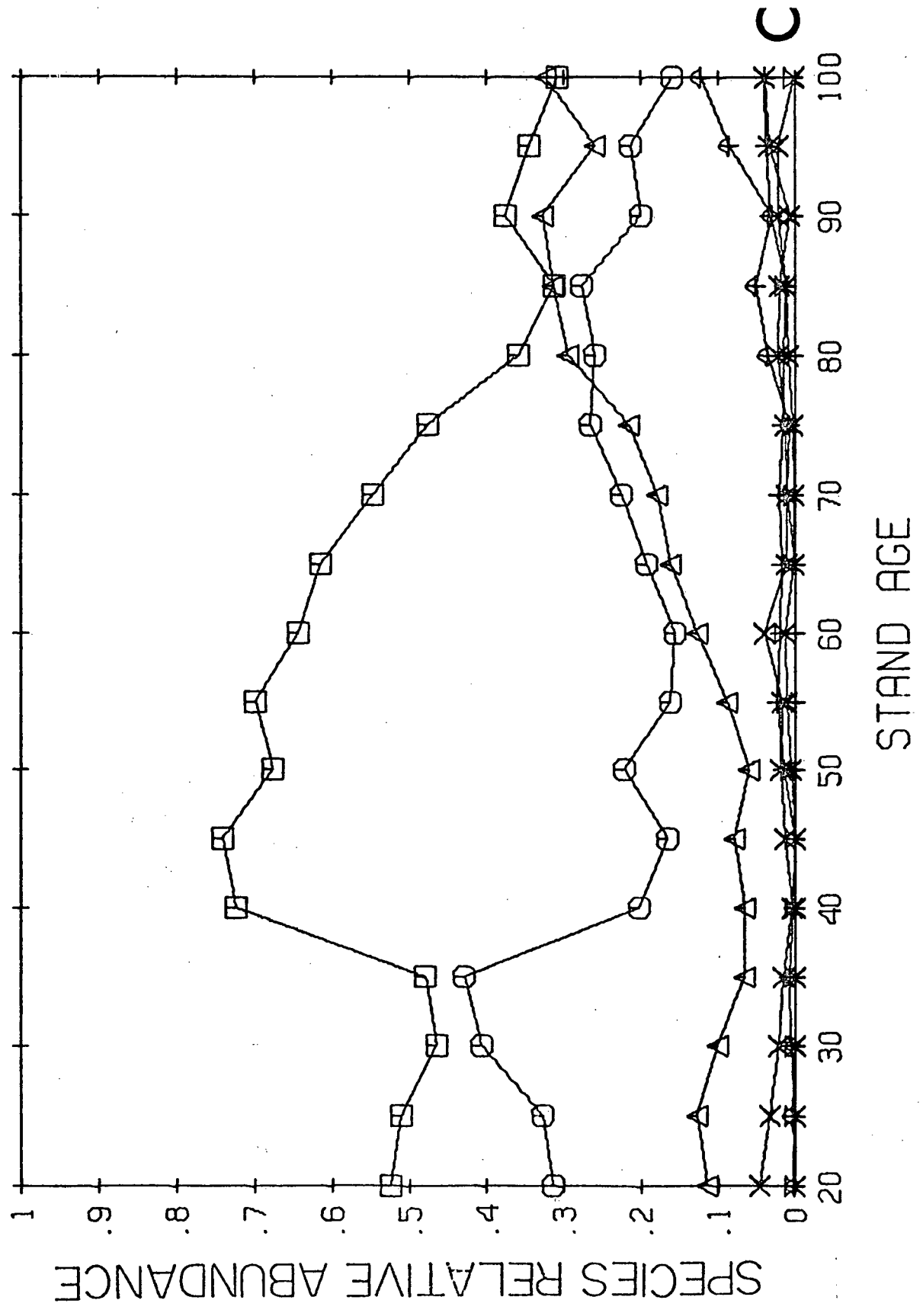
DRY DOUGLAS-FIR



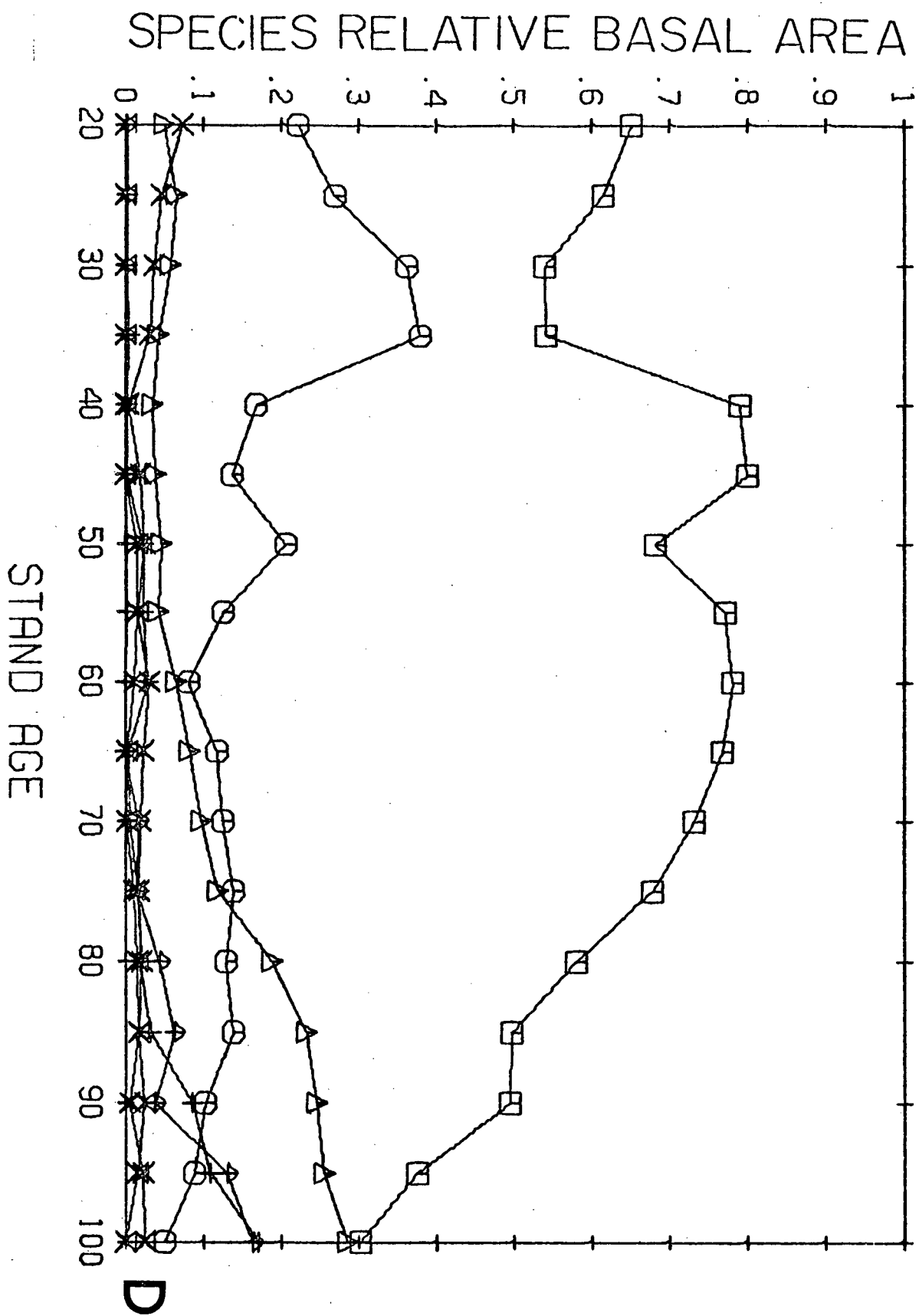
DRY DOUGLAS-FIR



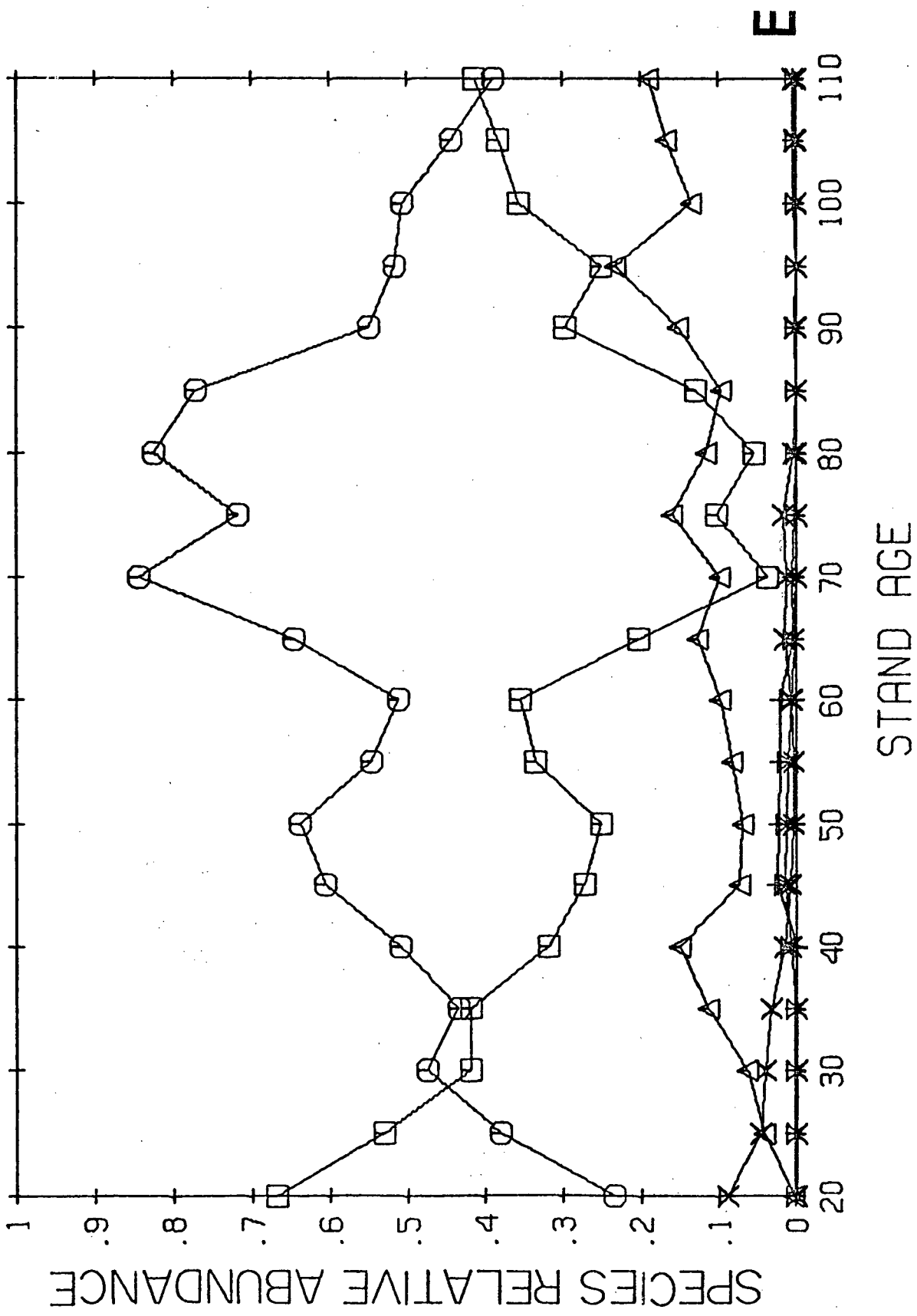
WET DOUGLAS-FIR



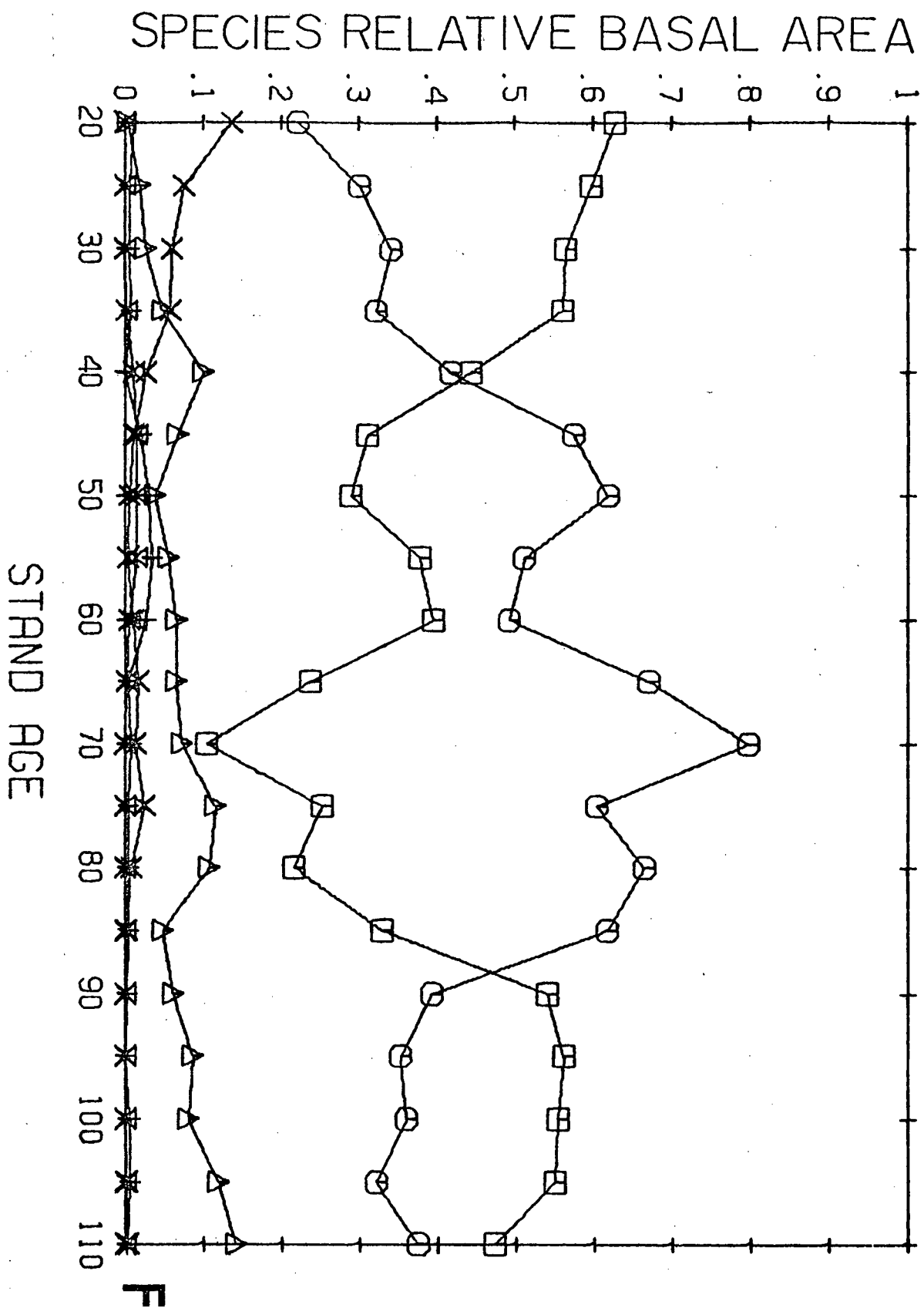
WET DOUGLAS-FIR



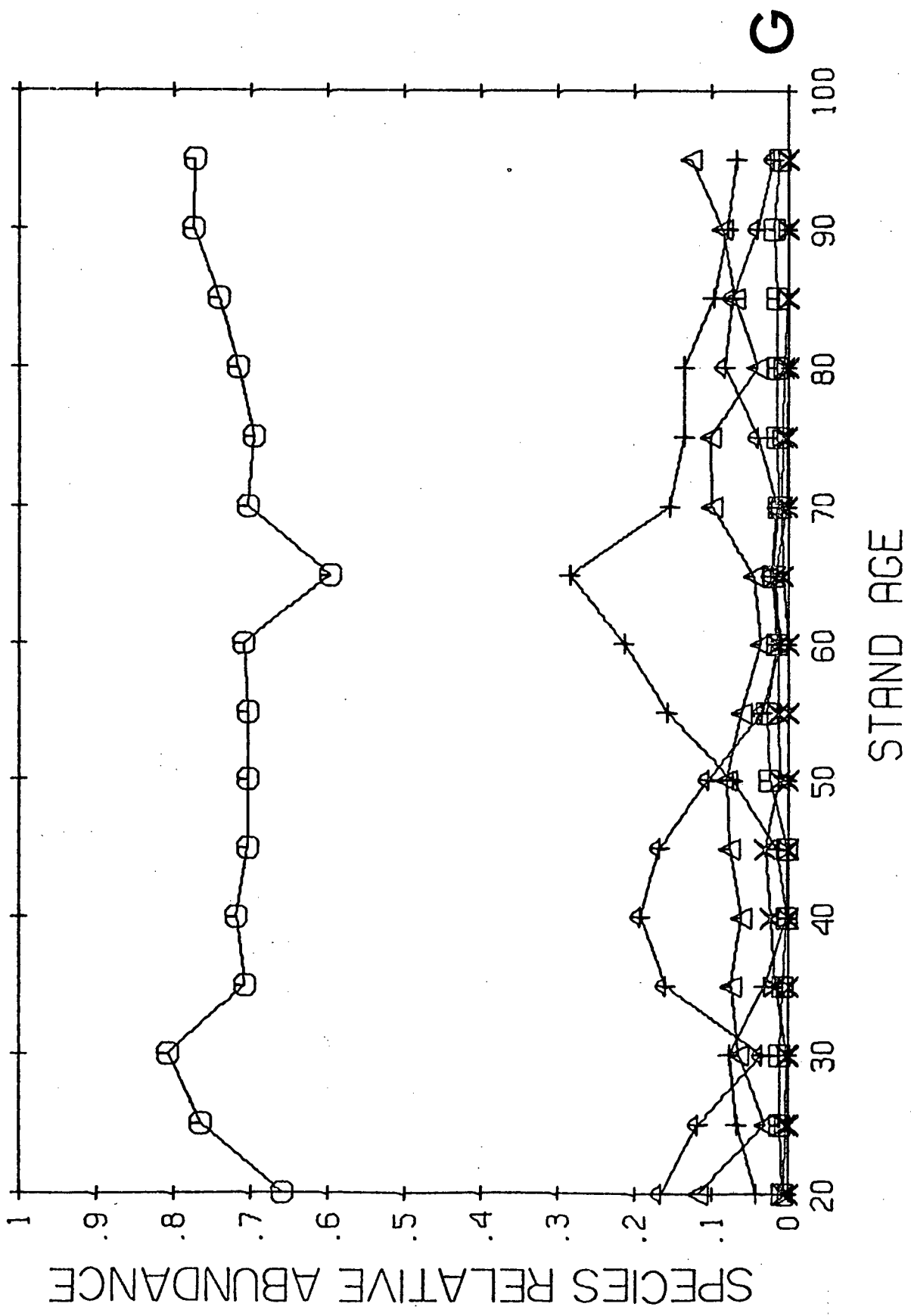
DRY WESTERN HEMLOCK



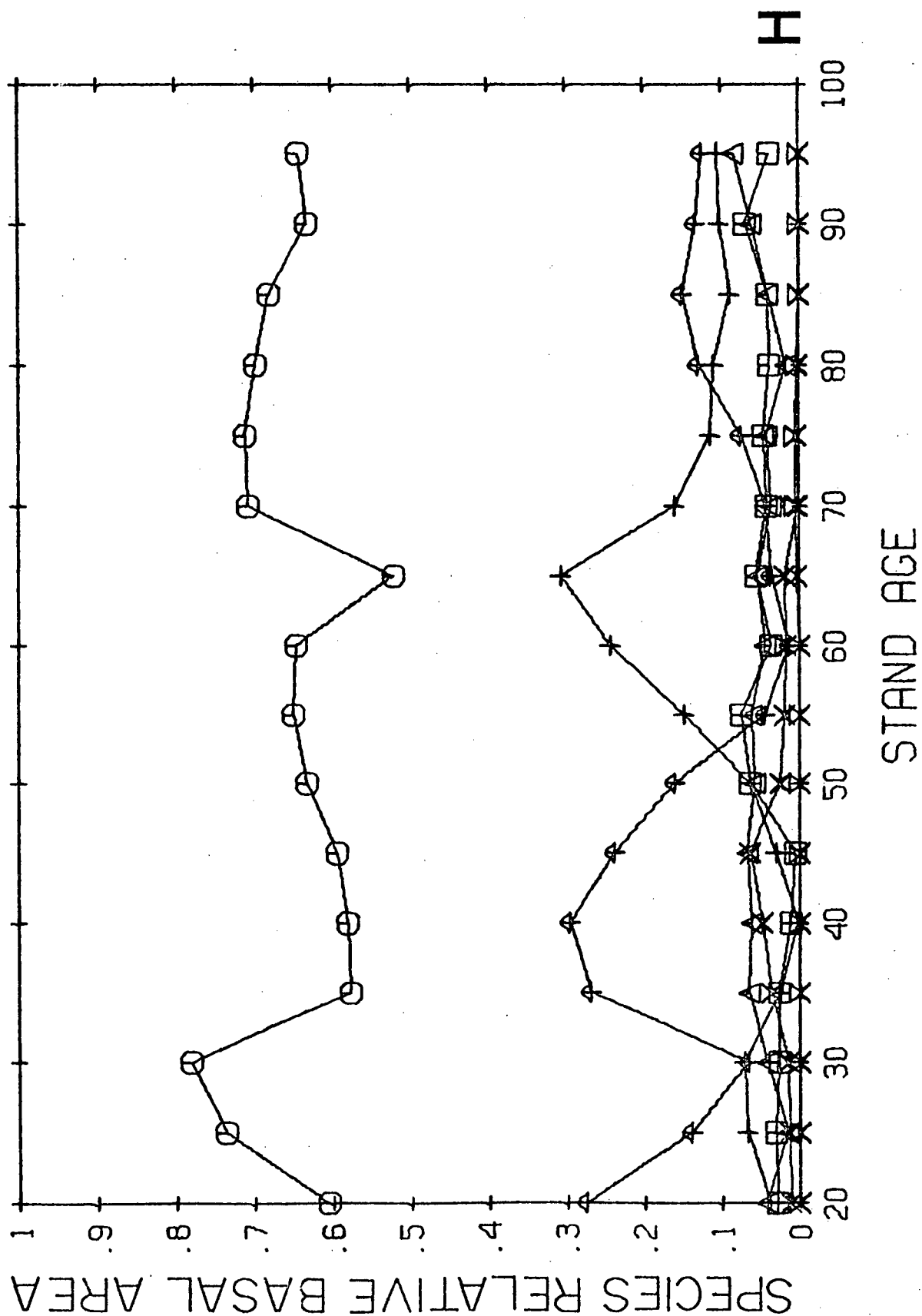
DRY WESTERN HEMLOCK



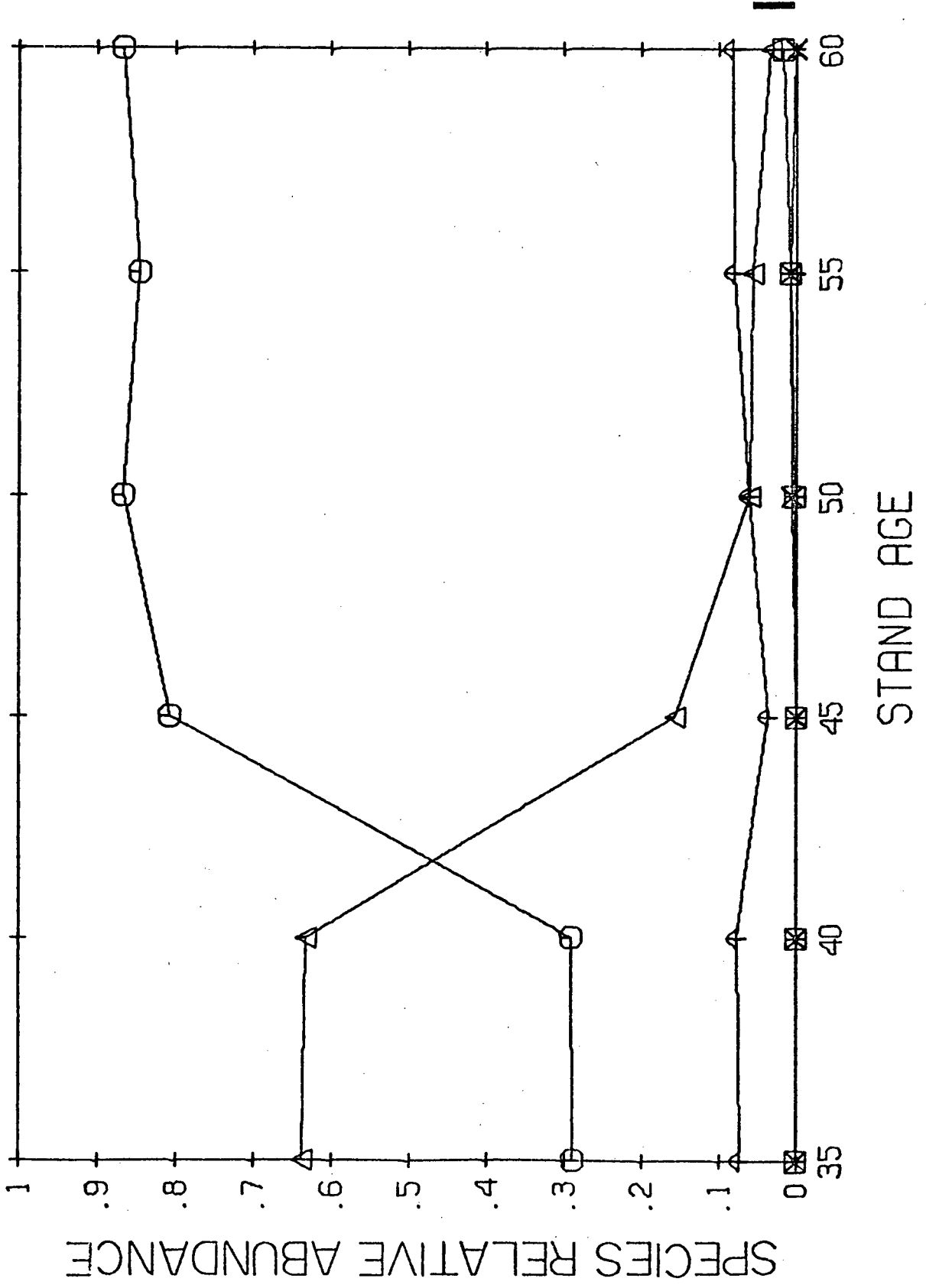
WET WESTERN HEMLOCK



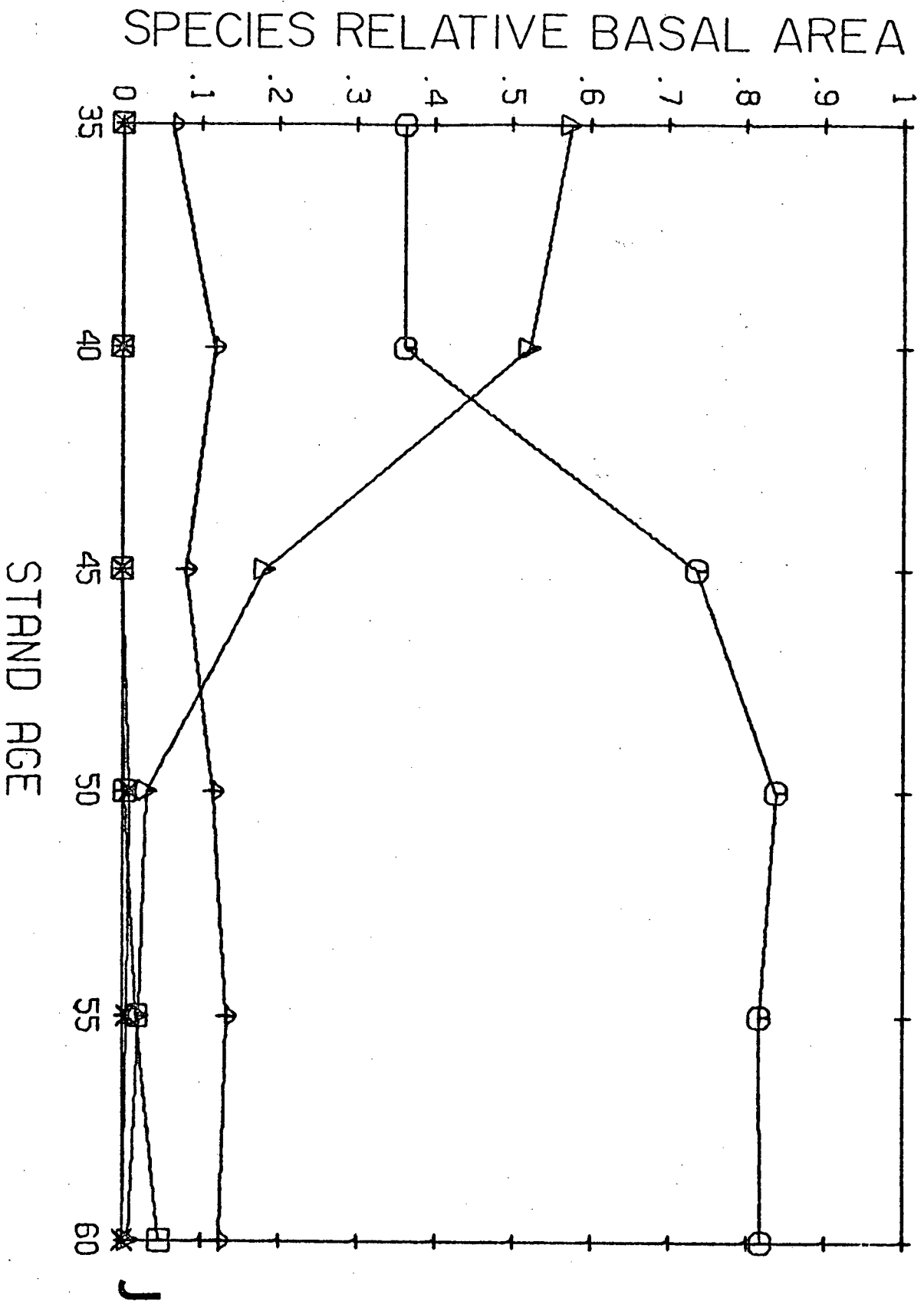
WET WESTERN HEMLOCK



FOG WESTERN HEMLOCK



FOG WESTERN HEMLOCK



increasing to reach 10% relative abundance by age 90. The recent work of Packee (1976) describes the succession from early invasion by herbs and shrubs up to the tree stratum climax. Although he gives no quantitative assessment, these results generally agree with his description. He recognizes the increase of T. plicata in the appropriate forest type, and he points out that Quercus garryana Dougl. and Arbutus menziesii Pursh. may be locally important. These last two species were extremely rare (< 1%) in the data set.

The Wet Douglas-fir Subzone is also the domain of P. menziesii, but T. heterophylla may locally be abundant at early stages, and T. plicata at later stages (Figures 6 C and D). The decline of P. menziesii after age 60 is exaggerated for reasons mentioned above. A. rubra invades early and tends to decrease, P. sitchensis, A. grandis, and A. macrophyllum are few. Packee (1976) contends that P. sitchensis is seral and suggests a climax of P. menziesii -- T. heterophylla and locally on the moister sites, T. plicata -- T. heterophylla -- A. grandis.

Western Hemlock Zone

T. heterophylla is generally more abundant in the Dry Western Hemlock Subzone, even though P. menziesii may reach a relative abundance of 0.68 (Figures 6 E and F). A. rubra is low and decreases fast, while T. plicata increases steadily. A. grandis and A. macrophyllum are barely perceptible. Packee (1976) recognizes that both A. rubra and P. menziesii are early invaders and he describes the climax as mainly P. menziesii (on dry sites) and T. heterophylla, with T. plicata locally.

In the Wet Western Hemlock Subzone, T. heterophylla is the most abundant, A. rubra and P. menziesii are not very abundant invaders, P. sitchensis is seral and A. amabilis may form a local climax with T. plicata and T. heterophylla (Figures 6 G and H). These results agree with packee's (1976) description, with the exception of P. sitchensis which he seems to place later in succession (although he gives no time scale).

The Fog Western Hemlock Subzone is not very well described by the data set, since there are only 19 observations, all between ages 35 and 60 (Figures I and J). It shows an early invasion by T. plicata, T. heterophylla, and P. sitchensis. After 45 years, T. heterophylla reaches a relative abundance of over 80%. P. menziesii and A. rubra show a relative abundance of about 1%. Packee (1976) assesses A. rubra as the main pioneer, followed by either P. sitchensis or P. sitchensis -- T. heterophylla (and occasionally P. menziesii), and a climax dominated by T. heterophylla, locally associated with T. plicata, A. amabilis, or P. sitchensis.

Plot type classification

The results of the classification described previously are presented for each subzone in Tables 5 to 9. The tables show the number of plots in each plot type, all the tree species accounting for 1% or more of the mean basal area, the mean basal area (and standard deviation) and the relative basal area for each species.

The Dry Douglas-fir Subzone is subdivided into four plot types (Table 5): Pm, Pm+, PmTp+, and PmTpTh+. In all plot types, P. menziesii

Plot Type	N	Species (>1% B.A.)	mean B.A. (s) (m ² /h)	mean E.A. (%)
<hr/>				
1) Fm	61	<u>P. menziesii</u>	41.6 (9.8)	99.2
2) Fm+	34	<u>P. menziesii</u>	23.4 (13.0)	64.6
		<u>P. contorta</u>	7.4 (11.9)	19.6
		<u>A. rubra</u>	4.2 (7.1)	14.0
3) FmTp+	23	<u>P. menziesii</u>	23.8 (9.2)	79.9
		<u>T. plicata</u>	3.7 (3.5)	10.8
		<u>A. rubra</u>	1.3 (2.4)	4.3
		<u>A. grandis</u>	0.3 (0.6)	1.8
		<u>T. heterophylla</u>	0.7 (0.9)	1.7
		<u>P. contorta</u>	0.7 (1.8)	1.4
4) FmTpTh+	7	<u>P. menziesii</u>	32.4 (14.6)	65.7
		<u>T. plicata</u>	10.8 (6.2)	21.3
		<u>T. heterophylla</u>	4.8 (2.3)	9.3
		<u>A. rubra</u>	1.6 (1.1)	3.8

TABLE 5

Forest plot types of the Dry Douglas-fir Subzone.

The mnemonics for the plot types are derived from the first letter of the genus and species of each species occurring in each observation with an abundance of at least 5% of the basal area for the observation. A plus sign (+) indicates that other species are present with an abundance of at least 1% of the basal area, but not necessarily in each observation. Values in brackets are the standard deviations of the basal area.

accounts for at least 65% of the basal area. P. contorta is typical of the Pm+ plot type, and T. plicata is typical of both PmTp+ and PmTpTh+ plot types. T. heterophylla is slightly abundant (9.3%) only in PmTpTh+. The Wet Douglas-fir Subzone has six plot types (Table 6): Pm+, PmTh+, PmTp+, PmThTp+, PmThAgTp+, and ThTp+. P. menziesii occurs in all but the last plot type, with at least 41% of the basal area in each. T. heterophylla with 20.5% to 56.5% of the basal area is a major species in four plot types and T. plicata accounts for at least 14% in the last four plot types.

There are six plot types in the Dry Western Hemlock Subzone (Table 7): Th+, PmTh, PmThAr+, PmThTp, ThTp+, and Pm+. P. menziesii is the most abundant species in four out of six plot types, with at least 51% in basal area, and T. heterophylla is the most abundant in the two other plot types, with a minimum of 75% in basal area. A. rubra and T. plicata are the only other two species which can qualify as major species. The Wet Western Hemlock Subzone is subdivided into seven plot types, the highest number of all subzones (Table 8). They are: Th, ThPs+, ThAa, ThTp+, ThPsTp+, ThTpPm+, and ThPm+. T. heterophylla is the predominating major species in all plot types, T. plicata is major in three, and P. menziesii and P. sitchensis in two. Only two plot types were found in the Fog Western Hemlock Subzone (Table 9): ThPs+ and ThTp+. There are only 19 observations in this subzone and this is insufficient to reveal its full diversity. T. heterophylla is by and large the most abundant in both plot types. P. sitchensis is also found in both. P. menziesii occurs in ThPs+ only, and T. plicata in ThTp+ only.

Plot Type	N	Species (>1% B.A.)	mean B.A. (s) (m ² /h)	mean B.A. (%)
<hr/>				
1) Pm+	110	<u>P. menziesii</u>	36.6 (11.3)	95.5
		<u>A. rubra</u>	1.2 (3.2)	3.1
2) PmTh+	57	<u>P. menziesii</u>	26.7 (13.1)	73.9
		<u>T. heterophylla</u>	8.3 (11.8)	20.5
		<u>A. rubra</u>	1.7 (4.5)	4.5
3) PmTp+	38	<u>P. menziesii</u>	28.4 (8.9)	73.3
		<u>T. plicata</u>	6.6 (6.6)	13.9
		<u>P. sitchensis</u>	2.6 (8.7)	3.6
		<u>A. grandis</u>	1.8 (6.4)	3.2
		<u>A. rubra</u>	1.4 (2.7)	2.6
		<u>A. macrophyllum</u>	1.1 (3.0)	2.2
		<u>T. heterophylla</u>	0.6 (0.8)	1.1
4) PmThTp+	61	<u>P. menziesii</u>	26.8 (17.6)	54.4
		<u>T. heterophylla</u>	12.6 (10.0)	27.1
		<u>T. plicata</u>	8.3 (8.5)	16.5
		<u>A. macrophyllum</u>	0.8 (2.8)	1.3
5) PmThAgTp+	16	<u>P. menziesii</u>	26.0 (17.5)	41.0
		<u>T. heterophylla</u>	11.7 (11.8)	21.5
		<u>A. grandis</u>	11.9 (8.4)	20.0
		<u>T. plicata</u>	8.4 (4.1)	16.5
		<u>A. macrophyllum</u>	0.8 (1.5)	1.2
6) ThTp+	27	<u>T. heterophylla</u>	22.8 (19.9)	56.5
		<u>T. plicata</u>	15.6 (16.7)	29.3
		<u>P. sitchensis</u>	7.2 (11.5)	10.9
		<u>A. rubra</u>	1.1 (1.7)	1.8

TABLE 6

Forest plot types of the Wet Douglas-fir Subzone.

See Table 5 for explanations.

Plot Type	N	Species (>1% B.A.)	mean E.A. (s) (m ² /h)	mean E.A. (%)
1) Th+	25	<u>T. heterophylla</u>	52.1 (11.6)	98.1
		<u>A. rubra</u>	0.5 (1.3)	1.0
2) PmTh	72	<u>P. menziesii</u>	24.6 (14.7)	61.6
		<u>T. heterophylla</u>	18.6 (17.3)	37.0
3) PmThAr+	27	<u>P. menziesii</u>	21.3 (13.5)	50.8
		<u>T. heterophylla</u>	17.1 (15.8)	35.1
		<u>A. rubra</u>	4.2 (3.7)	10.3
		<u>A. grandis</u>	1.1 (2.0)	3.2
4) PmThTp	48	<u>P. menziesii</u>	31.1 (18.9)	51.5
		<u>T. heterophylla</u>	17.6 (12.5)	32.4
		<u>T. plicata</u>	8.7 (6.0)	14.7
5) ThTp+	17	<u>T. heterophylla</u>	37.2 (10.2)	75.3
		<u>T. plicata</u>	10.6 (7.5)	21.6
		<u>A. rubra</u>	0.5 (1.2)	1.2
		<u>A. grandis</u>	0.8 (3.2)	1.2
6) Pm+	38	<u>P. menziesii</u>	30.7 (14.6)	92.2
		<u>A. rubra</u>	1.7 (4.5)	5.0
		<u>A. macrophyllum</u>	0.7 (2.5)	1.7
		<u>T. heterophylla</u>	0.4 (0.6)	1.1

TABLE 7

Forest plot types of the Dry Western Hemlock Subzone.

See Table 5 for explanations.

Plot Type	N	Species (>1% B.A.)	mean E.A. (s) (m ² /h)	mean B.A. (%)
<hr/>				
1) Th	70	<u>T. heterophylla</u>	61.6 (12.2)	97.7
2) ThPs+	56	<u>T. heterophylla</u>	34.5 (17.7)	52.5
		<u>P. sitchensis</u>	28.8 (20.7)	41.0
		<u>A. rubra</u>	3.4 (6.8)	5.7
3) ThAa	65	<u>T. heterophylla</u>	36.4 (21.4)	57.4
		<u>A. amabilis</u>	26.8 (21.0)	42.0
4) ThTp+	16	<u>T. heterophylla</u>	28.5 (16.0)	57.7
		<u>T. plicata</u>	21.2 (23.7)	31.4
		<u>A. amabilis</u>	6.1 (11.9)	10.5
5) ThPsTp+	32	<u>T. heterophylla</u>	23.7 (14.0)	38.2
		<u>P. sitchensis</u>	21.8 (19.4)	32.3
		<u>T. plicata</u>	12.4 (7.8)	21.2
		<u>A. rubra</u>	4.9 (4.9)	8.3
6) ThTpPm+	17	<u>T. heterophylla</u>	29.2 (13.2)	58.1
		<u>T. plicata</u>	9.7 (6.4)	20.8
		<u>P. menziesii</u>	9.2 (7.8)	17.2
		<u>A. rubra</u>	1.3 (2.1)	3.6
7) ThPm+	40	<u>T. heterophylla</u>	52.1 (14.7)	74.4
		<u>P. menziesii</u>	16.4 (12.5)	22.0
		<u>P. sitchensis</u>	1.0 (3.0)	1.5
		<u>T. plicata</u>	0.6 (1.0)	1.0

TABLE 8

Forest plot types of the Wet Western Hemlock Subzone.

See Table 5 for explanations.

Plot Type	N	Species (>1% B.A.)	mean B.A. (s) (m ² /h)	mean F.A. (%)
<hr/>				
1) ThPs+	12	<u>T. heterophylla</u>	60.9 (8.4)	83.2
		<u>P. sitchensis</u>	11.1 (7.9)	14.3
		<u>P. menziesii</u>	1.6 (4.9)	1.9
2) ThTp+	7	<u>T. heterophylla</u>	40.8 (24.7)	63.6
		<u>T. plicata</u>	16.8 (15.2)	29.4
		<u>P. sitchensis</u>	2.9 (4.5)	5.0
		<u>A. rubra</u>	1.1 (2.8)	1.7

TABLE 9

Forest plot types of the Fog Western Hemlock Subzone.

See Table 5 for explanations.

There is one important comment to make about this classification method. The major species were used to build its skeleton, since, by definition, these species occur in all observations. To avoid an infinite number of classes, minor species were grouped, and each one does not necessarily occur in each observation. For example, in the Dry Douglas-fir Subzone (see Table 5), the name of the second plot type, Pm†, indicates that each observation has to contain P. menziesii, and either P. contorta or A. rubra, or both. This, unfortunately, inflates the standard deviation of the minor species in Tables 5 to 9, but the advantage of a limited number of classes far outweighs this inconvenience. In any case, minor species account for, at most, only 5% of the total basal area.

Analysis of basal area growth variation

There are five species that occur in more than one plot type and in all plots in each case, within one or more subzones: P. menziesii, T. heterophylla, T. plicata, P. sitchensis, and A. amabilis. Since they are major species, i.e. they occur in all observations of the plot types where they are found, it is possible to study the variation of their basal area growth among various plot types as described previously. Different plot types are assumed to represent different competition regimes. Since minor species do not occur in all observations, analysis of variance can be performed only on the subset of plots in which they do occur. This explains the discrepancies in mean basal area for these species between the set of tables describing the plot types (Tables 5 to 9) and the set of tables of anova results (Tables 11, 13, 15, 17, and 19).

All data shown in this analysis represent means for all plots of a plot type, or overall means when indicated. The stand age is given in case it might be correlated with growth variables; a positive correlation with growth increment could override the treatment effect. Site indices are mentioned for P. menziesii and T. heterophylla, wherever both species occur; site index is used as a general indication of site productivity and could also override the effect of the treatment (plot type). Since the forest is immature, the five-year increment in basal area should be proportional to basal area, so a ratio of the five-year increment over basal area is also given (as a percentage). This percent five-year increment is the most critical variable, since it is independent of the abundance of the species, and is reasonably linear over the period of time considered in this study. A significant difference in the basal area itself among plot types would be indicative of the fitness of the species to each plot type. Finally the ratio (in percent) of the basal area increment of a species (DBA) over the total basal area (all species) indicates a rate of change of a species over the whole community.

The results of this analysis are discussed separately for each subzone. When there is a significant difference among treatments (plot types), the extremes are given, otherwise the overall mean is used. Where age attributes vary significantly, their correlation with basal area growth attributes is given, if relevant. It is assumed that significant differences in growth attributes are due to treatments, i.e. difference in competition regimes, only when there is no significant difference in age attributes or no significant correlation between age attributes and growth attributes.

Since minor species occur on fewer plot types than major species, and in fewer observations, very few significant differences among plot types were found for either their age attributes or growth attributes. For minor species, only results with some relevance to succession will be discussed.

Dry Douglas-fir Subzone

Major species (Table 10)

Four plot types constitute this subzone, and P. menziesii occurs in all of them (Table 5 and 10). Stand age ranges from 46.0 to 57.9 years, and P. menziesii site index has an overall mean of 25.9 m. The five-year basal area increment of P. menziesii shows no significant difference among plot types, its basal area shows a significant difference (23.4 - 41.6 m²/h); and the ratios of these two variables vary significantly from 6.4% to 14.6%. The percent rate of increase shows no significant correlation ($p = 0.05$) with age or with basal area. Assuming that the difference is due to the competition regime, the data show that the rate of increase (DBA) of P. menziesii is the smallest in the plot types (Pm, PmTp+) where P. menziesii is the most abundant species, and the greatest in the plot types (Pm+, PmTpTh+) where A. rubra shows its highest decrease. This suggests that P. menziesii growth is favoured by the opening of the forest when the mortality of A. rubra becomes high, after 40 or 50 years. As P. menziesii takes over A. rubra, P. contorta and T. plicata increase concurrently, thus preventing P. menziesii from being the absolute dominant, except in the Pm plot type.

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/Tot BA (%/5y)
<u>P. menziesii</u>								
1) Pm	46.0	26.6	-	2.0	41.6	6.4	41.9	6.3
2) Pm+	50.0	24.8	-	3.6	23.4	14.6	35.8	10.4
3) PmTp+	50.9	26.0	-	1.8	23.3	8.1	30.6	6.5
4) PmTpTh+	57.9	24.4	-	3.7	32.4	12.7	49.7	8.8
Overall	48.6	25.9	-	2.5	32.9	9.3	38.6	7.6
F-ratio	3.1	0.9	-	0.7	26.6	2.6	9.5	0.8
	**	NS	-	NS	***	*	***	NS
<u>T. plicata</u>								
1) PmTp+	50.9	26.0	-	1.2	3.7	53.6	30.6	4.4
2) PmTpTh+	57.9	24.4	-	2.8	10.8	29.1	49.7	5.9
Overall	52.5	25.6	-	1.6	5.4	47.9	35.0	4.7
F-ratio	1.4	0.5	-	9.0	15.2	1.5	9.4	0.7
	NS	NS	-	***	***	NS	***	NS

TABLE 10

One-way analysis of variance of the major species across different plot types of the Ery Douglas-fir Subzone.

Data represent means for all observations of a particular plot type. Characteristics of plot types are given in Table 5. Pm = P. menziesii. Th = T. heterophylla. 'SI 50' = site index at base age 50. 'DBA' = Delta BA = first difference in basal area between two observations at 5 years interval. 'BA' = basal area of the subject species. 'Total BA' = total basal area of all the species in each observation.

Probability levels are as follows: * = $p < 0.10$, ** = $p < 0.05$, *** = $p < 0.01$, NS = not significant.

T. plicata occurs in two plot types where stand age averages 52.5 years, and P. menziesii site index, 25.6 m. The five-year increment varies significantly ($1.2 - 2.8 \text{ m}^2/\text{h}/5\text{y}$), but is proportional to basal area ($3.7 - 10.8 \text{ m}^2/\text{h}$), and their ratios are not significantly different. The very high rate of increase of T. plicata ($47.9\%/5\text{y}$) indicates a gradual succession of T. plicata over P. menziesii, resulting in a transition from the Pm plot type to PmTp+. The same conclusion was reached in the stand-type succession data presented in the previous chapter. The graphs of species relative abundance across age (see Figures 6 A and B) show in fact that T. plicata increases at the detriment of P. menziesii. In some stands, the transition goes from Pm to Pm+ where P. contorta may reach a relative abundance of 20%. This trend is also in agreement with the succession data (previous chapter), and with the graph of species relative abundance across age (Figures 6 A and B).

Minor species (Table 11)

A. rubra shows a significant difference in rate of increase over total basal area ($-0.5 - 1.6\%/5\text{y}$) correlated with stand age ($r = -0.98$, $p = 0.1$). This fall in the relative basal area rate of increase confirms the pioneer role of A. rubra in the community. Its rate of increase relative to the community becomes negative ($-0.5\%/5\text{y}$) in PmTp+, where P. menziesii attains $6.5\%/5\text{y}$ and T. plicata, $4.4\%/5\text{y}$. P. contorta is found more abundantly in the plot type without T. plicata (Pm+) than in the one with this species (PmTp+). This suggests different basic requirements for these species, and Krajina (1969) points out that T. plicata prefers eutrophic soils and hygric conditions, whereas P. contorta cannot tolerate

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<u>A. rubra</u>								
1) Pm+	46.0	26.8	-	0.4	7.6	-5.1	34.7	1.6
2) PmTp+	61.1	29.5	-	-0.1	3.4	-2.7	37.8	-0.5
3) PmTpTh+	57.9	24.4	-	0.2	1.6	-6.6	49.7	0.3
Overall	52.3	27.0	-	0.2	5.3	-4.8	38.5	0.8
F-ratio	5.7 ***	1.8 NS	-	2.5 *	2.9 *	0.0 NS	3.7 **	2.7 *
<u>P. contorta</u>								
1) Pm+	55.0	21.9	-	0.6	14.8	7.4	36.8	1.4
2) PmTp+	68.8	30.5	-	-0.1	4.2	1.8	50.1	-0.1
Overall	57.6	23.5	-	0.4	12.8	6.3	39.3	1.1
F-ratio	3.6 *	8.4 ***	-	1.2 NS	2.5 NS	0.5 NS	7.0 **	1.0 NS
<u>T. heterophylla</u>								
1) PmTp+	55.0	27.7	-	-0.1	1.2	1.2	36.9	-0.1
2) PmTpTh+	57.9	24.4	-	-0.9	4.8	-9.5	49.7	-0.8
Overall	56.0	26.5	-	-0.4	2.4	-2.6	41.4	-0.3
F-ratio	0.2 NS	1.9 NS	-	1.1 NS	27.0 ***	0.3 NS	3.3 *	0.4 NS

TABLE 11

One-way analysis of variance of the minor species across different plot types of the Dry Douglas-fir Subzone.

Data represent means for all occurrences of the subject species in a given plot type. Characteristics of plot types are given in Table 5. For abbreviations, see Table 10.

eutrophic soils and requires drier conditions. T. heterophylla is analysed as a minor species here although it is a major one in the PmTpTh* plot type. No significant differences were found between the two plot types, except, of course, that T. heterophylla is more abundant in the plot type where it is a major species. Figures 6 A and B show a decreasing proportion of A. rubra basal area, previously observed in the succession data, and a low and stable relative abundance of P. contorta and T. heterophylla.

Wet Douglas-fir Subzone

Major species (Table 12)

P. menziesii is found in 5 out of 6 plot types within which stand age ranges from 40.9 to 71.3 years, P. menziesii site index averages 26.7 m., and T. heterophylla site index varies from 18.3 to 27.4 m. The five-year basal area increment has an overall mean of 2.3 m²/h/5y, basal area ranges from 26.0 to 36.5 m²/h, and the rate of increase shows no significant difference among plot types, with an overall mean of 10.6%/5y. In addition, the rate of basal area increase as a ratio of the whole community shows no significant difference. The situation is similar for T. heterophylla, but here basal area increment shows a significant difference (0.02 - 2.5 m²/h/5y) as well as the basal area (8.3 - 22.8 m²/h), yet their ratio is not significantly different and has an overall mean of 5.9%/5y. On the other hand, the ratio of basal area increment over total basal area is significant and T. heterophylla reaches the highest rate of increase in the ThTp* plot type, the only one where there is no P. menziesii, suggesting mutual site incompatibility.

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<u>P. menziesii</u>								
1) Pm+	46.0	26.6	-	2.5	36.5	9.1	38.4	8.4
2) PmTh+	40.9	27.5	23.9	2.4	26.7	13.5	37.1	8.8
3) PmTp+	57.0	25.2	18.3	2.6	28.4	10.5	42.4	7.3
4) PmThTp+	61.1	26.2	22.4	1.7	26.8	10.7	48.8	4.8
5) PmThAgTp+	71.3	29.5	27.4	1.9	26.0	9.4	59.1	3.3
Overall	51.1	26.7	23.4	2.3	30.8	10.6	42.1	7.3
F-ratio	16.9 ***	1.9 NS	4.2 ***	0.5 NS	8.6 ***	0.8 NS	11.8 ***	1.6 NS
<u>T. heterophylla</u>								
1) PmTh+	40.9	27.5	23.9	0.6	8.3	7.2	37.1	2.2
2) PmThTp+	61.1	26.2	22.4	0.02	12.6	3.2	48.8	1.1
3) PmThAgTp+	71.3	29.5	27.4	0.5	11.7	1.5	59.1	1.0
4) ThTp+	55.6	21.3	22.9	2.5	22.8	11.9	47.2	8.1
Overall	54.0	27.1	23.4	0.7	12.7	5.9	45.4	2.7
F-ratio	12.9 ***	1.5 NS	2.6 *	6.3 ***	7.8 ***	0.6 NS	8.2 ***	7.6 ***
<u>T. plicata</u>								
1) PmTp+	57.0	25.2	18.3	1.5	6.6	40.0	42.4	3.6
2) PmThTp+	61.1	26.2	22.4	1.2	8.3	22.8	48.8	3.3
3) PmThAgTp+	71.3	29.5	27.4	1.3	8.4	15.9	59.1	2.5
4) ThTp+	55.6	21.3	22.9	1.4	15.6	10.9	47.2	3.1
Overall	60.1	26.3	23.1	1.3	9.2	24.4	48.0	3.3
F-ratio	2.1 NS	2.0 NS	3.4 **	0.2 NS	4.9 ***	3.3 **	3.1 **	0.2 NS

TABLE 12

One-way analysis of variance of the major species across different plot types of the Wet Douglas-fir Subzone. Data represent means for all observations of a particular plot type. Characteristics of plot types are given in Table 6. For abbreviations, see Table 10.

T. plicata has a very significant difference in rate of growth among plot types, from 10.9 to 40.0%/5Y. Its lowest rate of increase is in the ThTp+ plot type, exactly where T. heterophylla exhibits its highest rate of increase. The highest rate of increase for T. plicata appears in the PmTp+ plot type, where P. menziesii is the most abundant among all plot types in which these two species coexist, and in which T. heterophylla is practically absent. Moreover, there is a significant correlation of 0.99 ($p = 0.05$) between the rate of increase of T. plicata and the relative abundance (% BA, Table 6), of P. menziesii in the 3 plot types where these species co-occur (PmTp+, PmThTp+, PmThAgTp+), and the rate of increase is consistently 2 to 4 times higher for T. plicata than for P. menziesii. These observations indicate that the conditions which favour P. menziesii do not favour T. heterophylla, and that T. plicata has some potential to succeed P. menziesii, at least locally, where T. heterophylla is infrequent. This can also be observed in the graph of the species relative abundance (see Figures 6 C and D), and this trend was revealed by the succession data of the previous chapter.

Minor Species (Table 13)

No significant differences were found in rates of increase of minor species. A. rubra deserves a comment. The stand age varies greatly among plot types, and is negatively correlated with the rate of increase in basal area ($r = -0.92$, $p = 0.1$). Although the difference in rate of increase in basal area is not significant, it is noteworthy that it shows successively an increase (5.6%/5Y) and then a decrease (-6.4%/5Y) with time. This suggests that the pioneer role of A. rubra observed in the

Plct Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<u>A. rubra</u>								
1) Pm+	42.4	28.6	- ¹	-0.05	4.6	6.2	39.4	0.4
2) PmTh+	38.6	31.4	29.0	0.5	6.9	5.6	40.3	1.4
3) PmTp+	70.8	29.1	18.3	-0.4	4.1	-10.7	49.5	-0.6
4) ThTp+	79.2	-	20.3	-0.2	2.5	-6.4	60.8	-0.5
Overall	53.5	29.4	22.5	-0.02	4.6	0.7	45.3.	0.3
F-ratio	23.1 ***	1.2 NS	7.0 ***	1.4 NS	1.9 NS	1.4 NS	7.5 ***	2.1 NS
<u>P. sitchensis</u>								
1) PmTp+	77.5	28.2	18.3	3.2	25.0	12.2	67.9	4.4
2) ThTp+	83.6	-	20.0	1.7	17.7	6.7	60.0	2.4
Overall	82.0	28.2	19.6	2.1	19.6	8.2	62.1	3.0
F-ratio	0.9 NS	- -	0.3 NS	1.0 NS	1.0 NS	0.7 NS	0.6 NS	0.9 NS
<u>A. grandis</u>								
1) PmTp+	65.0	31.0	-	0.7	11.5	7.8	51.8	1.2
2) PmThAgTp+	71.3	29.5	27.4	1.1	11.9	14.2	59.1	2.1
Overall	69.5	29.9	27.4	1.0	11.8	12.5	57.1	1.8
F-ratio	0.5 NS	0.3 NS	- -	1.4 NS	0.0 NS	1.4 NS	1.6 NS	1.7 NS

¹ Missing values for Fir or Hemlock Site Index are due to the absence of the species in the plot type.

Table 13...

(Cont'd)

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
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A. macrophyllum

1) PmTp+	65.6	29.7	-	0.4	5.0	10.0	49.4	0.8
2) PmTpTh+	69.1	25.8	23.7	0.1	4.7	29.0	48.2	0.5
3) PmThAgTp+	67.5	33.5	36.6	0.2	3.0	7.9	58.5	0.4
Overall	67.6	28.5	26.0	0.2	4.5	18.7	50.4	0.6
F-ratio	0.1 NS	3.9 **	22.7 ***	0.8 NS	0.2 NS	0.8 NS	0.4 NS	0.6 NS

TABLE 13

One-way analysis of variance of the minor species across different plot types of the Wet Douglas-fir Subzone.

Data represent means for all occurrences of the subject species in a given plot type. Characteristics of plot types are given in Table 6. For abbreviations, see Table 10.

Dry Douglas-fir Subzone is similar in the Wet Douglas-fir Subzone. The graph of species relative abundance agrees well with this view (Figures 6 C and D), and the succession data showed the same behaviour. P. sitchensis, A. grandis, and A. macrophyllum do not show significant difference in any of the growth variables.

Dry Western Hemlock Subzone

Major species (Table 14)

T. heterophylla is the most important species in this subzone and occurs in 5 out of 6 plot types. Stand age (37.8 - 67.6 y), P. menziesii site index (26.3 - 39.6 m), and T. heterophylla site index (24.3 - 28.0 m) are all significantly different. Basal area increment (0.9 - 4.3 m²/h/5y) and basal area (17.1 - 52.1 m²/h) also vary significantly, and are correlated ($r = 0.94$, $p = 0.05$), yet neither one shows any significant correlation with stand age, or site index. The percent rate of increase is highly significantly different among plot types, with the highest values in the two plot types where T. plicata is absent and P. menziesii present (PmTh, PmThAr+), and the smallest values where T. heterophylla is either forming pure stands (Th+) or where T. plicata is abundant (PmThTp, ThTp+). This indicates that P. menziesii does not offer much competition to T. heterophylla, and that T. heterophylla and T. plicata compete strongly with T. heterophylla.

All variables for P. menziesii are significantly different among plot types. The mean stand age goes from 33.2 to 67.6 years. The basal area increment is negatively correlated with stand age ($r = -0.96$, $p = 0.05$)

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<u>T. heterophylla</u>								
1) Th+	56.0	39.6	27.4	4.3	52.1	9.1	53.1	8.9
2) PmTh	45.4	30.6	25.5	2.2	18.6	21.9	43.9	6.4
3) PmThAr+	37.8	32.1	28.0	1.2	17.1	14.9	44.2	4.0
4) PmThTp	67.6	26.3	24.3	0.9	17.6	6.2	58.2	2.2
5) ThTp+	49.7	27.4	26.9	3.0	37.2	9.3	49.4	6.8
Overall	51.7	29.6	26.0	2.1	24.2	14.1	49.3	5.3
F-ratio	9.6 ***	6.9 ***	2.9 **	11.2 ***	32.2 ***	6.8 ***	5.0 ***	5.4 ***
<u>P. menziesii</u>								
1) PmTh	45.4	30.6	25.5	3.3	24.6	20.1	43.9	13.2
2) PmThAr+	37.8	32.1	28.0	3.6	21.3	21.3	44.2	11.2
3) PmThTp	67.6	26.3	24.3	1.2	31.1	7.3	58.2	2.6
4) Pm+	33.2	27.2	-	5.2	30.7	22.3	33.5	20.9
Overall	47.5	29.0	25.5	3.2	27.1	17.4	45.5	11.7
F-ratio	18.8 ***	10.0 ***	3.7 **	6.5 ***	3.5 **	7.4 ***	12.0 ***	15.1 ***
<u>T. plicata</u>								
1) PmThTp	67.6	26.3	24.3	0.8	8.7	12.1	58.2	1.8
2) ThTp+	49.7	27.4	26.9	1.0	10.6	9.5	49.4	2.2
Overall	62.9	26.3	25.2	0.8	9.2	11.4	55.9	1.9
F-ratio	8.7 ***	0.0 NS	0.2 NS	0.3 NS	1.2 NS	0.3 NS	4.1 **	0.3 NS

TABLE 14

One-way analysis of variance of the major species across different plot types of the Dry Western Hemlock Subzone.

Data represent means for all observations of a particular plot type. Characteristics of plot types are given in Table 7. For abbreviations, see Table 10.

and shows its lowest value ($1.2 \text{ m}^2/\text{h}/5\text{y}$) in the oldest plot type (PmThTp). The percent rate of increase is also the lowest in the oldest plot type. However, this plot type (PmThTp) is also the only P. menziesii plot type with a large proportion of T. plicata (14.7%), and T. plicata is at its best rate of increase ($12.1\%/5\text{y}$). It seems apparent in the older plots that the conditions favour a rapid basal area growth for T. plicata reflecting both a large diameter increment and good regeneration of this species, while P. menziesii grows much slower than in other plot types. The consequences can be seen on the graph of species relative abundance for the Dry Western Hemlock Subzone (Figures 6 E and F).

Minor species (Table 15)

A. rubra and A. grandis are minor species in the Dry Western Hemlock Subzone (Table 15). Both basal area and basal area increment over basal area are significantly different for A. rubra. Even though stand age is not significantly different among plot types, there is a significant negative correlation between stand age and basal area ($r = -0.97$, $p = 0.05$). Moreover, the two oldest plot types show a very high mortality for A. rubra indicated by a rate of increase of $-31.6\%/5\text{Y}$ in the Th+ plot type, and $-73.4\%/5\text{y}$ in the PmTp+. This again reflects the pioneer behaviour of A. rubra whose relative abundance is decreasing constantly when plotted against age (Figures 6 E and F), as previously shown in the stand-type succession data. A. grandis covers a very small basal area in the PmThAr+ plot type ($2.5 \text{ m}^2/\text{h}$), and slightly more in PmTp+ ($6.6 \text{ m}^2/\text{h}$); this difference is not significant.

Plct Type	Stand Age (years)	Fm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
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A. rubra

1) Th+	50.0	-	29.7	-0.8	3.0	-31.6	55.3	-1.7
2) PmThAr+	38.3	32.3	28.0	-0.1	4.9	4.9	44.1	0.8
3) ThTp+	51.3	27.4	26.7	-1.0	2.1	-73.4	46.7	-2.4
4) Pm+	24.0	33.5	-	0.6	12.9	4.0	34.5	1.9
Overall	39.0	32.4	28.0	-0.2	5.5	-8.0	44.3	0.3
F-ratio	1.9 NS	1.0 NS	0.5 NS	0.9 NS	12.1 ***	6.8 ***	1.4 NS	1.5 NS

A. grandis

1) PmThAr+	49.2	29.1	27.8	0.5	2.5	14.6	49.2	2.0
2) PmTp+	50.0	-	30.5	0.7	6.6	5.3	61.6	1.1
Overall	49.3	29.1	28.3	0.5	3.0	13.3	51.0	1.8
F-ratio	0.0 NS	- -	0.7 ***	0.1 NS	2.4 NS	0.4 NS	0.6 NS	0.2 NS

TABLE 15

One-way analysis of variance of the minor species across different plot types of the Dry Western Hemlock Subzone.

Data represent means for all occurrences of the subject species in a given plct type. Characteristics of plot types are given in Table 7. For abbreviations, see Table 10.

Wet Western Hemlock Subzone

Major species (Table 16)

T. heterophylla is found in all of the 7 plot types, and accounts for well over half the total basal area, except in ThPsTp+ where it is only 38.2% (Table 8). The stand age varies from 42.8 to 60.6 years, and the T. heterophylla site index, from 21.5 to 29.9 m. The only correlation worth mentioning indicates a slowly diminishing percent rate of increase with stand age ($r = -0.70$, $p = 0.1$). T. heterophylla basal area increment as a ratio of total basal area has an overall mean of 4.8%/5y, but as a ratio of T. heterophylla basal area, it varies among plot types. It has its highest rate of increase (13.7%/5y) in the ThPs+ plot type, where P. sitchensis also reaches its highest value. This high rate of increase for both species is probably due to the youth of this plot type, and to high fitness to site conditions, but it might also reveal a lack of intense competition between T. heterophylla and P. sitchensis. Among 5 plot types, Th, ThAa, ThTp+, ThPsTp+, and ThTpPm+, the rate of increase of T. heterophylla is very stable (circa 7.5%/5y), the lowest rate of increase (3.5%/5y) is found in the ThPm+ plot type, where P. menziesii is the most abundant. This indicates either mutual site incompatibility or strong competition between these two species, and this hypothesis is reinforced by the observation that P. menziesii shows its lowest rate of increase (3.0%/5y) in this same plot type, and its highest (14.2%/5y) in the ThTpPm+, where T. heterophylla is significantly less abundant (see Table 8).

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<u>T. heterophylla</u>								
1) Th	54.6	-	29.0	3.2	61.6	6.1	63.0	6.0
2) ThPs+	42.8	-	28.3	3.0	34.5	13.7	67.2	6.4
3) ThAa	57.1	-	26.5	2.7	36.4	7.3	63.5	5.0
4) ThTp+	60.6	-	21.5	1.3	28.5	7.9	56.0	3.6
5) ThPsTp+	43.3	-	26.1	1.6	23.6	8.6	62.9	2.7
6) ThTpPm+	47.6	-	29.9	1.6	29.2	7.4	49.4	4.4
7) ThPm+	59.3	-	29.8	1.6	52.1	3.5	70.8	2.2
Overall	52.2	-	27.7	2.5	41.9	7.9	63.8	4.8
F-ratio	6.2 ***	-	7.3 ***	2.0 *	32.4 ***	2.6 **	3.6 ***	1.7 NS
<u>T. plicata</u>								
1) ThTp+	60.6	-	21.5	0.8	21.2	10.5	56.0	2.3
2) ThPsTp+	43.3	-	26.1	1.7	12.4	12.4	62.8	3.3
3) ThTpPm+	47.6	-	29.9	0.6	9.7	2.6	49.5	1.4
Overall	48.7	-	26.0	1.2	13.8	9.4	57.7	2.6
F-ratio	5.4 ***	-	8.6 ***	3.6 **	3.5 **	3.5 **	2.1 NS	1.5 NS
<u>P. menziesii</u>								
1) ThTpPm+	47.6	-	29.9	1.1	9.2	14.2	49.5	2.2
2) ThPm+	59.3	-	29.8	0.5	16.4	3.0	70.7	0.7
Overall	55.8	-	29.8	0.6	14.2	6.4	64.4	1.2
F-ratio	3.5 *	-	0.0 NS	1.2 NS	4.8 **	3.8 *	26.8 ***	3.4 *

Table 16...

(Cont'd)

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<hr/>								
<i>P. sitchensis</i>								
1) ThPs+	42.8	-	28.4	3.9	28.8	17.9	67.2	6.9
2) ThPsTp+	43.3	-	26.1	3.3	21.8	15.3	62.8	5.1
Overall	43.0	-	27.5	3.6	26.3	17.0	65.6	6.3
F-ratio	0.0	-	4.6	0.7	2.4	0.9	0.9	1.2
	NS	-	**	NS	NS	NS	NS	NS

TABLE 16

One-way analysis of variance of the major species across different plot types of the Wet Western Hemlock Subzone.

Data represent means for all observations of a particular plot type. Characteristics of plot types are given in Table 8. For abbreviations, see Table 10.

T. plicata occurs as a major species in 3 plot types, where stand age goes from 43.3 to 60.6 years, and T. heterophylla site index, from 21.5 to 29.9 m. Basal area rate of increase, basal area, and percent rate of increase all vary significantly among plot types. There is no significant correlation between any of these variables. Total basal area and T. plicata increment over total basal area do not vary significantly. The lowest basal area rate of increase (2.6%/5y) for T. plicata is found in the ThTpPm+ plot type, the only plot type where P. menziesii coexists with T. plicata, and where P. menziesii achieves its best rate of increase (14.2%/5y). This can be interpreted as a superior competitive ability of P. menziesii over T. plicata in this plot type, or by better response of P. menziesii to the site conditions. P. sitchensis is found in two plot types, but none of the growth variables reflect any significant difference.

There is a strong predominance of T. heterophylla over all plot types. T. heterophylla can either form the climax by itself or by association with A. amabilis or T. plicata. This is also what is suggested by the graph of species relative abundance against stand age (Figures 6 G and H), where T. heterophylla accounts for 60 to 70% of the total basal area at all ages. P. sitchensis and A. amabilis fluctuate around the 15% level, and P. menziesii, T. plicata and A. rubra, around the 5% level. The succession data of the previous chapter showed much the same, with emphasis on the possibility of A. amabilis taking over the low frequency stand-types at older stand ages.

Minor species (Table 17)

A. rubra appears again as a minor species, and its basal area and basal area increment display no significant difference among plot types. Although its basal area is slightly larger in older plot types, its rate of increase becomes negative (-2.1%/5y), and A. rubra is deemed to be outcompeted by seral and climax species, as in all previously considered subzones. Its behaviour is shown in Figures 6 G and H. A. amabilis is a major species in ThAa, but a minor one in ThTp+; for this reason it is discussed as a minor species. Only the T. heterophylla site index shows a significant difference between the two plot types, but no significant correlation with other variables can be established. It was found that A. amabilis occupies 42.0% of the total basal area in the ThAa plot type (Table 8), and constitutes a climax with T. heterophylla. Packee (1976) points out that A. amabilis will become a climax dominant in the colder portion of the subzone, provided no major disturbance occurs, but will be of lesser importance in more maritime (lower elevation) portions of the subzone.

Fog Western Hemlock Subzone

Major species (Table 18)

T. heterophylla is the only species found in all observations. All variables show significant differences between the two plot types, but there are too few observations to detect any significant correlations. T. heterophylla has a rate of increase of 0.3%/5y in the ThPs+ plot type, and 12.8%/5y in the ThTp+ plot type. This indicates that T. heterophylla

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<u>A. rubra</u>								
1) ThPs+	46.0	-	27.9	0.3	9.1	-2.1	67.9	0.7
2) ThPsTp+	40.0	-	25.6	0.6	7.9	6.7	60.1	1.2
3) ThTpPm+	26.7	-	35.1	0.6	3.7	14.9	40.8	1.7
Overall	41.0	-	27.8	0.5	7.9	3.8	61.1	1.0
F-ratio	10.2 ***	-	10.5 ***	0.5 NS	1.6 NS	2.4 NS	8.7 ***	0.8 NS
<u>A. amabilis</u>								
1) ThAa	57.1	-	26.4	2.1	26.8	9.2	63.5	3.6
2) ThTp+	53.3	-	19.8	1.4	16.3	12.8	69.2	4.0
Overall	56.8	-	25.9	2.1	25.9	9.5	64.0	3.6
F-ratio	0.2 NS	-	7.0 ***	0.7 NS	1.4 NS	1.1 NS	0.3 NS	0.1 NS

TABLE 17

One-way analysis of variance of the minor species across different plot types of the Wet Western Hemlock Subzone.

Data represent means for all occurrences of the subject species in a given plot type. Characteristics of plot types are given in Table 8. For abbreviations, see Table 10.

Plct Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DBA/ Tot BA (%/5y)
<hr/>								
1) ThPs+	51.7	-	36.3	0.2	60.9	0.3	74.0	0.3
2) ThTp+	43.6	-	29.2	3.3	40.8	12.8	61.8	5.6
Overall	48.7	-	33.7	1.3	53.5	4.9	69.5	2.2
F-ratio	12.2 ***	-	20.0 ***	13.6 ***	6.8 **	18.0 ***	8.0 **	16.1 ***

TABLE 18

One-way analysis of variance of major species on different plot types of the Fog Western Hemlock Subzone.

Data represent means for all observations of a particular plot type. Characteristics of plot types are given in Table 9. For abbreviations, see Table 10.

might outcompete T. plicata, and P. sitchensis might later interfere with the progression of T. heterophylla. Since T. plicata was found only in the ThTp+ plot type, it is impossible to compare its performance, but the graph of species relative abundance (Figure 6) indicates that the high rate of increase of T. heterophylla allows it to overtake T. plicata later. T. plicata then falls to the level of 10% relative abundance (Figures 6 I and J), and P. sitchensis increases slightly to reach a level under 10%. P. menziesii and A. rubra are merely traces (<2%). The stand-type data showed that in fact P. sitchensis was never abundant enough to constitute a stand-type and that T. heterophylla overtakes T. plicata by age 45. In the previous chapter, the unlikeliness of the rarity of T. plicata was discussed and was attributed to insufficient sampling in this subzone. The role of major climax species as stated by Packee (1976) was agreed upon.

Minor species (Table 19)

P. sitchensis is considered a minor species for the same reason given for A. amabilis in the Wet Western Hemlock Subzone. Its basal area is significantly larger in ThPs+ where it is a major species, 13.3 m²/h, against 5.1 m²/h in ThTp+ where it is a minor species. However, its rate of increase is smaller, though not significantly in the ThPs+ plot type, where T. heterophylla is more abundant. This reflects antagonism between T. heterophylla and P. sitchensis. Figures 6 I and J indicate that the proportion of its basal area over all the plots of the subzone fluctuates very little around the 10% level. The stand-type data showed that P. sitchensis was never the most abundant species in

Plot Type	Stand Age (years)	Pm SI 50 (m)	Th SI 50 (m)	DBA (m ² /h/5y)	BA (m ² /h)	DBA/BA (%/5y)	Total BA (m ² /h)	DEA/ Tot BA (%/5y)
<hr/>								
<i>P. sitchensis</i>								
1) ThPs+	52.0	-	36.9	0.8	13.3	6.0	75.7	1.0
2) ThTp+	40.0	-	31.2	1.0	5.1	11.7	60.4	1.7
Overall	48.6	-	35.3	0.8	10.9	7.6	71.3	1.2
F-ratio	23.5 ***	-	10.0 ***	0.1 NS	5.0 **	2.2 NS	8.4 **	0.8 NS

TABLE 19

One-way analysis of variance of the minor species across different plot types of the Fog Western Hemlock Subzone.

Data represent means for all occurrences of the subject species in a given plot type. Characteristics of plot types are given in Table 9. For abbreviations, see Table 10.

any stand.

Site index variation

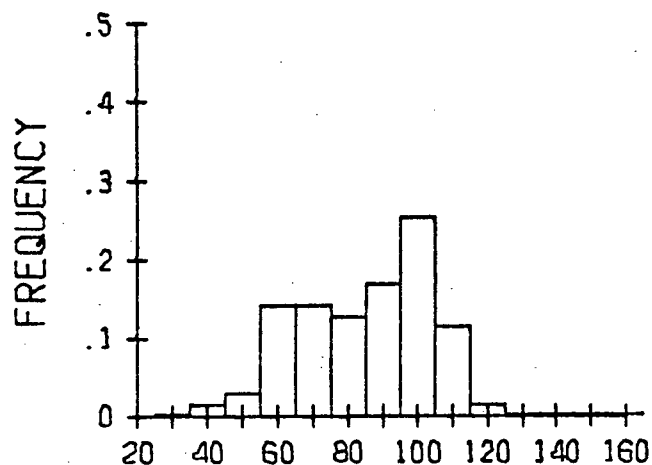
Site index variation was never significantly correlated with basal area growth. Although site index of even-aged stands is considered an expression of site quality (Curtis et al. 1974), its evaluation takes only age and height into account. The absence of correlation between site index and basal area growth does not invalidate site index as a measure of site productivity since height is as important as basal area in the computation of productivity. It seems rather to suggest, as is generally accepted, that basal area growth and height growth are controlled by different site factors. Perhaps height growth is more sensitive to physico-chemical site factors while basal area growth is more sensitive to biotic factors such as composition and density of vegetation.

The distribution of site indices in 10 feet (3.03 m) classes, at age 50, are given per subzone, for P. menziesii and T. heterophylla (Figure 7 and 8), and the subzone means and standard deviations are listed (Table 20). There is a significant difference ($p = 0.01$) among the subzone means for P. menziesii and T. heterophylla site indices, showing an increase in site index from the driest to the moistest subzone. Packee (1976) demonstrated that the mean annual moisture deficit with 200 mm of soil water storage capacity was the most suitable variable for differentiating subzones. Moisture deficit (Table 20) has a significant correlation with P. menziesii site index ($r = 0.95$, $p = 0.05$), and with T. heterophylla site index ($r = 0.82$, $p = 0.1$). This strongly

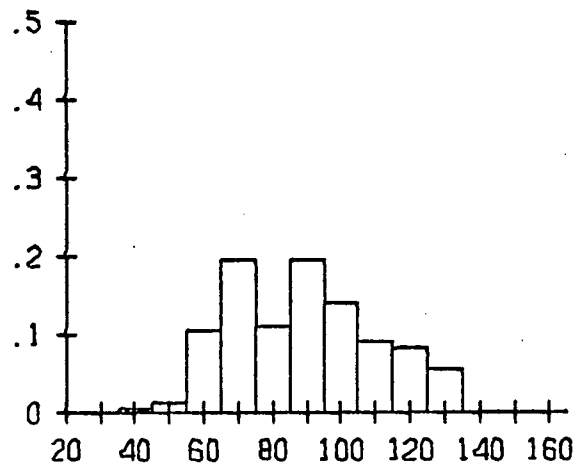
FIGURE 7

Site index distribution per 10 feet (3.03 m) classes for P. menziesii at age 50. The computation is based on a regression curve developed by MacMillan Bloedel Limited (1975 Internal Report).

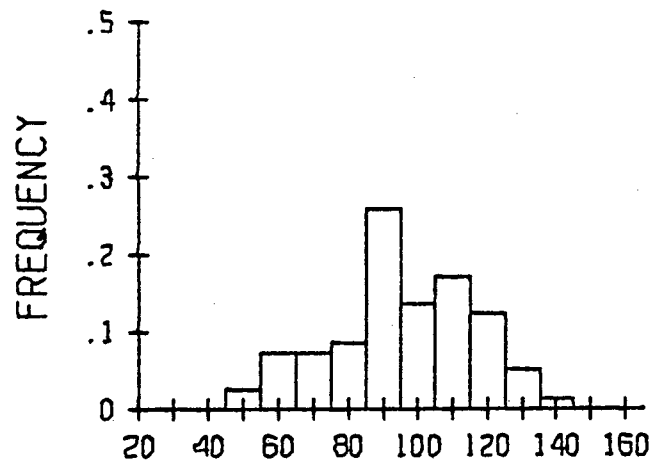
DRY DOUGLAS-FIR



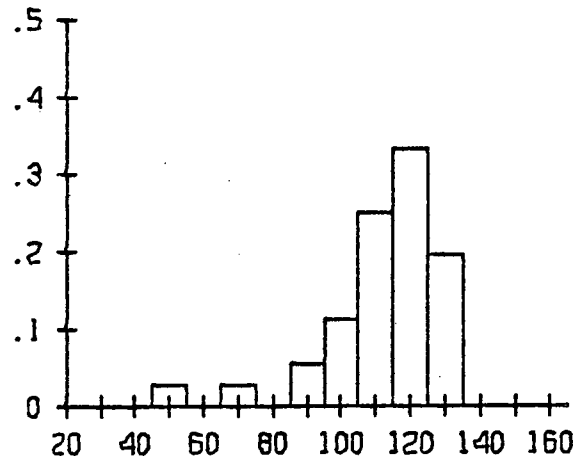
WET DOUGLAS-FIR



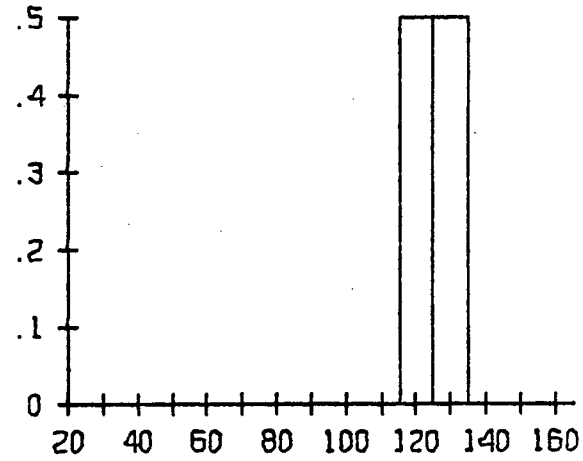
DRY WESTERN HEMLOCK



WET WESTERN HEMLOCK



FOG WESTERN HEMLOCK

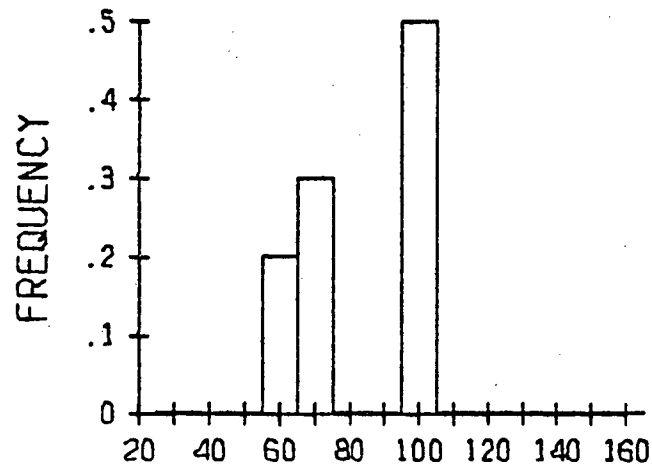


P. menziesii SITE INDEX (50)

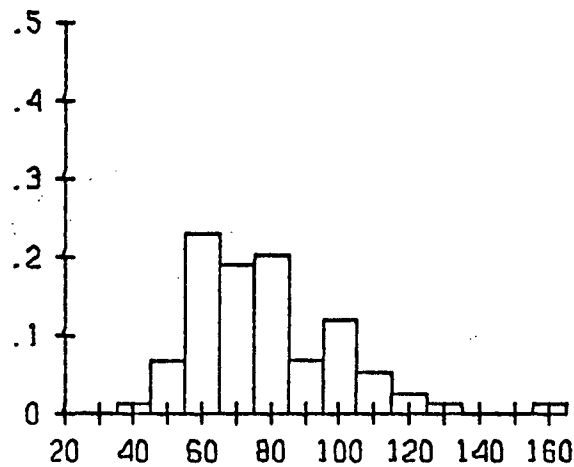
FIGURE 8

Site index distribution per 10 feet (3.03 m) classes for T. heterophylla at age 50. The computation is based on a regression curve developed by MacMillan Bloedel Limited (1975 Internal Report).

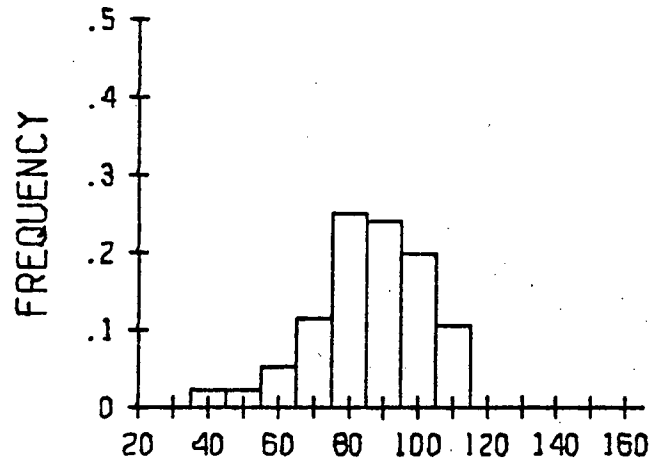
DRY DOUGLAS-FIR



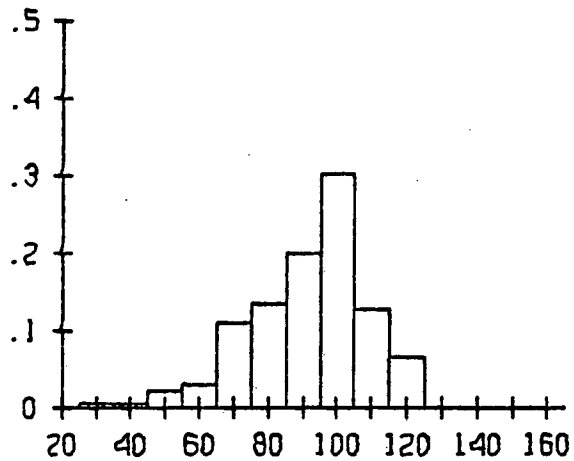
WET DOUGLAS-FIR



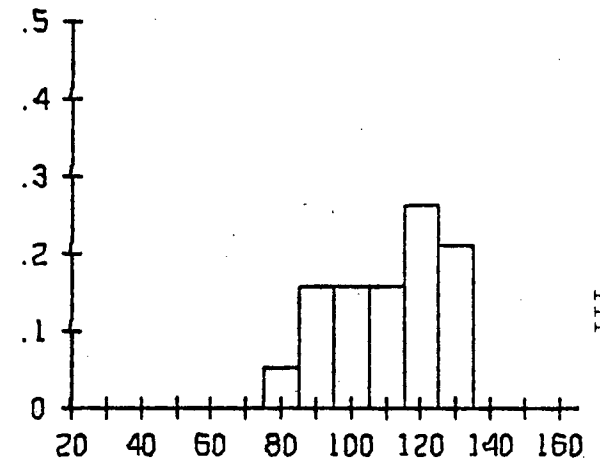
DRY WESTERN HEMLOCK



WET WESTERN HEMLOCK



FOG WESTERN HEMLOCK



T. heterophylla SITE INDEX (50)

SUBZONE	Pm SITE INDEX			Th SITE INDEX			MD
	n	mean	s	n	mean	s	mean
		(m)			(m)		(mm)
<hr/>							
Dry Douglas-fir Subzone	71	25.9	(5.6)	10	25.3	(5.6)	134
Wet Douglas-fir Subzone	143	27.1	(6.4)	74	23.9	(6.6)	93
Dry Western Hemlock Subzone	82	29.1	(6.2)	96	26.2	(4.8)	62
Wet Western Hemlock Subzone	36	34.2	(5.2)	229	28.0	(5.0)	27
Fog Western Hemlock Subzone	2	38.1	(2.2)	19	33.7	(4.8)	4

TABLE 20

Mean site indices and mean annual moisture deficit per subzone.

Site indices for P. menziesii and T. heterophylla at age 50 (MacMillan Bloedel Limited 1975 Internal Report). MD is the mean annual moisture deficit with 200 mm of soil water storage capacity (Packee 1976). Values in brackets are the standard deviations of site indices.

suggests that moisture availability is one of the main determinants in height growth for P. menziesii and T. heterophylla, and likely for the other species in this analysis.

CONCLUSION

Biogeoclimatic Subzones can be objectively subdivided into plot types which are statistically defined on the basis of present canopy vegetation. Differences in plot types are assumed to modify the dynamics of competition and the basal area growth performance of species. Quantitative differences among plot types were found in the rate of basal area growth of species which cannot be solely attributed to site index as a measure of productivity nor to site age. Results of analysis of variance are particularly conclusive for the major species, P. menziesii, T. heterophylla, T. plicata, and P. sitchensis, and for two minor species, P. contorta and A. rubra. No significant effect of P. menziesii and T. heterophylla site index on basal area growth could be detected at the plot level. Significant differences in site index appear at the subzone level and seem to reflect the soil moisture regime.

Biotic and abiotic site factors vary greatly within one Biogeoclimatic Subzone. The data did not allow testing for exact site factors that favor the growth of a species while inhibiting the growth of another. At early stages of secondary succession, species invasion and particularly, species establishment are controlled by abiotic site conditions.

Later on, tree composition creates a situation where species, just because they grow, have to compete for resources. Therefore, tree composition is an image of both abiotic site factors allowing or not the presence of various species, and biotic components allowing or not their coexistence. The inferences on succession drawn from these results agree with the species relative abundance observed throughout the rotation period and with the stand-type succession data of the previous chapter. Moreover, species performance might vary from one Biogeoclimatic Subzone to another, within similar plot types. The presence of P. menziesii in the Wet Douglas-fir Subzone, for instance, seems to correspond with a poor growth of T. heterophylla. No such observation was made in the Dry Western Hemlock Subzone, whereas the opposite for T. heterophylla was found in the Wet Western Hemlock Subzone. The relationships between these results suggest that the overall forest succession observed and modelled at the subzone level is partly due to the dynamics of interspecies competition observed at the plot level.

This study has brought forward some evidence that basal area growth of a species varies according to tree composition as characterized by plot types. It was not meant to assess the relative contribution of the variation due to abiotic factors with that due to competition; however, it is very likely that both are equally important.

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Analysis and modelling of interspecies competition
during forest secondary succession.

Pierre Bellefleur

CHAPTER III

The relationships between multi-species competition
and single tree replacement.

ABSTRACT

The effect of interspecies competition was examined on a single tree basis. The data consisted of over 2,000 observations from 12 Permanent Sample Plots where the coordinates of each tree were known. Indices of competition representing horizontal and vertical forest structure were computed for each tree. Regression models of yearly diameter increment were built to evaluate the contribution of diameter, age, site index, subzone location, several competition indices and interactions of some of these terms, for P. menziesii, T. plicata, and T. heterophylla. The most significant variables affecting tree growth, mortality, and regeneration, were determined by analysis of variance.

The results of the regression models showed that estimates based on present site conditions were significant only when used alone, without variables indicative of the past history of the tree. It was found that the relationship between the competition regime and the present state of a tree seems to be cause and effect applied over the entire life-span of the tree. The most powerful indicators of the impact of competition were found in the tree itself, and were evaluated by its diameter and long-term diameter increment in comparison with the whole population. Mortality and regeneration of each species were found to vary through time in response to the immediate neighborhood of the individual tree; this seems to be the mechanism which generates succession at the population level.

RÉSUMÉ

On a examiné l'effet de la compétition interspécifique au niveau de l'arbre. Les données forment plus de 2,000 observations provenant de 12 parcelles permanentes où l'on connaît les coordonnées de chaque tige. On a calculé des indices de compétition tenant compte de la structure horizontale et verticale de la forêt pour chaque arbre. On a construit des modèles de régression de l'accroissement annuel en diamètre pour évaluer la contribution du diamètre, de l'âge, de l'indice de site, de la location de la sous-zone, de plusieurs indices de compétition et des interactions de quelques-uns de ces termes pour P. menziesii, T. plicata et T. heterophylla. On a déterminé les variables les plus significatives pour la croissance, la mortalité et la régénération par analyse de variance.

Les résultats des modèles de régression ont montré que les prédictions basées sur les conditions actuelles du site sont significatives seulement si utilisées seules, sans l'inclusion de variables reflétant le passé de l'arbre. On a trouvé que la relation entre le régime de compétition et l'état actuel de l'arbre en est une de cause à effet durant la vie entière de l'arbre. C'est dans l'arbre lui-même que l'on a trouvé les meilleures indications de l'impact de la compétition qui est révélé par son diamètre et son accroissement en diamètre en comparaison de la population. On a trouvé que la mortalité et la régénération de chaque espèce varient selon le voisinage immédiat de chaque arbre; il semble que ce soit là le mécanisme qui engendre la succession au niveau de la population.

INTRODUCTION

The effect of interspecies competition on succession is often taken for granted, on the basis of biological common sense (Dansereau 1957, Horn 1974), and many conclusions about its importance are based on speculation (Miller 1967). The lack of knowledge about interspecies competition obscures the mechanisms which lead to the inhibition of growth as population density increases (Stewart and Levin 1973). Competition, as a process of plant population dynamics, has been concealed by more obvious processes, like succession, and has therefore been neglected by investigators (Pickett 1976). Fluctuations in population density should be explained by processes acting at the community level (Decker 1959). The attempt to elucidate the mechanism of succession at the physiological level of the plant represents a step below the population level and leaves partly unexplained the events observed in the community.

The importance of interspecies competition in population dynamics has been stressed by many investigators, yet statistical evidence is lacking to confirm the hypothesis of underlying mechanisms by which competition would lead to succession. This hypothesis requires a demonstrated modification of the response of an individual plant to the presence of different competitors in its immediate neighborhood. Moreover, it should be shown that particular combinations of plants can inhibit the growth of a specific plant and induce its mortality.

This chapter attempts to test the following hypotheses for a forest community of Coastal British Columbia. (1) The growth, the suppression,

and the regeneration of a single tree are related to the forest composition in its immediate neighborhood. (2) The decrease in rate of growth of a tree is progressive and can be used to predict its mortality. (3) The relationship between rate of growth and forest composition is species-specific. (4) The replacement of dead trees by trees of the same or different species can be predicted by the neighborhood composition. (5) Dead trees are frequently replaced by trees of other species and this mechanism generates the succession observed at the level of the forest stand.

DESCRIPTION OF THE DATA

The data consists of a set of 12 Permanent Sample Plots from the data bank of MacMillan Bloedel Limited, Forestry Division. The plots belong to the four major Biogeoclimatic Subzones of Coastal British Columbia; two plots are in the Dry Douglas-fir Subzone, six in the Wet Douglas-fir Subzone, three in the Dry Western Hemlock Subzone, and one plot is in the Wet Western Hemlock Subzone. Nine plots have an area of 0.04 hectare and three, 0.08 hectare. Plot parameters were measured three or four times at five-year intervals. Their forest density ranges from 1,317 to 1,947 stems per hectare, and the site index (base age 50) varies from 14 to 38 m for P. menziesii, and from 12 to 33 for T. heterophylla. The age of the plots ranges from 15 years at the first measurement to 114 years at the last measurement. Standard inventory-type parameters, described in Chapter I, were measured for each tree. In

addition, the position of each tree was calculated and recorded on stem maps.

Since the main goal of this study is the analysis of forest inter-species competition, sample plots were chosen on the basis of tree species diversity. The number of tree species per plot varies from three to six; a total of nine species were found: P. menziesii, T. plicata, T. heterophylla, A. rubra, A. grandis, and less abundantly, A. macrophyllum, Pinus monticola Dougl., Cornus nuttallii Audubon, and Prunus emarginata Dougl.

THE CHOICE OF AN APPROACH

Literature Review

There are a variety of deterministic models for single species: Pinus taeda L. (Clutter 1963), P. menziesii (Newnham 1964, Paillé 1970, Goulding 1972, Bella 1971, Mitchell 1971, Arney 1972), Picea glauca (Mitchell 1969), P. contorta (Lee 1967), T. heterophylla (Lin 1969). These models use either a tree-distance dependent or tree-distance independent approach (Munro 1973), and they all deal with intraspecies competition. The main feature common to these models is the concept of "zone of influence" (Krajicek et al. 1961, Vézina 1963, Opie 1968). The zone of influence of a tree is defined as an area on the ground representing the vertical projection of the crown or of the roots. It is, therefore, the assumed horizontal extent to which a tree can gather light, water and nutrients. Pertinent reviews of forest stand simulation modelling are numerous (Jaquette 1972, Honer 1972, Franklin et al. 1972, Smith 1973, Munro 1973).

Plant physiological modelling (Hesketh and Jones 1976, McKinion et al. 1975), although extremely rich in details about the mechanics of a plant, reveal little about plant to plant interaction, and even less about a multi-species situation. Agricultural plant modelling is also concerned primarily with monocultures (Stern 1965, Mead 1967).

There are several models concerned with forest multi-species modelling (Nelson 1965, Duncan et al. 1967, Waggoner and Reifsnyder 1968, Botkin et al. 1970, Whittaker et al. 1974, Stout et al. 1975). In these, the investigator is usually faced with a number of parameters varying together to determine, at any instant, part of the behaviour of a group of species. Multiple regression techniques are therefore widely used, and have proven to be quite powerful. However, multi-species models are mostly developed at the level of the whole stand, using a tree-distance independent approach. This approach is sufficient for growth and yield studies, but inadequate to examine plant to plant interaction.

In view of the objectives of this study, a tree-distance dependent approach seems to be necessary to investigate the response of a single plant to a number of biotic parameters. Multiple regression and analysis of variance can then be applied to evaluate the variability and relative importance of various parameters.

Methods

Height growth and diameter growth show different physiological responses. The latter is more sensitive to the density of the forest (Kramer and Kozlowski 1960) and is of the greatest interest for

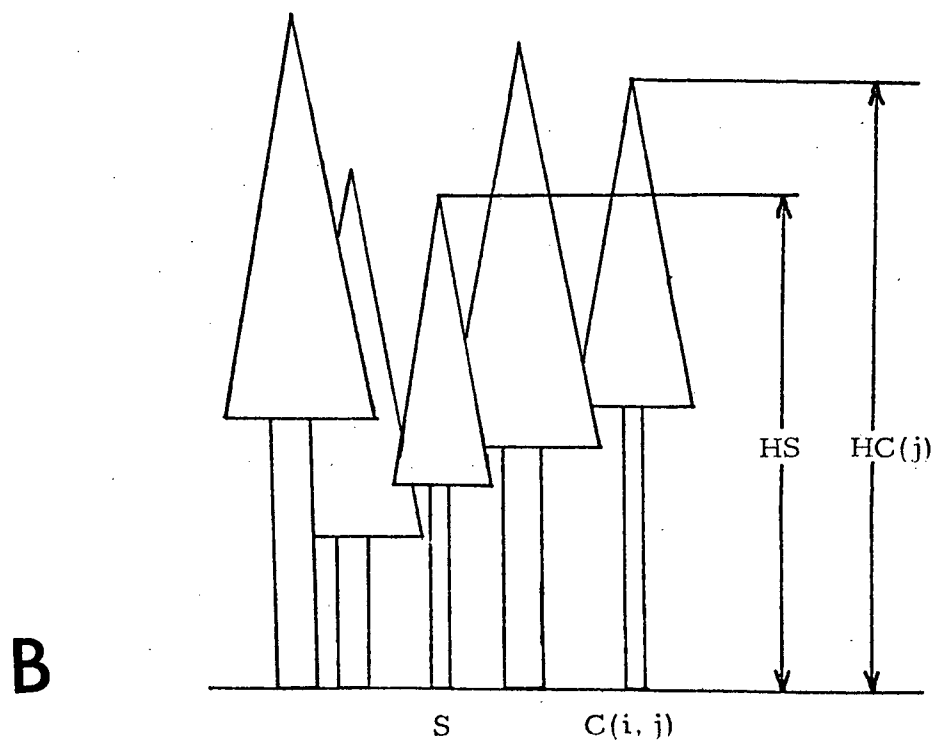
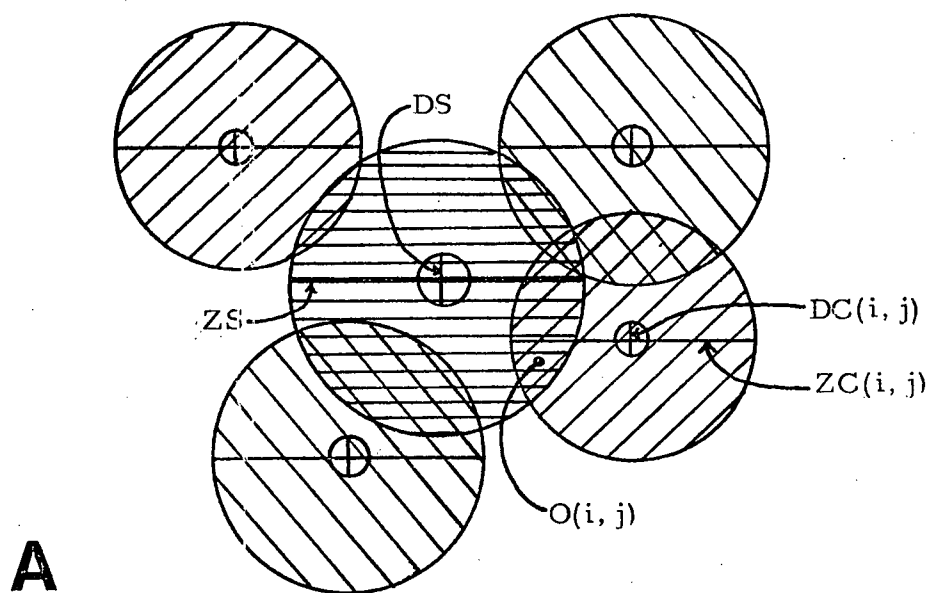
competition studies. The hypothesis that the rate of growth of a single tree is related to competition from different species in its neighborhood implies a precise measurement of competition due to each. Two main types of competition index are found in the forest literature. The first type is based on individual tree competition and usually evaluates intraspecies competition. The second type deals with interspecies competition, but is generally calculated at the species level. For this study, an index of competition based on single trees was derived from the idea of intraspecies competition indices by extension of the concept from one to several species. The classical approach is presented by Bella (1969) and Moore et al. (1973).

If the subject tree is denoted S and its diameter DS , there exists a zone of diameter ZS , proportional to DS , defined as the zone of influence of S (Figure 9 A). Similarly, each competitor j of species i , denoted $C(i,j)$, has a diameter $DC(i,j)$ and a zone of influence of diameter $ZC(i,j)$. When ZS is overlapped by $ZC(i,j)$, it is assumed that S and $C(i,j)$ compete for the same resources within the area of overlap $O(i,j)$. The summation of overlap of trees of species 1 is $\text{Sum } (O(1,j))$, for $j = 1 \dots n$, where n is the number of competitors of species 1 with subject tree S . The ratio of the area of overlap of species 1 to the area of S is $\text{Sum } (O(1,j))/AS$, for $j = 1 \dots n$, where AS is the area of the zone of influence of S . The ratio of the overlap due to all species is therefore $\text{Sum } (O(i,j))/AS$, for $j = 1 \dots n$ and $i = 1 \dots m$, where m is the number of species competing with S . The computation of the area of overlap was adapted for multi-species from Arney (1972).

FIGURE 9

A. Geometrical representation of the areas of overlap between a subject tree and its competitors. DS = DBH of the subject tree. ZS = diameter of the zone of influence of the subject tree. $DC(i,j)$ = DBH of the j th tree of the i th competing species. $ZC(i,j)$ = diameter of the zone of influence of the j th tree of the i th competing species. $C(i,j)$ = area of overlap between the j th tree of the i th competing species and the subject tree. Refer to text for formulae.

B. Geometrical representation of the height ratio of the competing trees over the subject tree. S = subject tree. $C(i,j)$ = j th tree of the i th competing species. HS = height of the subject tree. $HC(j)$ = height of the j th tree. Refer to text for formulae.



The potential area of overlap due to unknown competitors located outside the plot borders creates a bias (Monserud and Ek 1974, Martin et al. 1977). The method of mirror image from the border was used, with the reflection line passing through the border, and the calculated overlap was weighted in proportion to the distance of the subject tree from each of the two closest borders. Since sample plots are rectangular, this procedure performed satisfactorily when compared with evaluation using distance and size of trees outside the borders.

A simple index of vertical competition was also calculated. The height of the subject tree is denoted H_S , and the height of a competitor $H_C(j)$ (Figure 9 B). No species distinction was made for the competitors' height. The average height of the competitors is $\text{Sum}(H_C(j))/n$, for $j = 1 \dots n$ and the height ratio of competitors over subject tree is $\text{Sum}(H_C(j))/n/H_S$, for $j = 1 \dots n$. The purpose of this index is to indicate whether the subject tree is taller than its competitors (index ≤ 1) or is under their shade (index > 1), and in what proportion.

The DBH (diameter at breast height) of each tree was measured at five-year intervals and the average yearly DBH increment was calculated. The age of each tree was evaluated from regression equations based either on measured age, for canopy trees, or on DBH, for ingrowth trees. The status of the tree was recorded as ingrowth (DBH ≤ 4 cm at last measurement), live, or dead. The subzone to which the plot belongs was recorded as a presence-absence factor.

To evaluate the influence of the presence of n different species on the diameter growth of a subject tree, regression equations of the

following form were built:

$$\text{INCREMENT } (i,j) = f(\text{Sum } (O(1,i)), \text{Sum } (O(2,i)) \dots \text{Sum } (O(n,i)))$$

for each subject tree i of each species j . Other predictors such as DBH^2 and DBH/age were also used in some models. The purpose of the exercise was not to reach a high coefficient of determination (R^2), but to determine the contribution of various predictors in the equation. Predictor contribution was tested by analysis of variance of the additional sum of squares due to the predictor. Finally, the statistical significance of interactions between predictor "species overlap ratio" and predictor "subzone" were tested.

RESULTS AND DISCUSSION

Regression models

To find out the usefulness of distinguishing between the overlap ratio due to each competing species, as opposed to the total overlap ratio, two simple regression models were built (Table 21, Model 1 and 2). Model 1 pools all competitor species into overall overlap (SUMOR); Model 2 separates overlaps by competitor species (OPM, OTP, etc). Both models include DBH, age, and subzone location as additional independent variables. The analysis of variance (Table 22, Model 2 versus Model 1) confirms the significance of additional sum of squares due to additional factors considered in Model 2, with the exception of T. plicata model. It is, therefore, useful to know exactly which species is competing against P. menziesii and T. heterophylla. T. plicata appears less sensitive to

1) $Y = (K, DBH, AGE, SUMOR, DDF, WDF, DWH, WWH) B$

$$R^2 (Pm) = 0.645 \quad (Tp) = 0.508 \quad (Th) = 0.410$$

2) $Y = (K, DBH, AGE, OPM, CTP, CTH, OAG, OAR, OAM, DDF, WDF, DWH, WWH) B$

$$R^2 (Pm) = 0.656 \quad (Tp) = 0.513 \quad (Th) = 0.430$$

3) $Y = (K, DBH, AGE, OPM, CTP, CTH, DDF, WDF, DWH, WWH) B$

$$R^2 (Pm) = 0.655 \quad (Tp) = 0.510 \quad (Th) = 0.425$$

4) $Y = (K, DBH, AGE, SUMOR*HR, OPM, CTP, CTH, DDF, WDF, DWH, WWH) B$

$$R^2 (Pm) = 0.655 \quad (Tp) = 0.510 \quad (Th) = 0.425$$

5) $Y = (K, DBH, AGE, OPM, CTP, CTH) B$

$$R^2 (Pm) = 0.630 \quad (Tp) = 0.486 \quad (Th) = 0.413$$

6) $Y = (K, DBH, AGE, OPM, CTP, CTH, DDF, WDF, DWH, WWH, OPM*DDF, CTP*DDF, OPM*WDF, CTP*WDF, OTH*WDF, CPM*DWH, CTP*DWH, OTH*DWH, OPM*WWH, CTP*WWH, CTH*WWH) B$

$$R^2 (Pm) = 0.664 \quad (Tp) = 0.508 \quad (Th) = 0.427$$

7) $Y = (K, DBH, DBH^2, DBH/AGE, SUMOR, OPM, CTP, CTH, FSITE, HSITE, DDF, WDF, DWH, WWH) B$

$$R^2 (Pm) = 0.765 \quad (Tp) = 0.684 \quad (Th) = 0.506$$

Table 21...

(Cont'd)

TABLE 21

Regression models used in this study. R^2 is given for three subject species: P. menziesii, T. plicata, and T. heterophylla respectively. Variable names are as follows:

AGE: breast age of the tree (years)
 E: vector of regression coefficients
 DBH: diameter at breast height (mm)
 DDF: Dry Douglas-fir Subzone (0 or 1)
 DWH: Dry Western Hemlock Subzone (0 or 1)
 FSITE: site index for P. menziesii, (age 50) (m)
 HSITE: site index for T. heterophylla, (age 50) (m)
 HR: height ratio
 K: the constant 1
 CAG: overlap ratio due to A. grandis
 CAM: overlap ratio due to A. macrophyllum
 CAR: overlap ratio due to A. rubra
 CPM: overlap ratio due to P. menziesii
 CTH: overlap ratio due to T. heterophylla
 OTP: overlap ratio due to T. plicata
 SUMOR: total overlap ratio (all species)
 WDF: Wet Douglas-fir Subzone (0 or 1)
 WWH: Wet Western Hemlock Subzone (0 or 1)
 Y: average yearly diameter increment
 in the last five years (mm)

Model	Source	df	MS	F-ratio
MODEL 2 versus MODEL 1				
<u>P. menziesii</u>	Additional Regression	5	12.15	4.04 ***
	Error	657	3.01	
<u>T. plicata</u>	Additional Regression	5	4.10	0.80 NS
	Error	377	5.16	
<u>T. heterophylla</u>	Additional Regression	4	4.58	3.55 ***
	Error	400	1.29	
MODEL 3 versus MODEL 1				
<u>P. menziesii</u>	Additional Regression	2	26.92	8.94 ***
	Error	660	3.01	
<u>T. plicata</u>	Additional Regression	2	4.82	0.93 NS
	Error	380	5.15	
<u>T. heterophylla</u>	Additional Regression	2	6.44	4.99 ***
	Error	402	1.29	
MODEL 4 versus MODEL 3				
<u>P. menziesii</u>	Additional Regression	1	1.05	0.35 NS
	Error	659	3.01	
<u>T. plicata</u>	Additional Regression	1	0.17	0.03 NS
	Error	379	5.16	
<u>T. heterophylla</u>	Additional Regression	1	0.12	0.09 NS
	Error	401	1.30	

Table 22...

(Cont'd)

Model	Source	df	MS	F-ratio
MODEL 3 versus MODEL 5				
<u>P. menziesii</u>	Additional Regression Error	4 660	34.75 3.01	11.54 ***
<u>T. plicata</u>	Additional Regression Error	4 380	24.61 5.15	4.78 ***
<u>T. heterophylla</u>	Additional Regression Error	3 402	3.51 1.29	2.72 ***
MODEL 6 versus MODEL 3				
<u>P. menziesii</u>	Additional Regression Error	11 649	4.62 2.98	1.55 NS
<u>T. plicata</u>	Additional Regression Error	11 369	0.78 5.32	0.15 NS
<u>T. heterophylla</u>	Additional Regression Error	8 394	0.31 1.32	0.23 NS
MODEL 7 versus MODEL 3				
<u>P. menziesii</u>	Additional Regression Error	4 656	158.7 2.06	77.03 ***
<u>T. plicata</u>	Additional Regression Error	4 376	177.7 3.36	51.68 ***
<u>T. heterophylla</u>	Additional Regression Error	4 398	18.49 1.12	16.51 ***

TABLE 22

Analysis of variance table on regression models. The analysis tests the significance of the variation accounted for by the first model over and above that accounted for by the second model.

this level of detail in this model. The large number of predictors in the models, and the low occurrence of some species made the solution of the models possible only for three species: P. menziesii, T. heterophylla, and T. plicata. Model 3 (Table 21) shows that it is possible to delete the low frequency species as predictors in Model 2, and still obtain a more powerful model than Model 1. Model 4 tests an agglomerate index of competition, defined as total overlap ratio times the height ratio. The underlying hypothesis is that the average yearly increment should be inversely proportional to the total overlap ratio, as well as to the height ratio, since the overlap on both the horizontal and the vertical plane of the crown is assumed detrimental to diameter increment. Analysis of variance shows that this predictor does not add significant information (Table 22, Model 4 versus Model 3).

The necessity of including the Biogeoclimatic Subzone from which each observation came was tested by removing this information from Model 3 (Table 21, Model 5). The analysis of variance supports the hypothesis that the additional information provided by the subzone location is highly significant (Table 22, Model 3 versus Model 5). Model 6 was derived from Model 3 to test a possible interaction between the overlap ratios and the Biogeoclimatic Subzones. It was hypothesized that P. menziesii, T. plicata, and T. heterophylla might have a totally different impact as competitors from one subzone to another (Table 21, Model 6). The analysis of variance indicates, however, that these interactions are not significant (Table 22, Model 6 versus Model 3). Some predictors were added to Model 3 to test their significance. DBH^2 was included as a

reflection of the geometric increase of basal area; DBH/Age as an indicator of the average growth over the life of the tree; P. menziesii and T. heterophylla site indices, as indicator of site productivity; and finally the total overlap ratio was reintroduced in the model to represent the residual bits of information due to competitors other than P. menziesii, T. plicata, and T. heterophylla (Table 21, Model 7). As expected, the inclusion of these four predictors was very highly significant (Table 22, Model 7 versus Model 3). This model gives high multiple correlation coefficients ($R = 0.87$ for P. menziesii, $R = 0.83$ for T. plicata, and $R = 0.71$ for T. heterophylla), and is well suited to estimate the yearly DBH increment for these species over a large diversity of situations. Interestingly enough, predictors like partial and total overlaps, and subzone location are not significant in this model (Appendix C, Model 7), while they were significant in models where DBH^2 and DBH/Age were not introduced as predictors. Site indices were significant in only half of the cases. The highest predictive power, achieved by DBH^2 and DBH/Age, has a clear biological meaning. DBH^2 is directly proportional to basal area and represents the cumulative growth of the tree over its entire lifespan. DBH/Age gives the average DBH increment over the life of the tree and reveals the history of its failures or successes. The predictors carry so much of the past growth history of the tree that other predictors representing only present conditions are insignificant in comparison. When the strong predictors are not included in the model, weak predictors become significant since they describe the present conditions through subzone location, site index, and competition regime.

Mortality and regeneration analysis.

All dependent variables mentioned above were submitted to one-way analyses of variance to test for possible differences among species and among status (ingrowth, live, dead) of stems within each species. Two useful types of indicators were found. Mortality indicators are variables that show significant differences between live and dead stems of the same age and species; since some measurements were made just before the death of trees, it is possible to compare each variable, DBH for instance, between live and dead stems and to predict the probability of mortality of a live stem whose value for that variable approaches the average value of dead stems. Regeneration indicators are competition indices that show significant differences between species in the category of the ingrowth stems; they indicate the conditions under which a given species does and does not regenerate.

Mortality indicators

P. menziesii is the only species whose dead stems show a DBH significantly smaller than the average for live stems (Table 23). The overlap ratio due to T. plicata is significantly smaller on dead stems than on live ones while the overlap ratio due to T. heterophylla is significantly larger on dead stems. This indicates that a surrounding of T. heterophylla is generally associated with the suppression and death of P. menziesii stems. The average yearly DBH increment over the five years preceding death is significantly smaller, indicating a progressive growth reduction before death. The average growth rate over the total lifespan of the tree, DBH/Age, is also significantly smaller for dead stems, which strongly suggests a long and progressive accumulation of the effects of

INDICATOR	STATUS	Pm	Tp	Th	Ag	Ar
YINC	Live	2.7	2.5	1.8	1.8	.84
	Dead	.93	0.1	0.9	-	-.5
	F-ratio	11***	2.1 NS	8.1***	-	4.0***
DBH	Live	234	178	165	274	244
	Dead	175	178	182	266	200
	F-ratio	12***	0.0 NS	1.1 NS	0.1 NS	0.5 NS
DBH/AGE	Live	3.8	2.9	2.5	4.8	4.0
	Dead	2.5	2.2	2.4	4.8	2.3
	F-ratio	11***	0.5 NS	0.2 NS	0.0 NS	4.4 **
OPM	Live	.36	.49	.42	.25	.17
	Dead	.36	.51	.63	.67	.07
	F-ratio	0.0 NS	0.0 NS	3.9 **	1.8 NS	0.2 NS
OTP	Live	.18	.30	.20	.05	.02
	Dead	.04	.28	.17	.01	.11
	F-ratio	3.7 **	0.0 NS	0.1 NS	0.7 NS	2.2 NS
OTH	Live	.18	.16	.18	-	.10
	Dead	.40	0.0	.10	-	.23
	F-ratio	4.6 **	0.6 NS	1.4 NS	-	1.2 NS
SIZER	Live	.94	1.6	1.3	1.1	.95
	Dead	1.1	2.7	1.9	2.5	1.5
	F-ratio	1.5 NS	2.4 NS	10***	12***	3.8 *

TABLE 23

One-way analysis of variance of mortality indicators between live and dead stems. Refer to Table 21 for definition of indicators. Pm=P. menziesii, Tp=T. plicata, Th=T. heterophylla, Ag=A. grandis, Ar=A. rubra.

the neighborhood competitors.

No mortality indicator shows any statistical significance in the case of T. plicata. However, there were only four dead T. plicata stems out of 377 observations. The low number of observations in this class indicates clearly that the mortality in T. plicata occurs later than in P. menziesii, since the average age of T. plicata is not significantly lower than P. menziesii.

Three indicators are significant for T. heterophylla. The average yearly increment in the five years preceding death is only half of the value for live stems. The overlap ratio due to P. menziesii is significantly larger on dead stems. The height ratio of the competitors is also significantly higher around dying stems. Therefore stems which are overlapped and are shorter than the average, and with a DBH increment smaller than the average, die.

The height ratio is the only valid indicator for A. grandis. Yet the overlap ratio due to P. menziesii, although not statistically significant, is an indication that P. menziesii overlap is correlated with mortality in A. grandis.

The dead stems of A. rubra show that the average DBH increment over their entire lifespan, DBH/Age, is significantly smaller than for live stems; this indicates that the competition effect of surrounding stems was acting for a long time. In the five years preceding mortality, the average DBH increment becomes nil. The competitors around dead stems are, on the average, 1.5 times as tall, as opposed to 0.95 around live stems.

Regeneration indicators

One-way analysis of variance among species indicates that A. rubra regenerates a new stem only when the total overlap ratio is near zero (Table 24). This confirms the pioneer role of A. rubra which was already demonstrated in the two previous chapters. The height ratio further indicates that the competitors are shorter, as would be expected during early stages of succession.

P. menziesii also requires low total overlap ratio to grow a new stem. The overlap ratio due to P. menziesii, T. heterophylla, and T. plicata, respectively, reflects the order in which these species will compete against P. menziesii. The height ratio larger than 1 means that other stems were present before or concurrently with P. menziesii; it is only logical to suggest that A. rubra was preceding it.

The next less tolerant species in regard to total overlap is T. heterophylla. Yet the overlap ratio due to P. menziesii suggests that this latter species was present first and surrounds the new stems of T. heterophylla. The height ratio of 2.0 indicates the head start of early invaders, either preceding or growing faster than T. heterophylla. T. plicata is less abundant as a neighbor of the new stems of T. heterophylla, and will play its role later.

Next in overlap tolerance is A. grandis, which occurs only in the Dry Douglas-fir Subzone. P. menziesii is therefore its main competitor and no co-occurrence with T. plicata nor with T. heterophylla was observed in the sample. The height ratio classifies A. grandis as a late invader likely to succeed P. menziesii locally.

INDICATOR	Pm	Tp	Th	Ag	Ar	F-ratio
SUMOR	.53	.94	.76	.93	.02	20.0 ***
OPM	.37	.46	.45	.93	.001	10.5 ***
OTP	.18	.38	.16	-	.02	9.7 ***
OTH	.32	.25	.26	-	.002	2.9 **
HR	1.2	2.2	2.0	1.7	.85	50.0 ***

TABLE 24

One-way analysis of variance of regeneration indicators between species. Refer to Table 21 for definition of indicators. Ingrowth data only were used in this analysis. Pm=P. menziesii, Tp=T. plicata, Th=T. heterophylla, Ag=A. grandis, Ar=A. rubra.

The most tolerant regenerator in regard to overlap is T. plicata which can regenerate even when 94% of its zone of influence is overlapped. The most severe competitor on a new stem of T. plicata is P. menziesii, followed by T. plicata and finally T. heterophylla. The very high height ratio for T. plicata indicates that all competitors are, on the average, 2.2 times as tall as the ingrowth of T. plicata. This height ratio is the largest of all species, which suggests that T. plicata is the species able to regenerate the latest in the stand. This is an indication of a very high shade tolerance, and therefore, of the presence of T. plicata in the older vegetation. The capacity of T. plicata to tolerate a broad spectrum of moisture conditions is also a selective advantage for regeneration under dense cover.

Succession trends

A typical dead stem of P. menziesii has a smaller DBH than the average stem; its life average DBH increment is smaller than live stems; its DBH increment in the five years preceding death is very small; its most severe competitors are T. heterophylla and P. menziesii stems, and the competing stems are taller. P. menziesii ingrowth requires good sunlight exposure as indicated by its low tolerance to total overlap ratio, which makes it a typical pioneer to be succeeded by more shade-tolerant species. The requirement for good sunlight exposure further suggests tolerance to drier sites.

For A. rubra, the typical dead stem has a life average DBH increment smaller than live stems; the DBH increment is highly reduced during the five years preceding death and the dead stems are much shorter than the

average. The ingrowth stem does not tolerate any overlap and is only slightly shorter than the surrounding stems. Therefore, among the sample plots, A. rubra is an early invader which is rapidly replaced by seral or climax species. It competes with other pioneers such as P. menziesii. It was shown, in Chapter I (Figure 5), that A. rubra can hold out P. menziesii in a small proportion of the stands ($< 5\%$), until about age 60.

The dead stems of T. heterophylla do not show a life average DBH increment any smaller than other stems; their DBH increment preceding mortality is very reduced; their most severe competitors are P. menziesii stems, and the dead stems can be much shorter than their competitors. The ingrowth can tolerate a large amount of overlap, usually provided by stems of P. menziesii and older T. heterophylla stems, and grows in deep shade, with high surrounding competitors. T. heterophylla is therefore a seral species likely to remain in the climax vegetation, and is preceded, on these sample plots, by A. rubra or P. menziesii, or both. T. heterophylla can also be present as a pioneer if conditions are unsuitable for, or there is no seed source of P. menziesii.

The dead stems of A. grandis, on the sample plots, have only one characteristic which distinguishes them from the average live stem: they are very much shorter than the surrounding stems. The ingrowth can tolerate a large amount of overlap, all coming from P. menziesii in this case, and from stems which are much taller. A. grandis was found only in the Dry Douglas-fir Subzone among the sample plots and was found locally with P. menziesii in the older vegetation.

Within the sample, there were only four dead stems of T. plicata and they showed no significant characteristic (Tables 23). Yet this low mortality on plots 114 years old is itself an indication that T. plicata will persist during later stages of succession. The ingrowth shows a very high tolerance to overlap (Table 24); its main competitors are P. menziesii and other stems of T. plicata; the height of the average competitor can be very much higher than the ingrowth. T. plicata seems the most shade tolerant among the five species analysed at the stem level and it occupies a place in the older vegetation in plots dominated by P. menziesii or T. heterophylla.

CONCLUSION

There is strong evidence that the growth of a single stem is affected by forest composition in its immediate neighborhood. Diameter growth increment is a result of site conditions and competition regimes, both past and present. The contribution of present site conditions was studied through tree composition, subzone location, and site index. Present competition regime was estimated by competition indices which took into account the horizontal distribution of the crowns and roots and the vertical distribution of the crowns of all tree species. It was found that three species - P. menziesii, T. heterophylla, and T. plicata - were most indicative of competition from crown and root overlap since they represented 92% of the total stem abundance in the sample plots. Cumulative effects of past site conditions and past competition regimes over

the lifespan of a tree were reflected by DBH, DBH^2 , and DBH/Age, which were the best predictors for diameter increment. Estimates based on present conditions were found significant only when used alone, without the predictors DBH^2 and DBH/Age.

No matter how small the competition indices were, and therefore sometimes statistically non-significant, it was the everyday impact created by detrimental competition which, in the long run, cumulated in terms of small DBH and small DBH increment. Although subzone location and overlap ratios were significant, in the absence of stronger predictors, their interaction was not significant. This indicates that the mechanism of competition might be the same in all subzones, and that differences in vegetation between subzones would be due to other factors, such as soil and climate of the subzone regulating the availability of solar radiation, water, and nutrients.

Regression models revealed that DBH, DBH^2 , and DBH/Age were the best predictors of present diameter increment; the analysis of mortality showed that a high competition index, a DBH below average, and a diameter increment below average were good indicators of mortality. These results are similar to those of Monserud (1976) who found that DBH, diameter increment, and competition index were the best variables to distinguish between live and dead stems, although the mortality function he derived from them was not species-specific. Mortality and regeneration indicators were strongly correlated with forest composition and structure (geometric position of each tree and distributions of DBH and height), and were species-specific. Pioneer and seral species could be recognized on

the basis of their tolerance to forest composition and structure in their surroundings. The correlation between high competition indices and mortality, and between low competition indices and regeneration in a species-specific manner points out a mechanism more likely dependent on the local competition regime around each stem than on site factors.

Starting from an assumed equal seed distribution, site conditions allow only some species to grow at first, and since competition is very severe on these early invaders, their density decreases quickly. Simultaneously, shade conditions (set by forest composition and structure) determine probabilities of regeneration of these species and invasion by other species. This mechanism applies to the lowest level of the forest population, a single tree, and its effects produce succession as can be observed at the plot level and at the Biogeoclimatic Subzone level. Abiotic characteristics of the subzone determine forest composition from which competition shapes the trend of succession by a mechanism independent of the subzone. It is, therefore, unnecessary to invoke more complex explanations to link together significant interactions from the single tree to the entire subzone.

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Analysis and modelling of interspecies competition
during forest secondary succession.

Pierre Bellefleur

CHAPTER IV

Synthesis and conclusion.

The perception of succession at the Biogeoclimatic Subzone level required observations over a long period of time. The level of resolution was rather broad and the observations revealed trends rather than details. Pioneer and seral roles of species could be identified in each subzone, although the rates of change might have been exaggerated due to unequal sampling intensity over space. Markov models were unable to duplicate the observed changes in tree species composition in adequate detail. The major problems that were unsolved at this level were linked with the variability in the kinds of disturbance which initiated succession, in the types of communities, and in the kinds of sites, and were further linked with the probability of species invasion. Therefore, this level of interpretation appeared essentially global and descriptive and did not suggest any specific population dynamic mechanisms. Its main value was the overview provided for each subzone and the comparison of patterns of succession among them.

Observations at the plot level made the community structure immediately obvious, no matter what scheme was used to classify communities. Tree composition was used to discriminate between communities since it was the only possible way to do so in the absence of data on understory vegetation. In addition, this way of defining communities offered the advantage of simplicity and field practicability. The growth of any given species could be clearly seen to vary from one community to another; this performance appeared to be subzone-specific. Trends in species succession could be inferred only indirectly at this

level, but they coincided closely with those observed at the Biogeoclimatic Subzone level. The long-term overview provided by the Biogeoclimatic Subzone level was, however, lost at the plot level. On the other hand, some mechanism of species replacement through either facilitation or inhibition emerged more or less clearly, since growth was affected by tree composition which, in turn, was affected by site factors and by intra- and interspecies competition. The plot level of interpretation was superior to the Biogeoclimatic Subzone level in its ability to reveal the structure of communities and the role they play in promoting species replacement.

Unfortunately, due to the absence of appropriate data on site factors, it was not possible to test whether or not abiotic factors such as microclimate, soil heterogeneity, and local topography played a more important role than plant to plant interactions. It seemed that this problem could be solved either by field experimentation or by observations at a level of interpretation where site factors could be kept relatively homogeneous.

With present inventory techniques of vegetation sampling, sample plots had to be chosen to be relatively homogeneous to represent typical communities and to maximize differences between them. This offered the invaluable advantage of ensuring a certain constancy of the site factors within any sample plot and made it reasonable to assume that all trees of a plot were subject to the same abiotic conditions.

It was shown that suppression and mortality of trees was strongly dependent upon the composition of the surrounding trees. Dead stems

showed a history of sub-standard growth which was correlated with competition from its neighbors suggesting that the accumulation of detrimental effects produced a stress which, in the long run, led to below-average growth. The conditions for regeneration were also determined by the neighboring vegetation and those conditions which were associated with the mortality of a tree of a given species could be associated with the regeneration of another species. At this level of interpretation, it was also possible to show that the best growth predictors reflected the past history of the tree, which is, not surprisingly, a non-Markovian conclusion. This general mechanism of selective suppression and selective replacement of stems seemed, furthermore, the same from one subzone to the other. The differences in vegetation between subzones should then be due to other factors, such as the availability of solar radiation, water, and nutrients.

The interpretation at the individual tree level was the only one which suggested a mechanism, broadly described as inter-tree competition, which was able to account for changes in the net rate of change of populations through mortality and regeneration. This mechanism is responsible for the repeatable sequence of dominant species observed at the two higher levels of interpretation. Whether competition can be qualified as a "mechanism" is debatable. If one looks at it from a physiological viewpoint, concepts such as nutrient cycling, ion exchange capacity, and allelopathic substances would suggest more hypotheses on the chemical mechanics of inhibition and facilitation. This,

however, is beyond the scope of this study which meant to investigate the forest from the population dynamics viewpoint. From this view, competition is indeed a mechanism since it accounts for part of the forces behind mortality and regeneration of species. It was not possible to demonstrate that facilitation mechanisms rather than inhibitory mechanisms such as competition are necessary to explain secondary succession.

APPENDIX A

Species names used in the analyses (after Krajina 1969)

CODE	BOTANICAL NAME	ENGLISH NAME
<hr/>		
Aa	<u>Abies amabilis</u> (Dougl.) Forbes	Amabilis fir
Ag	<u>Abies grandis</u> (Dougl.) Lindl.	Grand fir
Am	<u>Acer macrophyllum</u> Pursh	Broadleaf maple
Ar	<u>Alnus rubra</u> Bong.	Red alder
	<u>Arbutus menziesii</u> Pursh	Pacific madrona
	<u>Cornus nuttallii</u> Audubon	Western flowering dogwood
Ps	<u>Picea sitchensis</u> (Bong.) Carr	Sitka spruce
Pc	<u>Pinus contorta</u> Dougl.	Lodgepole pine
	<u>Pinus monticola</u> Dougl.	Western white pine
	<u>Prunus emarginata</u> Dougl.	Bitter cherry
Pm	<u>Pseudotsuga menziesii</u> (Mirb.) Franco	Douglas-fir
	<u>Quercus garryana</u> Dougl.	Garry oak
Tp	<u>Thuja plicata</u> Donn	Western redcedar
Th	<u>Tsuga heterophylla</u> (Raf.) Sarg.	Western hemlock

APPENDIX B

Transition matrices used in the Markov models. Rows and columns represent stand types in the order of the species list. Observations and estimates are counts. Transitions are probabilities of moving from the column stand-type to the row stand-type in a time interval of five years. The transition matrix has been multiplied by 10^3 .

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SPECIES:

THUJA PLICATA

ALNUS RUBRA

PSEUDOTSUGA MENZIESII

PINUS CONTORTA

STEMS

BASAL AREA

OBSERVATIONS:

9	0	1	0
0	3	0	0
0	0	103	0
0	0	0	9
9	3	104	9

1	0	0	0
0	4	1	0
0	0	111	0
0	0	0	8
1	4	112	8

ESTIMATES:

9	1	5	0
0	2	0	0
0	0	95	0
0	0	4	9
9	3	104	9

1	3	0	0
0	0	2	0
0	0	106	0
0	1	3	8
1	4	112	8

TRANSITIONS:

1000	115	30	0
0	885	0	0
0	0	950	0
0	0	20	1000

1000	400	0	0
0	500	15	0
0	0	970	0
0	100	15	1000

1000 1000 1000 1000

1000 1000 1000 1000

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SPECIES:

PSEUDOTSUGA MENZIESII
TSUGA HETEROPHYLLA
THUJA PLICATA
ALNUS RUBRA
ABIES GRANDIS
ACER MACROPHYLLUM
PICEA SITCHENSIS

STEMS**BASAL AREA****OBSERVATIONS:**

211	3	0	0	1	0	0	248	0	0	0	0	0	0	0
5	53	1	0	0	0	0	1	42	1	0	0	0	0	0
2	2	38	0	1	0	0	1	0	20	0	0	0	0	0
0	0	0	3	0	0	0	0	0	0	3	0	0	0	0
0	0	1	0	3	0	0	0	0	0	0	2	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0	0	7
218	58	40	3	5	2	1	250	42	21	3	2	1	7	

ESTIMATES:

180	3	0	0	0	0	0	228	0	0	3	0	0	0	0
30	53	1	2	0	0	0	1	29	1	0	0	0	0	0
8	2	24	0	1	0	0	21	0	20	0	0	0	0	0
0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
0	0	15	0	4	0	0	0	0	0	0	2	0	0	0
0	0	0	0	0	2	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	1	0	13	0	0	0	0	0	7
218	58	40	3	5	2	1	250	42	21	3	2	1	7	

TRANSITIONS:

896	52	0	0	100	0	0	952	0	0	500	0	0	0	0
80	914	25	250	0	0	0	4	850	50	0	0	0	0	0
24	34	775	0	200	0	0	44	0	950	0	0	0	0	0
0	0	0	750	0	0	0	0	0	0	500	0	0	0	0
0	0	200	0	700	0	0	0	0	0	0	1000	0	0	0
0	0	0	0	0	1000	0	0	0	0	0	0	1000	0	0
0	0	0	0	0	0	1000	0	150	0	0	0	0	0	1000
1000	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000

=====

SPECIES:

PSEUDOTSUGA MENZIESII
ALNUS RUBRA
TSUGA HETEROPHYLLA
THUJA PLICATA
ABIES GRANDIS

*STEMS**BASAL AREA**OBSERVATIONS:*

100	1	0	0	0
0	5	0	0	0
4	0	129	0	0
2	0	3	2	0
0	0	0	0	3
106	6	132	2	3

145	0	2	0	0
0	3	0	0	0
5	0	89	0	0
1	0	0	1	0
0	0	0	0	4
151	3	91	1	4

ESTIMATES:

98	1	0	0	0
0	5	0	0	0
6	0	129	1	0
2	0	3	1	0
0	0	0	0	3
106	6	132	2	3

145	0	4	0	4
0	2	0	0	0
5	0	87	0	0
1	0	0	1	0
0	1	0	0	0
151	3	91	1	4

TRANSITIONS:

933	167	0	0	0
0	833	0	0	0
48	0	977	200	0
19	0	23	800	0
0	0	0	0	1000
1000	1000	1000	1000	1000

960	0	32	0	500
0	800	0	0	0
33	0	968	0	0
7	0	0	1000	0
0	200	0	0	500
1000	1000	1000	1000	1000

SPECIES:

TSUGA HETEROPHYLLA
THUJA PLICATA
ABIES AMABILIS
PICEA SITCHENSIS
ALNUS RUBRA

STEMS**BASAL AREA****OBSERVATIONS:**

249	0	0	1	0
0	10	0	1	0
0	0	39	0	0
1	0	0	21	0
0	0	0	0	4
250	10	39	23	4

234	0	0	0	0
0	13	1	0	0
0	0	34	0	0
3	1	0	33	0
0	0	0	0	4
237	14	35	33	4

ESTIMATES:

249	0	0	1	1
0	6	0	1	0
0	4	39	5	0
1	0	0	16	0
0	0	0	0	3
250	10	39	23	4

234	0	4	0	0
0	13	1	0	0
0	0	30	20	0
3	1	0	13	0
0	0	0	0	4
237	14	35	33	4

TRANSITIONS:

996	0	0	43	100
0	800	0	43	0
0	200	1000	100	0
4	0	0	814	0
0	0	0	0	900

987	0	50	0	0
0	929	29	0	0
0	0	921	300	0
13	71	0	700	0
0	0	0	0	1000

1000 1000 1000 1000 1000

1000 1000 1000 1000 1000

=====

SPECIES:

TSUGA HETEROPHYLLA
THUJA PLICATA

STEMS

BASAL AREA

OBSERVATIONS:

17 0
0 3

17 3

17 0
0 3

17 3

ESTIMATES:

17 3
0 0

17 3

17 3
0 0

17 3

TRANSITIONS:

1000 550
0 450

1000 1000

1000 550
0 450

1000 1000

=====

5. FOG WESTERN HEMLOCK SUBZONE.

APPENDIX C

Partial regression coefficients (B) and F-ratios for Model 5 and Model 7. In all cases $F(0.05) = 5.02$ and $F(0.01) = 7.88$

MODEL 5

$Y = K + DBH + AGE + OPM + OTP + OTH$

P. menziesii $R^2 = 0.631$ $df = 1, 664$

B:	4.7	.014	-.075	-.65	0.26	.083
F:	253	628	454	25	3.3	.670

T. plicata $R^2 = 0.486$ $df = 1, 384$

B:	2.3	.019	-.044	-.30	-.58	.290
F:	44	310	97	2.5	11	1.1

T. heterophylla $R^2 = 0.413$ $df = 1, 405$

B:	2.7	.009	-.032	-.42	0.085	-.32
F:	152	176	142	18	0.6	5.1

APPENDIX C...

(Cont'd)

MODEL 7

$$Y = K + DBH + EBH^2 + DBH + SUMOR + OPM + OTP + OTH \\ + FSITE + HSITE + LDF + WDF + DWH + WWH$$

P. menziesii $R^2 = 0.765$ $df = 1, 656$

B: -.33 .004 -.001 1.04 -.28 -.19 0.07 -.03
 -.03 -.03 -.25 0.14 -.29 0.40
 F: 0.42 5.03 7.0 529 5.4 2.3 .32 0.10
 1.2 1.8 .38 .13 .57 1.0

T. plicata $R^2 = 0.684$ $df=1, 376$

B: 1.80 0.017 -.002 1.1 -.27 0.18 -.11 -.02
 -.09 -.12 0.27 1.4 -1.1 -.6
 F: 4.6 26 17 219 1.9 0.58 .43 .007
 4.1 6.3 .22 7.3 3.9 1.1

T. heterophylla $R^2 = 0.506$ $df = 1, 398$

B: .079 .009 -.002 .91 -.06 -.36 -.03 -.34
 -.09 .059 -.19 -.46 1.1
 F: .04 8.9 14 169 0.16 4.0 .05 3.9
 19 7.2 .81 6.1 .33