Ecosystem Development in Abies amabilis Stands of the Washington Cascades: Root Growth and its Role in Net Primary Production

by

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Abstract

ECOSYSTEM DEVELOPMENT IN *ABIES AMABILIS* STANDS OF THE WASHINGTON CASCADES: ROOT GROWTH AND ITS ROLE IN NET PRIMARY PRODUCTION

by Michael R. Keyes

Chairman of Supervisory Committee: Dr. Charles C. Grier
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Declining net primary production which accompanies ecosystem maturation is thought to result from the respiration of slowly accumulating woody biomass. This explanation was examined in light of recent studies which have shown that over half of ecosystem net primary production goes into the production and turnover of roots.

Five study sites in the Abies amabilis zone of the Cedar River watershed were chosen to represent a chronosequence. The stands studied were 3, 9, 23, 50, and 180 years of age. Regression equations were developed for foliage and root biomass. Aboveground and belowground community biomass and net primary production were estimated for all stands.

It was hypothesized that with the belowground portion of net production included, the assessment of conifer net primary production should be linearly related to its foliage biomass. This hypothesized relationship showed a strong linear correlation ($r^2=.99$). Although net primary production declined from 23.2 t ha^{-1} in 50 year-old to 13.8 t ha^{-1} in the 180 year-old stand, this was associated with a reduction in foliage biomass. In addition, a relatively higher proportion of total net production was apportioned to roots in this mature stand.

A more detailed examination of root phenology was conducted from rhizotrons which were constructed in the 23- and 180 year-old stands. Root tip initiations and elongation were monitored for a 23 month period between December, 1978 and November, 1980. Data from these rhizotrons were used to test the hypothesis that the seasonal duration of active root growth would not be reduced in the cool soil of the *Abies amabilis* zone, regardless of stand age. A corollary hypothesis was that duration of active angiosperm root growth occurs over a comparatively shorter growing season than in *Abies amabilis*.

Consistent with the study hypothesis, changes in root growth were not synchronous with soil temperature changes. Increasing numbers of new root tips were observed in the spring before soil temperatures warmed. Fall and winter activity was sustained despite the decline in soil temperature. Conifer roots were actively growing over a comparatively longer season than those of *Pseudotsuga menziesii* previously studied in the warmer soils of the Puget Lowlands. Angiosperm root growth occurred over a comparatively shorter growing season than *Abies amabilis*.

TABLE OF CONTENTS

Page

LIST OF FIGURES (continued)

LIST OF TABLES

LIST OF PLATES


Tiarella trifoliata
Cornus canadensis
Forest Floor
A Horizon
B Horizon
Abies amabilis
Toby Fairchild 1982

PROLOGUE

The Cure

The only cure for digging in the dirt is ideas;

the only cure for ideas is more ideas;

the only cure for more ideas is digging in the dirt.

Kenneth Burke

ACKNOWLEDGMENTS

For anyone who has traversed the snowfields in the upper reaches of the Washington Cascade range, the opportunity to witness serene beauty within an otherwise harsh environment, provides a basis for establishing a communion with nature incomparable in most usual human experience. Feelings of personal growth and mutual accomplishment extend far beyond any scholarly purpose. To the numerous people who have assisted me in the construction and operation phases of this forest experiment, I would like to express my gratitude: Yvonne Alexander, Greg Antos, Joby Fairchild, Tom Hinckley, Steve Hyzer, Hiromi Imoto, Cal Meier, Yashi Morikawa, Mary Jo Pellerito, Steve Piper, Mike Smith, and Milt Smith.

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CHAPTER I

INTRODUCTION

The study of ecological succession has paralleled the emergence of ecosystem théory (Golley, 1977). Succession within the ecosystem context may be viewed as a developmental attribute of ecological systems accompanied by and due to concomitant changes in bioenergetic pathways (Reiners, *et al.*, 1971). It is generally acknowledged that a climax or steady state condition is characterized by increasing biomass accumulations and declining production to biomass ratios (Margalef, 1968; Woodwell and Whittaker, 1968; Odum, 1969). No explicit bioenergetic proof which explains the apparent decline in net primary production with increasing ecosystem maturity has been advanced.

Studies of community metabolism and forest productivity are no longer in their infancy. A thorough coverage of research pertaining to forest productivity and community metabolism going back to early work on the stratified clip method by Monsi and Saeki (1953) has been reviewed by Kira and Shidei (1967). It has been hypothesized by Kira and Shidei (1967) that gross production is proportional to leaf biomass and that the amount of organic matter consumed by respiration would parallel woody biomass accumulation as succession progressed.

Theoretically, accumulating respiring woody tissue will narrow the difference between gross production and respiration until a steady state is attained, at which time they balance and net production equals zero. This appealing theory has been partly verified in an aquatic microcosm by Cooke (1967). The analogy between the work of Cooke (1967) and Kira and Shidei (1967) was suggested by Odum in his 1969 benchmark paper. This comparison led Odum (1969) to suggest that a gradual decline in net production results from increasing respiration with ecosystem maturity until respiration and gross production balance. Further theoretical or experimental work conducted during the course of the International Biological Program and in the years that followed have not addressed Kira and Shidei's (1967) theory.

The process of plant succession is controlled to such an extent by edaphic conditions that its interpretation and true significance can be understood only by a thorough knowledge of root relations (Weaver and Clements, 1938). Odum (1975) suggested that an ecosystem's long-term strategy is the evolution of autogenic processes which are in homeostasis with the environment. The relative competitive advantage which conifers maintain over their deciduous counterparts in the Pacific Northwest may result from their ability to (1) photosynthesize in cooler spring and fall seasons and (2) secure sufficient quantities of water and nutrients over this comparatively longer season of assimilation (Franklin and Waring, 1979). Unless coniferous root systems evolved an autogenic process to increase water absorption, net assimilation would be reduced in the spring and fall months in the *Abies amabilis* zone due to the cool soil temperatures which exist under the snow pack for 6 to 8 months of the year.

Although the role of roots in absorption has long been recognized, the cost associated with their production and maintenance has only recently been assessed. Ecosystem studies in temperate North America have demonstrated that as much as 70% of net primary production is not accounted for when belowground growth and mortality are not considered in net production estimates (Harris, *et al.*, 1978; Caldwell, 1979; Grier, *et al.*, 1981; Keyes and Grier, 1981). Consequently, conclusions concerning the bioenergetic basis for changes in forest productivity with ecosystem maturity may be misleading if belowground productivity is not considered.

Several hypotheses were examined during the course of this research. It was postulated that conifer net production and leaf biomass in *Abies amabilis* zone ecosystems are linearly related. This hypothesis was tested by determining above- and belowground assessments of net primary production in a chronosequence of *Abies amabilis* stands ranging from 3 to approximately 180 years of age. Total net primary production along this chronosequence has been contrasted with theoretical changes in community metabolism models advanced by Kira and Shidei (1967) and Odum (1969). A corollary objective of this study was to ascertain whether Abies amabilis zone ecosystems reach the comparably high productivities associated with other temperate coniferous forests.

Another hypothesis being examined proposed that the seasonal duration of active conifer root growth is not reduced in Abies amabilis ecosystems, irrespective of the stage in stand development. It was further postulated that a comparable duration of angiosperm root growth is not sustained over this relatively short growing season. In order to test this hypothesis, the seasonal growth patterns of morphologically different types of conifer roots were observed in two different aged Abies amabilis ecosystems using root observation chambers. The analysis of root phenology paid particular attention to the spring and early winter growth periods of conifer roots, which might be severely depressed by the lingering snow pack and lowered soil temperatures.

CHAPTER II

LITERATURE REVIEW

2.1.1 Production Relations

The dissipation of energy captured by green plants (primary producers) via photosynthesis is the connection common to virtually all organisms in the environment. Photoreduction of carbon dioxide and water is carried out using wavelengths between 400 and 700 nm. This narrow window in the solar emission spectrum accounts for nearly half the electromagnetic energy reaching the earth's surface (Whittaker, 1975; Anon., 1974). Binding solar energy into chemical bonds as organic carbon provides the primary source of energy for secondary producers such as animals and saprophytes.

Primary productivity refers to the rate at which energy is bound or organic material is created by photosynthesis (Whittaker, 1975). Although not always formally stated, primary productivity is expressed per unit time and per unit of the earth's surface area. Productivity can either be expressed in energy units such as calories or more commonly in dry weight of organic matter. Primary production is usually divided into two parts; gross primary production and net primary production. Gross primary production (GPP) is the total amount of carbohydrates produced by a community. Respiration by green plants in maintenance of living tissue is a major use of these carbohydrates and is termed autotrophic respiration (R_A). Carbohydrates manufactured during photosynthesis which are not utilized for metabolic needs may accumulate as plant tissue. This increase in measurable dry weight is defined as net primary production (NPP), where

$$NPP = GPP - R_A$$

The study of carbon storage and flow through measurements of net primary production provides a structural framework for comparisons of forest community energetics. Primary productivity is a measure of solar assimilation capacity and represents the most essential resource currency; chemically bound energy. Because accumulation of biomass parallels the growth and development of many forest ecosystems, its eventual distribution and flow into other components of the ecosystems are of interest to forest managers. Fuel, fiber, and food for other trophic levels, and stabilization of biogeochemical cycles through organic matter accumulation are among the many fates of forest primary productivity. Most consumers (including humans) have developed a preference for utilizing certain NPP components. Obviously, stemwood is of paramount concern to most foresters. Likewise, the impact of herbivorous consumption has gained recognition in intensive forest management. Stand structure and species composition are manipulated to reduce the impact of defoliation by such pests as the spruce budworm, mountain pine beetle, Douglas-fir tussock moth and balsam whooly aphid. A model for the prediction of bark beetle attacks and quantification of mortality has been enhanced by relationships developed in productivity studies (Grier and Waring, 1974; Waring and Pitman, 1980).

For organizational purposes, the productivity of the biosphere is conceptually divided into (1) aquatic (e.g., lakes, rivers, oceans, and estuaries) and (2) terrestrial biomes (e.g., grassland, boreal, and tropical). World estimates of global net primary production suggest that between 122 x 10^9 and 170 x 10^9 dry metric tons of organic matter are produced each year (Basilevich, et al., 1970; Leith and Whittaker, 1975) with approximately 55 x 10^9t ha^{-1} yr^{-1} produced in aquatic systems. Lifecycles and biomass accumulations are typically shorter in aquatic ecosystems. Along continental margins, oceanic production depends heavily on upwellings for enrichment and mixing in the photic zone. Without such mixing, sinking of nutrient-rich organisms carries valuable nutrients beyond reach of suspended autotrophs. Although the oceans occupy nearly two-thirds of the planet, mean productivities are less than one-fifth that of terrestrial ecosystems, where plant biomass accumulations of only 0 to 0.1 g m^{-2} exist (Whittaker, 1975).

Confidence limits have not been placed upon net primary production in the biosphere. Spatial and temporal variability of NPP in terrestrial ecosystems necessitate that typical estimates of NPP be selected from a broad range of values for any biome. The difference between the highest global estimates given by Basilevich, et al. (1970) and that compiled by Leith (1973) is a result of the rather subjective selections of appropriate weighing of average NPP estimates for different communities. Reported estimates are not always comparable due to different techniques used in NPP measurements. Gas-exchange measurement for terrestrial communities is often both an extensive and expensive undertaking; consequently, most production estimates are based upon measurements of growth or biomass accumulation (Whittaker and Marks, 1975).

Measurements of a forest's net production usually involve the application of a harvest technique. If aboveground net production in successional stands is to be assessed, dimension analysis (allometry) can be applied to the tree strata whereas herb and shrub productivities are best determined from sequential harvests (Whittaker and Marks, 1975). Variations in these harvest techniques are common because of the structural differences between ecosystems, the treatment of mortality, and budgetary constraints. A more detailed account of currently used harvest techniques is outlined by Grier and Logan (1977). Because of the obvious technical constraints on direct measurement of temporal sequences in successional studies of productivity, spatial sequences on adjacent sites are used to infer temporal changes (Drury and Nisbet, 1971).

Special techniques are used for productivity assessments of root systems. Sequential harvests using a soil coring device are most prevalent (Böhm, 1980; Harris, et al., 1979; Grier, et al., 1981). To document seasonal patterns of root production, root observation chambers (rhizotrons) have been used. This technique of observing root growth behind a transparent medium is not new. Root laboratories were established as early as 1900 in Germany (Kroemer, 1905) and in Russia in 1915 (Kolesnikov, 1971). Prototypes of modern observation laboratories were constructed in England in 1961 and 1966 at the East Malling Research Station (Rogers, 1969), in Africa (Huxley and Turk, 1967) and more recently in the United States (Taylor, et al, 1970; Fernandez and Caldwell, 1975; Caldwell, 1977; Keyes and Grier, 1981; Teskey and Hinckley, 1981). A significant aim of these later underground laboratories was to observe root growth under undisturbed soil conditions. Rhizotrons are less frequently used in estimating root production. However, both the harvest technique and rhizotrons were used by Keyes and Grier (1981) to examine root production and phenology in Pseudotsuga menziesii stands.

2.1.2 Factors Influencing Net Primary Production

Leith (1975) recognized two virtually ubiquitous conditions in plant communities; (1) species produce biomass in unequal amounts and (2) no single species carries out primary production for a whole community. The relative production profiles of species suggest that productivity of a community is shared spatially among the different species (Whittaker, 1975). There is a complimentary relationship between the productivity of tree and shrub strata. This is not surprising since net primary production is a community attribute. Long life cycles and stability of terrestrial plant communities are crucial to the development of biomass and sustained high primary productivity (Waring and Franklin, 1979).

Terrestrial and aquatic communities differ markedly in structure and function. The biomass of forest communities is often more than four orders of magnitude higher than that of rooted aquatic plants (Whittaker, 1975). Vertical stratification in plant communities is a method which allows for maximum utilization of photosynthetic tissues. Stratification is also a means of attaining greater leaf areas. Increased leaf areas in ecosystems may result from both growth and development of individuals of the same species and by the addition of genetically different individuals into different strata. The ability to accumulate annually the net products of photosynthesis provides a means of sustaining high levels of production.

Climate is a major determinant of the amount of solar radiation and heat available to plants for organic matter production. If water is not limiting, leaf area indices increase with latitude and production rates are also expected to rise (Kira, et al., 1969). Climate has been related to the gross production rate of forest ecosystems through its affect on the length of the growing season and on the total leaf area which a stand can support (Kira and Shidei, 1967). Longer growing seasons at lower latitudes appear to affect gross production rates much more than NPP. High gross production rates may be offset by increased respiration which is associated with warmer climates at low latitudes.

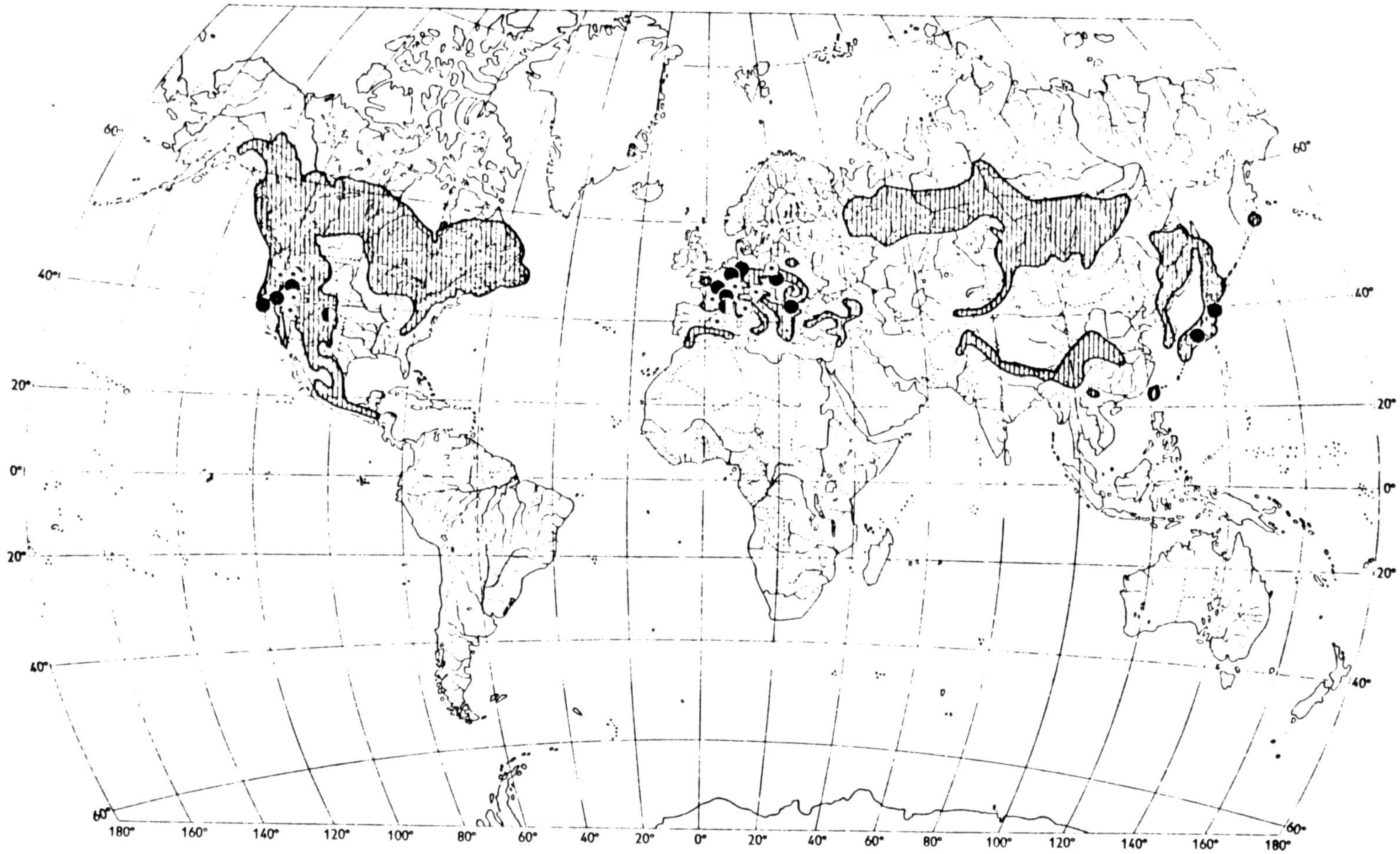
Moisture deficiencies over much of the earth's surface limit the production of plant communities. Commonly, plants use between 700 and 1000 grams of H_2O per gram of dry weight increment (Whittaker, 1975). Large amounts of water are needed for transpiration if the stomata are to remain open during daylight hours. In the absence of water, carbon dioxide absorption and assimilation on a diurnal or seasonal basis are proportionally retarded. Site water balance may dictate the potential productivity of a stand by determining the leaf area which a community can support (Grier and Running, 1977). In the absence of runoff, primary production is linearly correlated with precipitation rates from zero to approximately 700 mm per year (Leith, 1973). In areas with more than 700 mm of annual rainfall, primary productivity increases more slowly with increasing precipitation and becomes asymptotical approaching 4000 mm of annual rainfall.

Correlations of NPP with aspects of climate such as temperature or evapotranspiration has been reasonably successful (Rosenweig, 1968; Basilevich, et al., 1971; Gholz, 1982). Water is released into the atmosphere not only in the processes of transpiration and respiration but also by evaporation. As water is frequently in short supply, actual seasonal evaporation is usually lower than potential evaporation. Actual evapotranspiration (AET), which may effectively integrate both temperature and precipitation, has been related to net primary production (Whittaker, 1975). With increasing AET, Rosenweig (1968) showed an exponential rise in NPP. This correlation of NPP and AET is somewhat remarkable given that AET was only crudely estimated with no allowances made for soil water holding capacity or groundwater usage by vegetation. Strong correlations between NPP of Pacific Northwest communities and (1) site water balance (based on the actual extraction of soil water) and (2) minimum January air temperatures were presented by Gholz (1982).

Variability in NPP reported for forest stands growing under comparable climates can be ascribed to stocking, site, age, or differences in species composition. However, the apparent differences in primary productivity result in part from the varying proportion of NPP which is actually measured (Harris, et al., 1977; Grier, et al., 1981). Forest ecosystems may be much more efficient in the conversion of sunlight into organic material than was previously recognized. By neglecting the primary productivity occurring belowground, substantial errors in NPP assessments for some temperate forest ecosystems are becoming apparent. For instance, above- and belowground biomass and NPP above- and belowground were compared in two 40 year-old Pseudotsuga menziesii stands growing on sites of contrasting quality (Keyes and Grier, 1981). Seasonal determinations of fine root (<2 mm in diameter) biomass indicated that the proportion of NPP located belowground was two to three times higher on the "low site" than on the "high site." Overall, NPP, considering both above- and belowground components, was not greatly different between the two stands (Keyes and Grier, 1981). The increasing emphasis on belowground ecosystem processes was in part spurred by Harris and Kinerson (1973), who discovered that the seasonal fine root dynamics of 45 year-old yellow poplar (Liriodendron tulipifera L.) accounted for 9.0 t ha^{-1} yr^{-1} of the stand's NPP. A review of these and other root studies may be found in Harris, et al. (1979).

2.2 Characteristics of Montane Pacific Northwest Forests

The genus Abies is now widely distributed in montane to boreal forests of the Northern Hemisphere, as can be seen in Figure 1. Its distribution is continuous over large portions of North America, from west of the Yukon Territory, at 64°N latitude, to the mountains of Honduras, at 14°N latitude. The absence of Abies spp. in central continental America is indicative of Abies spp. less competitive status in arid climates dominated by grasslands and desert shrubs. Abies species are found in nearly pure stands at certain elevations and in



Abies: present distribution — ▭; distribution in the past — Eocene (or in Samland Oligocene) ⊕, Oligocene ◐, Miocene ⊙, Pliocene ●.

Acta Horti Bergiani. Band 20. N:o 4. 1963

Figure 1. Past and Present Distribution of Abies spp.

mixed stands above or below this band. For example, the current altitudinal distribution of Abies amabilis is shown in Figure 2.

There is general agreement among investigators of zonal montane vegetation in the Pacific Northwest that the distribution of forest communities is under the controlling influence of temperature and moisture. Piper (1906) concluded that the regional macroclimate is responsible for the distribution of vegetation over the entire region. Recent investigators have used indirect gradient analyses to discern the relative ecological differences between Tsuga heterophylla and Abies amabilis in the Washington Cascades (Fonda and Bliss, 1969; Thornburg, 1969; Kotar, 1972; Dyrness, et al., 1974; Long, 1976; Zobel, 1976). Dyrness, et al. (1974) suggested that the montane vegetation is ". . . arrayed along moisture and temperature gradients." Zobel and his coworkers have attempted to verify this indirect gradient analysis by assigning each of 16 stands a relative position with respect to temperature and moisture using the Temperature Growth Index (TGI) (Cleary and Waring, 1969) and a pressure bomb to determine maximum predawn moisture stress (PMS). Whereas PMS was successful in differentiating Tsuga heterophylla and Abies amabilis zones, it was less useful in separating communities within the Abies amabilis zone.

Until comparatively recently, detailed studies of production ecology were restricted to accessible and commercially important

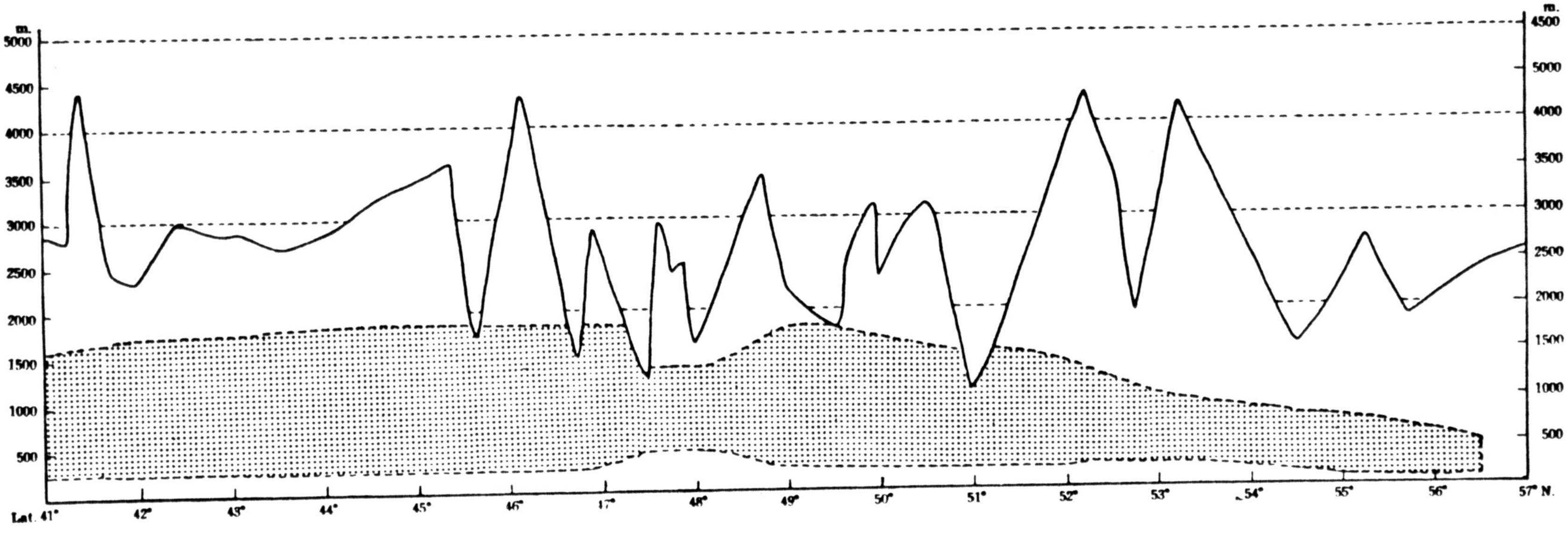


Figure 2. Altitudinal Distribution of Abies amabilis

lowland species. A detailed synthesis of most current synecological and relevant autoecological research is presented by Franklin and Dyrness (1973). Information available for the *Abies amabilis* zone, both in number of references and total pages, is comparatively scarce.

Physiologically, *Abies amabilis* appears unsuited to dry habitats. Krajina (1969) has suggested that *Abies amabilis* requires abundant soil moisture and, in general, an excess of 255 cm of yearly precipitation. Its susceptibility to moisture stress under conditions of high evaporative demand and low soil temperatures common in the spring were discussed by Hinckley and Ritchie (1972). Frozen soil conditions and hence the unavailability of moisture in the interior subalpine zone of British Columbia has been offered as an explanation for the absence of *Abies amabilis*. The geographic distribution which reflects the relatively narrow ecological amplitude of *Abies amabilis* is shown in Figure 3.

Provided that soil water is not limiting, cool soil temperatures may be advantageous for *Abies amabilis*. Its large seeds germinate rapidly following snowmelt (Thornburgh, 1969; Edwards, 1973). Kotar (1972) concluded that ". . . fast germination and rapid seedling establishment, especially establishment of root systems" were among the factors which enable *Abies amabilis* to succeed at higher elevations. He found that less moisture stress developed in *Abies amabilis* seedlings when compared with *Tsuga heterophylla* seedlings in controlled soil

Figure 3. Geographical Distribution of *Abies amabilis*

temperatures of 4°C. Following this moisture stress experiment, subsequent harvesting revealed that the Abies amabilis seedlings had twice the root/shoot ratio of Tsuga heterophylla (Kotar, 1972).

The structural development which distinguishes Abies amabilis zone ecosystems from lower elevation forests of the Tsuga heterophylla zone have not been investigated. Patterns of aboveground biomass accumulations in the lower Abies amabilis zone have been studied by Long (1976) using a chronosequence approach. Although successional trends were investigated with respect to dominance and diversity of both overstory and understory strata, the functional role of these structural changes has not been established. In contrast, both the functional and structural consequences of succession have been reported for Pseudotsuga menziesii in Tsuga heterophylla zone ecosystems using a chronosequence (Turner, 1976). Nutrient redistribution, foliar biomass, and the role of the understory in net primary production are discussed for Pseudotsuga menziesii by Turner and Long (1975) and Long and Turner (1975). A recent study by Grant (1980) found that height growth of Abies amabilis surpassed both Pseudotsuga menziesii and Tsuga heterophylla approximately 80 years after establishment.

Comparative productivity data for Abies amabilis zone ecosystems are scarce. Grier, et al. (1981) found aboveground net production in 23 and 180 year-old Abies amabilis stands to be 6.4 t ha^{-1} yr^{-1} and 4.5 t ha^{-1} yr^{-1}, respectively. With the inclusion of belowground net production, the total net primary production for these stands was reported to be 18.3 t ha^{-1} yr^{-1} for the 23 year-old and 16.8 t ha^{-1} yr^{-1} for the 180 year-old stands. However, Kira and Shidei (1967) have stated that primary productivity may amount to 25-35 t ha^{-1} yr^{-1} in most forest types provided that the stand is young in age, fully stocked, and has achieved canopy closure.

CHAPTER III

MATERIALS AND METHODS

3.1 Research Areas

All study sites were located in the upper reaches of Seattle's Cedar River watershed about 65 km southeast of Seattle, Washington (Figure 4). The west flowing Cedar River drainage is a 35,000 hectare catchment extending from about 1650 m elevation near the crest of the Cascade Mountains to about 200 m in the Puget Lowlands. The watershed was one of the intensive research sites of the Coniferous Forest Biome (Gessel, 1972). Weathered fragments of the Cougar Mountain formation from early Miocene lava flows underlie all study sites (Hirsh, 1975). The present topography results from downcutting of these andesitic rocks by alpine glaciers during the Pleistocene.

Soils of the upper Cedar River are generally spodosols formed from mixed parent material, having diagnostically thick forest floors accumulated over bleached A-horizons, and underlain by illuvial reddish-brown Bhir horizons. Although morphologically the soils of all sites studied are spodosols, technically they are classified as Inceptisols (Cryandepts), owing to the deposition of Mazama and Mt. St. Helens' Y and W ash (Ugolini, et al., 1974). A-horizons vary with tephra accretions from 4 to 13 cm in depth, and beneath this irregularly

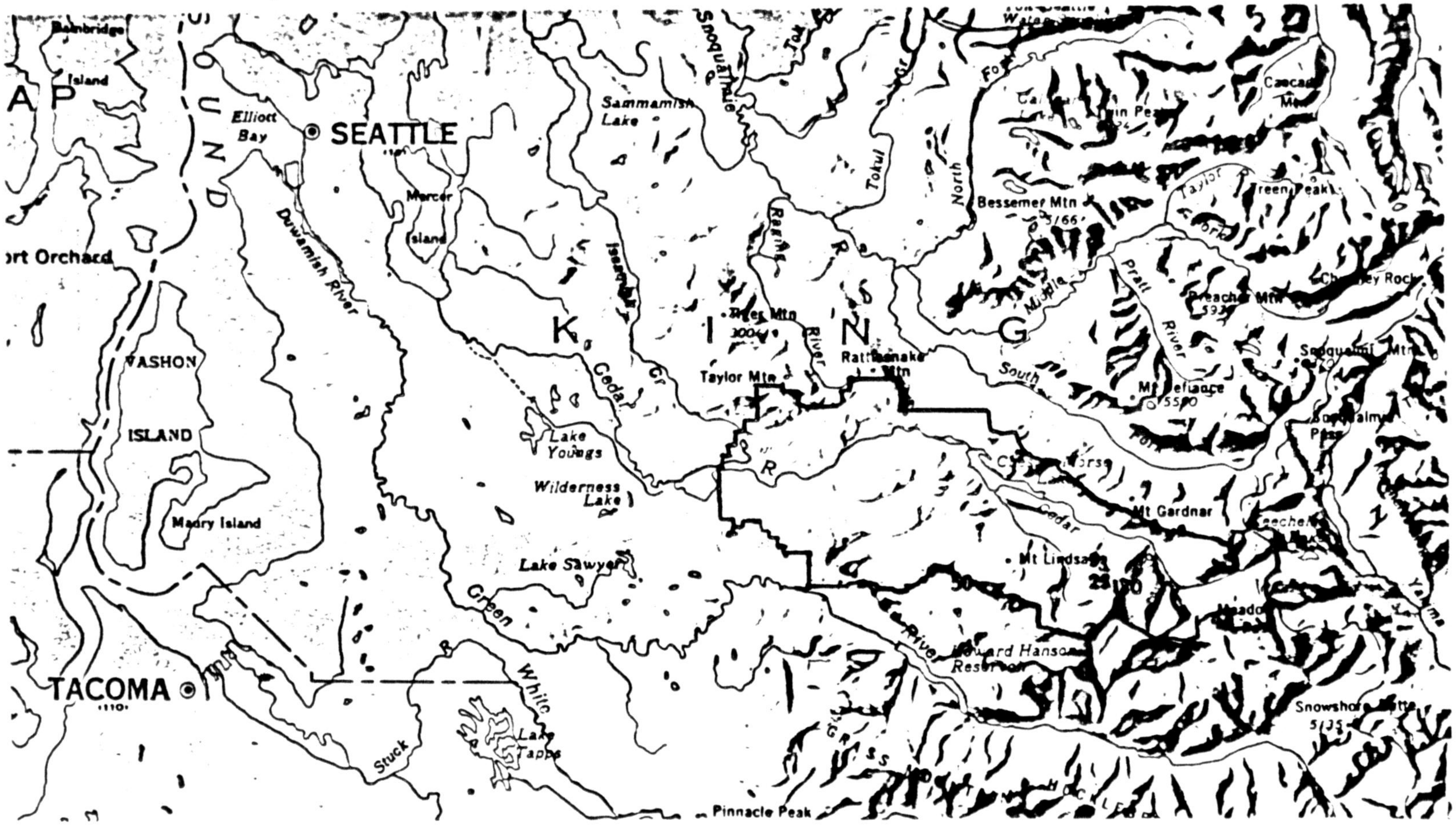


Figure 4. Research Areas in the Cedar River watershed, Washington Cascades

bleached horizon lies a B2-horizon formed from fractured andesite with volcanic ash filling the voids. Forest floor depths vary between 4 and 18 cm in mature stands and 3 cm or less in recent clearcuts.

Climate of the upper Cedar River is cool and humid. Mean annual temperature is 5.5°C with January and July averages of -3.2 and 14.4°C, respectively. Nearly 70% of the 230 cm annual precipitation falls as snow between mid-October and May. The relatively short, frost-free growing season averages 117 days long (NOAA, 1980).

Five sites were used to study structural and functional attributes of Abies amabilis zone ecosystems along a chronosequence. Young, previously clearcut, 3- and 9 year-old stands were located along Findley Ridge 1 km from the 23 year-old stand and 4 km from the 180 year-old stand in the Findley Lake basin. More detailed descriptions of the latter two stands can be found in Grier, et al. (1981). A 50 year-old stand which had been released following salvage logging of the overstory in 1970 was located on Boulder Ridge, 8 km to the west of Findley Ridge (Figure 4).

The sites were chosen to represent a gradient in time. As expected, the floristic representation as measured by species percent, cover age, constancy, diversity, or dominance varied considerably. However, differences in relief and parent material were minimized during site selection to focus on changes in community production structure with ecosystem maturity. Some characteristics of the study areas are listed in Table 1.

The forest composition of the study plots was representative of the *Abies amabilis* vegetation zone as described by Franklin and Dyrness (1973). The zonal climax of these stands based on constancy and coverage would be the *Abies amabilis*/*Vaccinium alaskaense* association. For the tree strata, *Abies amabilis* is the dominant conifer in each stand along the chronosequence. *Tsuga heterophylla* was found ubiquitously throughout the study areas in keeping with its role as a subclimax species in this cool and moist zone (Franklin and Dyrness, 1973). Common associates in the tree strata were in order of decreasing frequency: *Pseudotsuga menziesii*, *Tsuga mertensiana*, *Pinus monticola*, and *Abies procera*. Well-developed herb and shrub strata were found beneath all but the dense 50 year-old stand. Ericaceous genera formed a conspicuous shrub layer with *Vaccinium membranaceum*, *V. ovalifolium*, *V. alaskaense*, and *Menziesia ferruginea* being dominant. The herb layer was dominated by *Xerophyllum tenax* along with *Cornus canadensis*, *Linnaea borealis*, *Achlys triphylla*, *Clintonia uniflora*, and *Rubus pedatus*. In the 50- and 180 year-old stands, branch and stem eiphytes of *Alectoria spp*. (a lichen) were also prevalent.

Table 1. Selected Characteristics of Research Sites in <u>Abies</u> <u>amabilis</u> Stands of the Cedar River watershed of the Washington Cascade Range

Age (yrs)	Slope (%)	Aspect	Mean Diameter (range/cm)	Mean Height (range/cm)	Basal Area (m^2 Ha^{-1})	Conifer Stocking stems Ha^{-1}	Establishment ment (cause)	Elevation (m)	Forest floor depth(cm)
3	0-6	South West	0.51 (.2-4.1)	.22 (0.1-1.2)	2.8	38,200	clearcutting	1230	6
9	13-33	South West	0.75 (.2-5.2)	.36 (0.1-1.8)	8.7	53,900	clearcutting	1220	4
23	5-12	South West	2.6 (.5-7.0)	1.4 (0.3-2.6)	45.7	110,000	clearcutting	1140	6
50	11-28	South	18.8 (1.2-40.6)	10.4 (1.1-15.0)	82.5	9,300	selection (salvage)	1200	15
180	0.5	South West	37.8 (0.2-104)	22.1 (0.1-39.0)	74.3	510	natural (unknown)	1140	18

3.2.1 Stand Measurements

3-, 9-, and 23 year-old stands

Stem diameters of all conifer saplings were measured to the nearest tenth millimeter with vernier calipers at 15 cm above the soil surface in six 6 m x 6 m plots in the 3- and 9 year-old stands and in eight 6 m x 6 m plots in the 23 year-old stand. Mean diameter and length (or height) of all dead branches, logs, and stumps were recorded for all plots. Conifers less than 2 cm in diameter at the 15 cm measurement height were sampled along with understory herbs and shrubs in the 3- and 9 year-old stands. Thirty trees covering the range of stem diameters present were harvested. Disks at the measurement height of 15 cm were removed from conifer samplings for determination of diameter increment. Diameter increments for seedlings (< 2 cm in diameter) were measured at the root collar.

50- and 180 year-old stands

Stem diameters for all trees greater than 2 cm at 1.37 m (dbh) were measured in six 8 m x 8 m plots in the 50 year-old stand and eight 25 m x 25 m plots in the 180 year-old stand. In the 50 year-old stand, tree ages were determined from thirty increment cores taken at dbh from trees covering the range of stem diameters. Fifty-two increment cores were obtained from trees in the 180 year-old stand for age determination. In addition, the radial increments of all cores were also measured to obtain an average growth increment for the last five years. In addition, six trees in each stand were severed at the soil surface and the tree's age was measured and compared to the age at dbh. Based upon these results sixteen years were added to each core to correct breast height age to total age.

3.2.2 Biomass Determination

3- and 9 year-old stands

Sixteen *Abies amabilis* seedlings and saplings representing the full range of size classes were carefully excavated with a shovel in each stand. Soil was gently shaken from the root systems and the intact conifers were returned to the laboratory for aging and dimension analysis following procedures detailed by Whittaker and Woodwell (1971). Biomass regression equations for stemwood, branch, foliage, coarse root (>5 mm in diameter), and fine root (<5 mm) were developed and the summary statistics are tabulated in Appendix A.

23 year-old stand

Fifty-two trees ranging from 0.5 cm to 6.5 cm in diameter were taken from a 1 m x 6 m plot in this stand and destructively analyzed. Procedures and equations for aboveground biomass are found in Grier and Milne (1981). Coarse root biomass was estimated from the excavation of eight root systems. Each root system was dried in a kiln at

$70^{o}C$. The biomass of each root system was corrected for losses due to breakage by tallying the diameters of broken ends and applying a separate regression equation. More detailed discussion of this approach is provided by Santantonio, *et al*. (1978). Root biomass regression equations are included in Appendices A and B.

50- and 180 year-old stands

Published allometric relationships were used to estimate stemwood, stembark, and branch biomass in each stand (Gholz, *et al*., 1979). Separate regression equations were used to estimate biomass for each species.

Recently wind-thrown *Abies amabilis* located on Findley Ridge were used to establish an allometric relationship for coarse root biomass. Root masses of trees ranging from 19 to 84 cm in stem diameter (measured at stump height of 30 cm) were hand winched onto a pickup truck bed and transported to the University of Washington. Soil and detritus were removed. Broken ends of roots were tallied and a correction factor applied for broken root tip loss in accordance with the procedures described by Santantonio, *et al*. (1978). Root masses were cut into manageable sections and weighed on a 450 kg postal scale (accuracy ± 1 kg). After fresh weighing, extensive subsampling was undertaken to correct for moisture content and to ascertain possible changes in specific gravity due to the decay of smaller root portions.

3.2.2.1 Foliage Biomass--Branch sampling in the 50- and 180 year-old stands

Due to previous discrepancies in reported leaf biomass of the 180 year-old *Abies amabilis* stand (Turner and Singer, 1976; Grier, *et al*., 1981), an alternative approach utilizing both destructive and non-destructive methods was used to calculate foliar biomass. A total of 60 branches were harvested. Branches were removed from four sample trees in the 50 year-old stand and seven trees in the 180 year-old stand. These branches were used to assess foliage biomass and were removed from trees on which the diameter of basal branches had been measured. Crowns of the largest nine trees were vertically divided into three sections. Two branches were severed from the lower, middle, and upper sections of each tree. A total of 54 branches were removed from these nine trees. Three branches were destructively analyzed on each of the two smallest trees. Foliage-bearing twigs of each years' cohorts were weighed fresh in the field. Subsamples used for moisture content and foliage-to-twig ratio determination were randomly selected for subsequent oven drying at 70°C and needle removal. A branch-to-foliage regression equation was then developed (Appendix C). The regression of branch diameter on foliage weight for each branch of the eleven sampled trees was used to reconstruct the total foliage biomass for each tree. As illustrated in Appendix D, these

Abies amabilis trees had considerably less foliage than those reported by Gholz, *et al*. (1979).

3.2.2.2 Understory--Biomass Determination

Understory vegetation, which consisted of conifer seedlings, shrubs, and herbs, was harvested in six 1.5 m^2 plots located at the southeast corners of each of the 3- and 9 year-old study plots and in 34 randomly located 1 m^2 plots in both the 23- and 180 year-old stands. Only a trace of understory biomass was present in the 50 year-old stand. Harvest sampling for biomass determination was undertaken in early May following snowmelt and again in early August at the height of the growing season. Conifer seedlings less than 2 cm in diameter (at the measurement heights of 15 cm in the 3-, 9-, and 23 year-old stands and 1.37 m in the 180 year-old stand) were treated as shrubs. All plant material was dried at 70°C for 72 hours or until a consistent dry weight was achieved. Understory biomass reported herein is a two year average of August harvest samplings.

3.2.3 Woody Detritus and Forest Floor Detritus

Woody detritus of standing dead trees, fallen logs, and stumps was estimated by computing the volumes of each component on the plots from the midpoint diameter and length (or height). Volumes for standing dead trees were computed using tarif tables (Turbull, *et al*., 1963) to account for parabolic taper. Average specific gravity was obtained by removing cross-sections from 15 standing dead trees, fallen logs, and stumps in the stands sampled. Each volume was then multiplied by its average specific gravity. A more detailed treatment of the sampling procedure is detailed in Grier and Logan (1977).

The forest floor was randomly sampled at 40 locations in each stand. A circular frame held perpendicular to the slope and a sharp knife were used to remove organic material. Woody material >10 mm in diameter and roots >5 mm in diameter were removed from the forest floor samples after being dried at 70°C. All material was ground fine enough to pass through a 40 mesh screen and subsampled for weight loss on ignition (450°C).

3.2.4.1 Litterfall Collections

Litter traps lined with 100 mesh nylon net were used for collection of litterfall <1 cm in diameter in all stands. In the 3-, 9-, and 23 year-old stands a total of 192 24 cm diameter circular littertraps were employed for biannual collections of litterfall. A total of seventy larger littertraps (50 cm x 50 cm) were used in the 50- and 180 year-old stands. Litter was hand-sorted into the following categories: live and dead conifer needles, live and dead deciduous leaves, twigs, lichens and mosses, plant reproductive parts, insect frass and feces, and miscellaneous material. Eight 3 m x 10 m branchfall plots were established to collect branch litter < 10 cm in diameter in each stand. After plots were surveyed and boundaries marked with rope, all material greater than 1 cm in diameter was removed from the plots by raking prior to the first collection. Branches were collected immediately after snowmelt. Following field collection, all litterfall was dried at 70°C.

3.2.4.2 Fine Root Biomass Sampling

Fine root biomass was determined by periodic soil coring in the 23- and 180 year-old stands as part of the study reported by Grier, _et al_. (1981). Beginning in April, 1978 and continuing at three to eight week intervals until April, 1979, thirty soil cores were extracted from each stand. Additional soil coring was undertaken in these two stands in the fall of 1979 and again in the spring of 1980 for a closer examination of these periods of rapid fluctuating fine root biomass. Soil cores were taken with a 3.8 cm inside diameter (ID) sharpened steel tube which was driven into the soil to the B-horizon (approximately 35 cm).

Less intensive fine root sampling was conducted in the 3-, 9-, and 50 year-old stands. A larger corer (5.1 cm ID) was used for fine root biomass estimation in these three stands. Twenty-five cores were extracted from each of the stands in May, August, and October of 1979 and 1980.

Cores from all stands were placed in PVC transport tubes, sealed in plastic bags, and returned to the laboratory for sorting and weighing. In the laboratory, each core was divided into the forest floor, and A- and B-horizons. Each horizon was individually processed. Fine roots from the mineral horizons were washed over a 0.5 mm mesh sieve. Procedures used to process cores are described in detail in Grier, et al. (1981). Roots were then separated into two size categories based on their diameter: 0-2 mm and 2-5 mm. Angiosperm and conifer roots <5 mm were dried at 70°C and weighed for biomass determination. Biomass for roots >5 mm in diameter was obtained from regression equations developed in this study (Appendix A).

3.2.5 Computations

Net primary production (NPP) was estimated from the equation $NPP = \Delta B + L + G$, where ΔB equals above- and belowground plant tissue formed during the interval 1977 to 1978 (Grier, et al., 1981), L equals mortality (tree and shrub mortality, branchfall, litterfall, and fine root turnover) and G equals grazing loss of plant material to herbivore consumption. Grazing was estimated from measurements of insect frass, and feces of mice, vole, deer, and elk which were separated from other litterfall components from June, 1979 to June, 1980. Estimates indicated that grazing was less than 1% of NPP in all stands, and therefore were not included in estimates of NPP.

Biomass Increment (ΔB)

Biomass for all conifers in the stand was calculated for 1978 from regression equations on stem diameter. Biomass in 1977 was then estimated by recalculating the stem diameter for 1977 and then applying the regression equation. Biomass increment for stemwood, stembark, branch, and coarse roots were determined by subtracting biomass calculated for 1977 from that computed for 1978. Biomass increment of the shrub and herb layers was estimated from the difference between May and August harvests.

Mortality (L)

Tree, shrub and branch mortality was assessed in each stand annually. Litterfall was collected biannually. Fine root turnover was determined by summing differences statistically significant at the 95% level in fine root decrements between sampling dates. Significant differences were determined using the standard t-test as detailed in Grier, et al. (1981). The data presented are an average of two years of sampling.

3.3 Results

3.3.1 Ecosystem Structure

Figure 5 illustrates that bimodal patterns of diameter distributions were present in all but the 23 year-old stand. In the 3- and 9

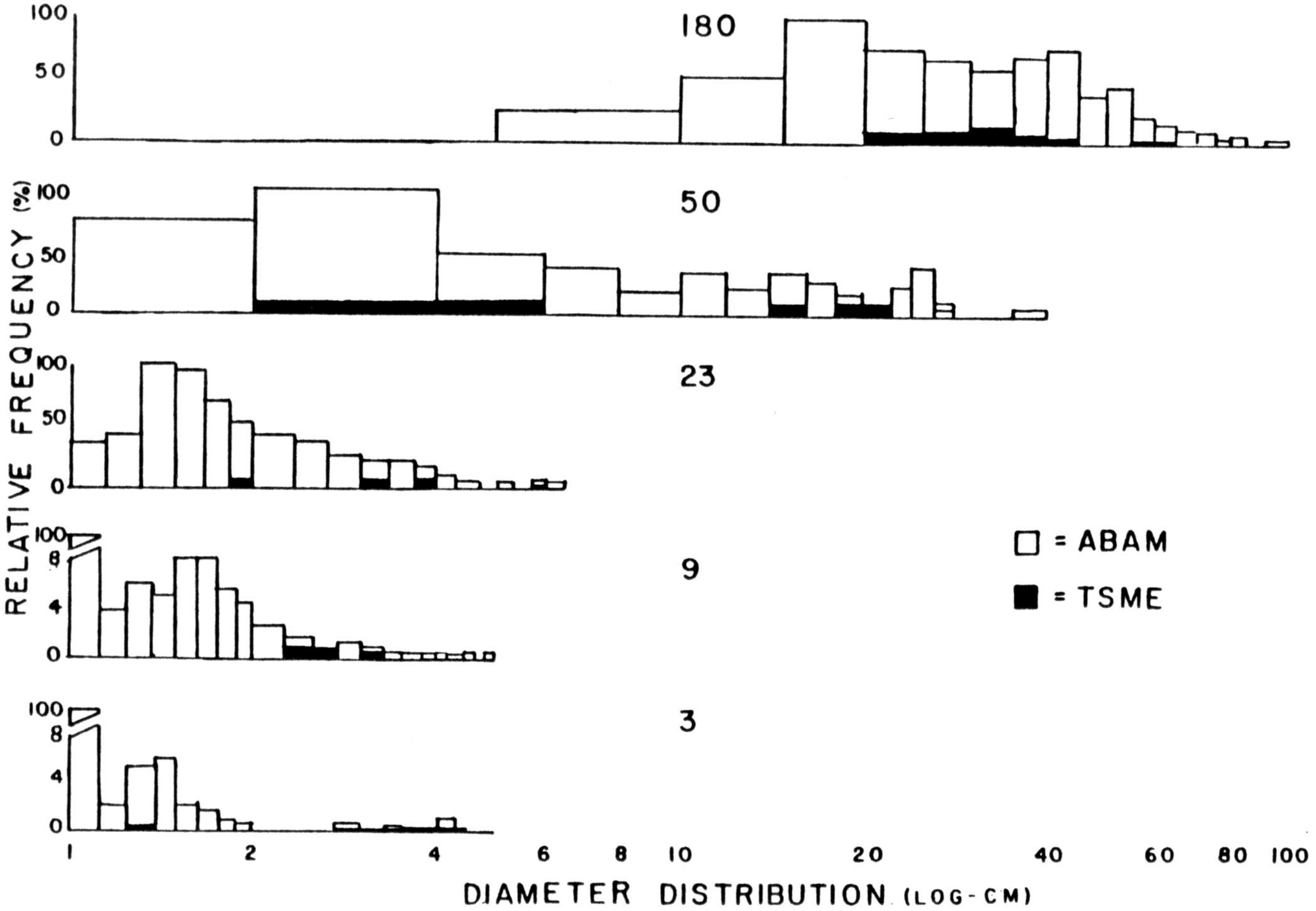


Figure 5. Conifer Diameter Distribution for Five *Abies amabilis* stands

year-old stands, seedlings less than 0.25 cm in diameter comprise the largest percentage of stems. In the 180 year-old stand, stems less than 5 cm were numerous. Relatively few small conifers are present in the 23- and 50 year-old stands. Tsuga mertensiana, although present in all stands, had no apparent peak diameter frequency. It was not found in the smaller diameter classes but was frequently present as saplings from 2 to 6 cm in diameter. Post logging Abies amabilis seedlings ranged from slightly less than 1 cm in diameter in the 3 year-old to slightly greater than 1 cm in the 9 year-old stand. Although a bimodal diameter frequency distribution was absent in the 23 year-old stand, its age structure (Figure 6) indicated that larger diameter classes were a composite of both post logging and advanced regeneration conifers.

Bimodal diameter frequency distributions with peaks about 20 cm apart were found for Abies amabilis in the 50 year-old stand. The two peaks for the largest diameter frequencies in the 180 year-old stand differed by nearly 25 cm, with 15 cm separating the seedlings from the sapling or pole-sized conifers.

Age structure indicates that these Abies stands became established in more than one distinct episode. The narrowest range of tree age and diameters was noted in the 23 year-old stand (Fig. 6). In contrast to the diameter distributions, which appear to overlap, more discrete modal frequencies in age were found. The age structure of all

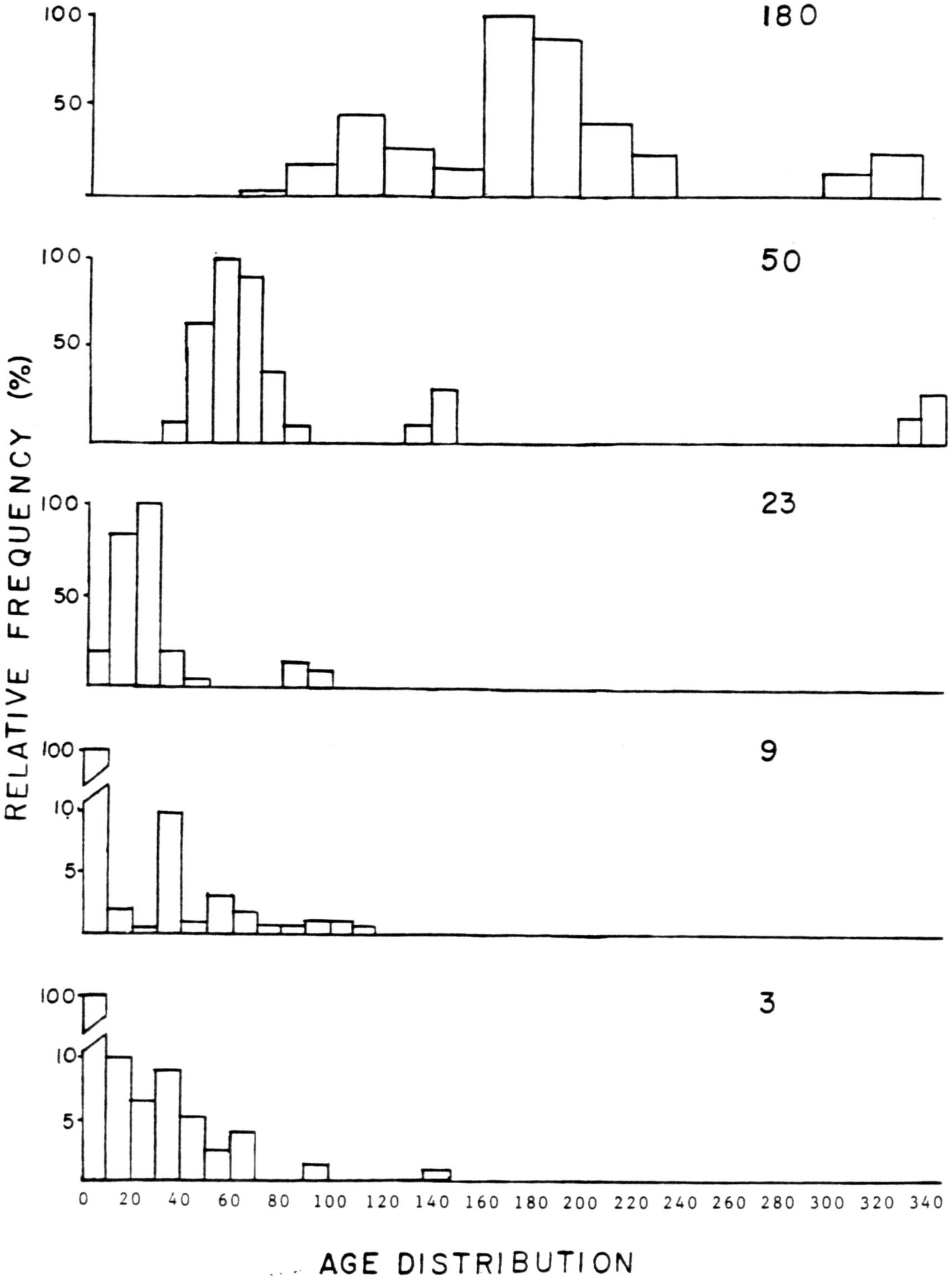


Figure 6. Conifer Age Distribution for Abies amabilis stands

other stands was not normally distributed. The majority of stems were apparently established over periods of 20 to 40 years. Patterns of establishment in intervals ranging from 70 to 85 years were exhibited in the 50- and 180 year-old stands. For example, the oldest stand had three modal ages: 0 to 20; 100 to 120; 180 to 200; and from 320 to 340.

Age and diameter relationships illustrated how these modal frequencies were related (Figure 7). The 3- and 9 year-old stands showed wide differences in age over a relatively narrow range in stem diameters, while in the 23 year-old stand a fairly tight matrix of diameters and age frequencies between 20 and 30 was present. Noticeable increases in diameter and a reduction in the range of ages were found in the 23 year-old stand.

Trees of a given age and diameter occupied a predictable crown class in the stratified canopy of the 180 year-old stand. Interestingly, some of the dominants were not the oldest trees but rather the largest for their respective age. Co-dominant trees were slightly "older" for their size. Not surprisingly, suppressed trees were the "oldest" of the small trees. Trees of the intermediate crown class were not well represented except in storm gaps and disturbed areas along the edges of these stands. The few intermediates that were present had modest diameters (<25 cm) and were 20 to 50 years younger than suppressed trees of the same diameter.

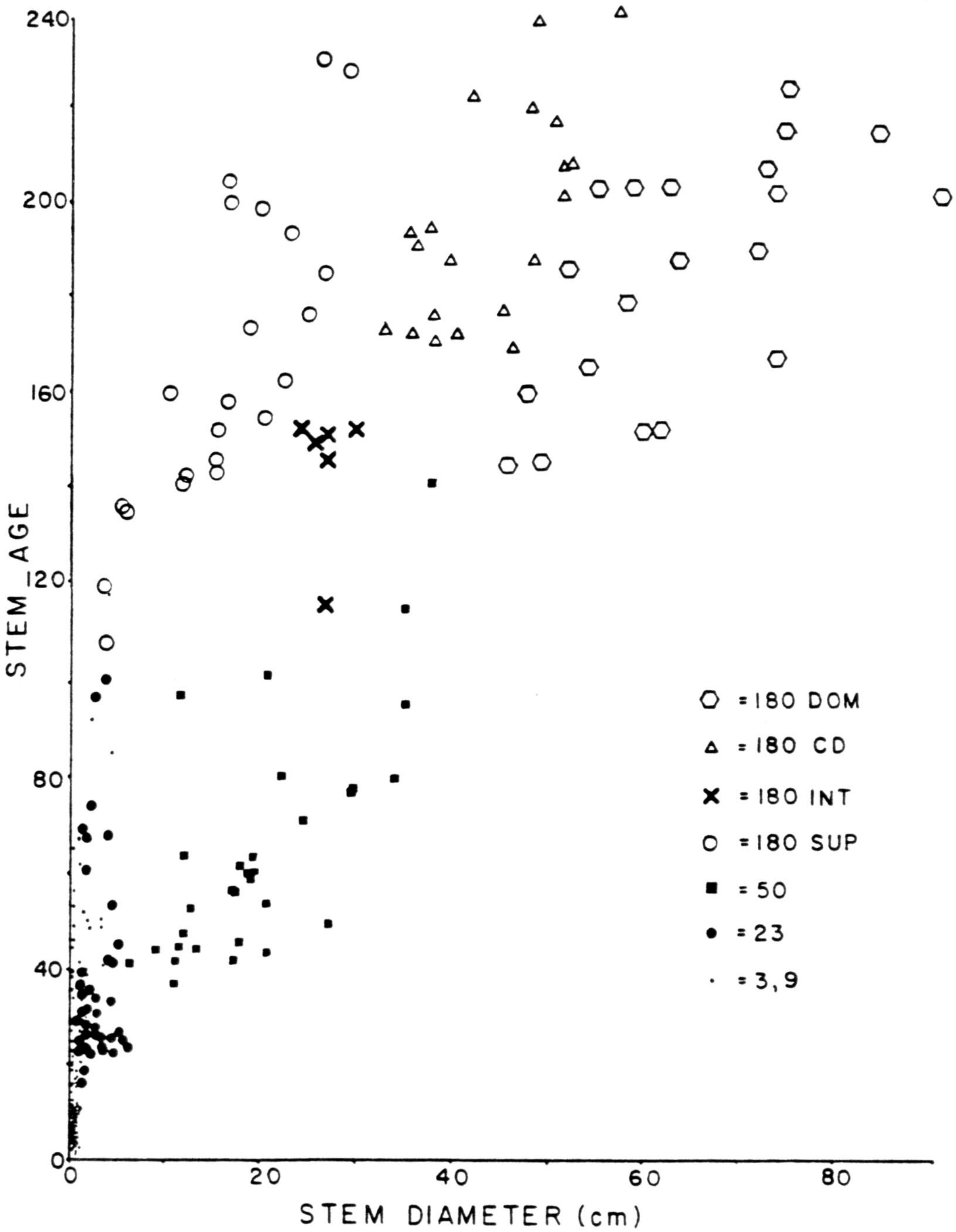


Figure 7. Stem Diameter and Age for Conifers in Five Different-Aged Stands in the Cedar River watershed, Washington Cascades

3.3.2 Organic Matter Distribution

Small increases in aboveground biomass of the tree strata from the time of clearcutting to about 25 years were followed by rapid biomass accumulation (Table 2). Aboveground conifer biomass of nearly 1 t ha^{-1} at three years after clearcutting rose to over 400 t ha^{-1} at 180 years of age. In the 3- and 9 year-old stands, most of the conifer biomass was advanced regeneration (Figure 6). Post-logging conifers, which were still seeding-in in the three youngest stands, rapidly increased as a proportion of total biomass. The distribution of foliage biomass, which was slow to accumulate, appeared to peak in the 50 year-old stand and was lower in the oldest stand examined. All other aboveground tree biomass components increased with increasing stand age. In contrast to aboveground conifer biomass, the biomass accumulation of the herb and shrub layers appeared to decline with increasing stand age. Dominance by Vaccinium spp. and Xerophyllum tenax dominated in the 3 year-old stand while a patchy structure of nearly pure conifer with Vaccinium spp. and Xerophyllum tenax in adjacent rhizominous clumps was found in the 23 year-old stand.

Total belowground biomass increased with increasing stand age but decreased in proportion to aboveground biomass. In the 3-, 9-, and 23 year-old stands, root biomass averaged 40% of aboveground biomass. This ratio of belowground to aboveground decreased to 25% between the 50- and 180 year-old stands. The coarse root fraction

Table 2. Organic Matter Distribution for Different-Aged *Abies amabilis* Stands in the Cedar River watershed in the Washington Cascade Range

	STAND AGE				
	3	9	23	50	180
ABOVEGROUND					
Biomass	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}
Stemwood	521	1440	25000	189000	294000
Stembark	79	213	2650	30500	62200
Live branch	158	517	7750	39300	67800
Foliage	308	930	13600	23200	14800
TOTAL	1066	3100	49000	282000	441800
Epipytes	T[a]	T	T	120	1700
Shrubs					
Stem	3400	2300	2240	T	10
Foliage[b]	596	428	250	T	T
Herb Layer	2150	3740	1310	T	12
TOTAL	6146	6468	3700	T	22
Total Living	7200	9570	52700	282000	442000
Dead Branches (attached)	85	290	2000	4900	7900
Standing Dead Trees (or stumps)	52260	38500	60500	12700	15700
Total Necromass	52300	38800	62500	17600	23600
Aboveground Total	58400	45300	105000	302000	466000
BELOWGROUND					
Trees					
Fine root	296	406	4670	5180	8010
Coarse root	415	658	13600	70700	98700
TOTAL	711	1010	17300	75800	107000
Shrub and Herb					
Fine root	2040	2510	3610	T	229
Coarse root	585	345	571	T	10
TOTAL	2620	3860	4180	T	239
Total Living	3330	4870	21500	75800	107000
Necromass					
Fallen logs	38100	31600	19900	255000	75000
Forest floor[c]	52900	36100	47800	105600	150000
Total Necromass	91000	67700	67700	362000	225000
Belowground Total Organic Matter	149000	103000	99200	437000	332000
Ecosystem Organic Matter (excluding soil)	208000	148000	205000	759000	798000

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[a] All shrub and herb foliage are peak growing season biomass.

[b] Amounts less than 10 kg ha^{-1} or less than 0.1% are indicated by T.

[c] Ash free dry weight at 70°C.

makes up an increasingly large percentage of belowground biomass in maturing stands. Fine root biomass, in contrast, appeared to increase rapidly from the time of clearcutting in the 3-, 9-, and 23 year-old stands. Although sample variation was high in the 3- and 9 year-old stands, statistically significant differences in conifer fine root biomass were found between these two stands. Although aboveground biomass decreased in the 3-, 9-, and 23 year-old stands, fine root biomass for the herb and shrub layers appeared to increase. Total fine root biomass was greater in the 180 year-old stand than in the 50 year-old stand due in part to the increased biomass of angiosperm roots. This simply reflected an increase of the understory biomass in the older stand.

The distribution of detritus in all but the 180 year-old stand reflects their logging history. Clearcutting of mature stands on the sites occupied by the 3-, 9-, and 23 year-old stands removed much of the aboveground biomass. High fallen log biomass in the 50 year-old stand has resulted from snags felled during salvage logging which were not subsequently yarded. During yarding of tree boles, the forest floor was extensively disturbed in the three younger stands.

3.3.3 Community Net Primary Production (NPP)

Major components of NPP are tabulated in Table 3 for all stands. Large differences in net production were present, ranging from 2.91 t ha^{-1} yr^{-1} at three years to the peak production of 23.2 t ha^{-1}

Table 3. Net Primary Production for Different-Aged Abies amabilis Stands of the Washington Cascade Range

	STAND AGE				
	3	9	23	50	180
Aboveground					
Biomass Increment	kg $ha^{-1}yr^{-1}$	kg $ha^{-1}yr^{-1}$	kg $ha^{-1}yr^{-1}$	kg $ha^{-1}yr^{-1}$	kg $ha^{-1}yr^{-1}$
Tree					
foliage	44	153	220	T	T
stemwood	153	260	2850	11900	1580
stembark	18	83	290	1190	360
branch	51	113	900	1200	380
TOTAL	266	609	3360	14300	2320
Shrub stem	588	755	60	T	T
Aboveground Biomass Inc.	854	1460	4360	14300	2320
Detritus Production					
Tree					
needlefall (current)	T	T	80	121	196
needlefall (senescent)	21	24	960	1750	834
dead branch	61	33	50	985	177
mortality	36	870	380	130	39
TOTAL	108	920	1470	2990	1150
Shrub and Herb					
leaffall	616	440	250	T	T
mortality (turnover)	398	660	320	T	50
TOTAL	1010	1010	570	T	50
Aboveground Detritus Production	1120	1880	2040	2990	1200
Aboveground Net Primary Production	1980	3390	6400	17300	3520
Belowground					
Biomass Increment					
Tree coarse root TOTAL	95	201	1780	2600	700
Detritus Production					
Tree fine root	50	75	5920	3300	9180
Shrub and Herb fine root	782	447	3480	T	390
TOTAL	832	522	9400	3300	9570
Belowground Net Primary Production	927	723	11200	5900	10300
Ecosystem Primary Production	2910	4110	17600	23200	13800

yr^{-1} for the 50 year-old stand. Between-plot variability was high in most stands, particularly in the recently harvested 3- and 9 year-old stands. Differences in NPP were observed among the stands. Net primary production increased with increasing stand age very rapidly following clearcutting and was highest in the 50 year-old stand. Net primary production in the 180 year-old stand was only 59% of the 50 year-old stand.

Net primary production closely paralleled leaf biomass throughout the chronosequence, as illustrated in Figure 8. The relative contribution of angiosperms to total NPP was highest (65%) in the 3 year-old stand and constituted a decreasing portion of NPP in the 9-, 23-, and 50 year-old stands, respectively. Aboveground NPP rose more slowly than belowground NPP for conifers in the three youngest stands. Root turnover by angiosperms was greatest in the 23 year-old stand. Peak conifer aboveground NPP was 17.3 t ha^{-1} yr^{-1} in the 50 year-old stand. Although leaf biomass declined between the 50- and 180 year-old stands, belowground NPP constituted a larger proportion of total NPP in the 180 year-old stand.

Shifts in the production allocation within both the above- and belowground compartments of the ecosystems were apparent in the _Abies amabilis_ stands. Production of root biomass ($<$5 mm coarse roots) increased rapidly from 3- to 9- and the 23 year-old stand, peaked in the 50 year-old stand and then declined (Figures 8 and 9). A similar

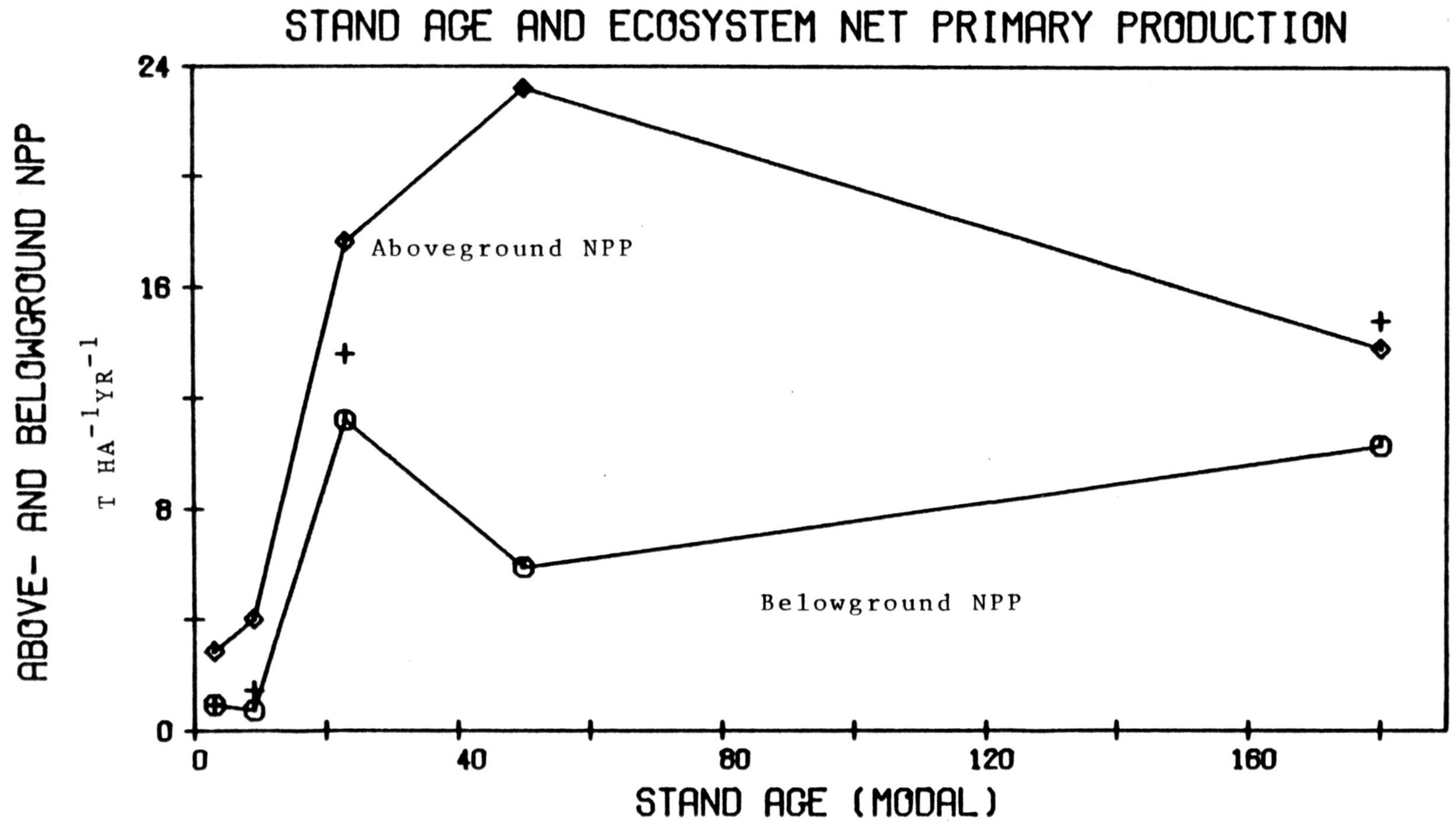

Figure 8. Above- and Belowground Net Primary Production Pattern with Ecosystem Development

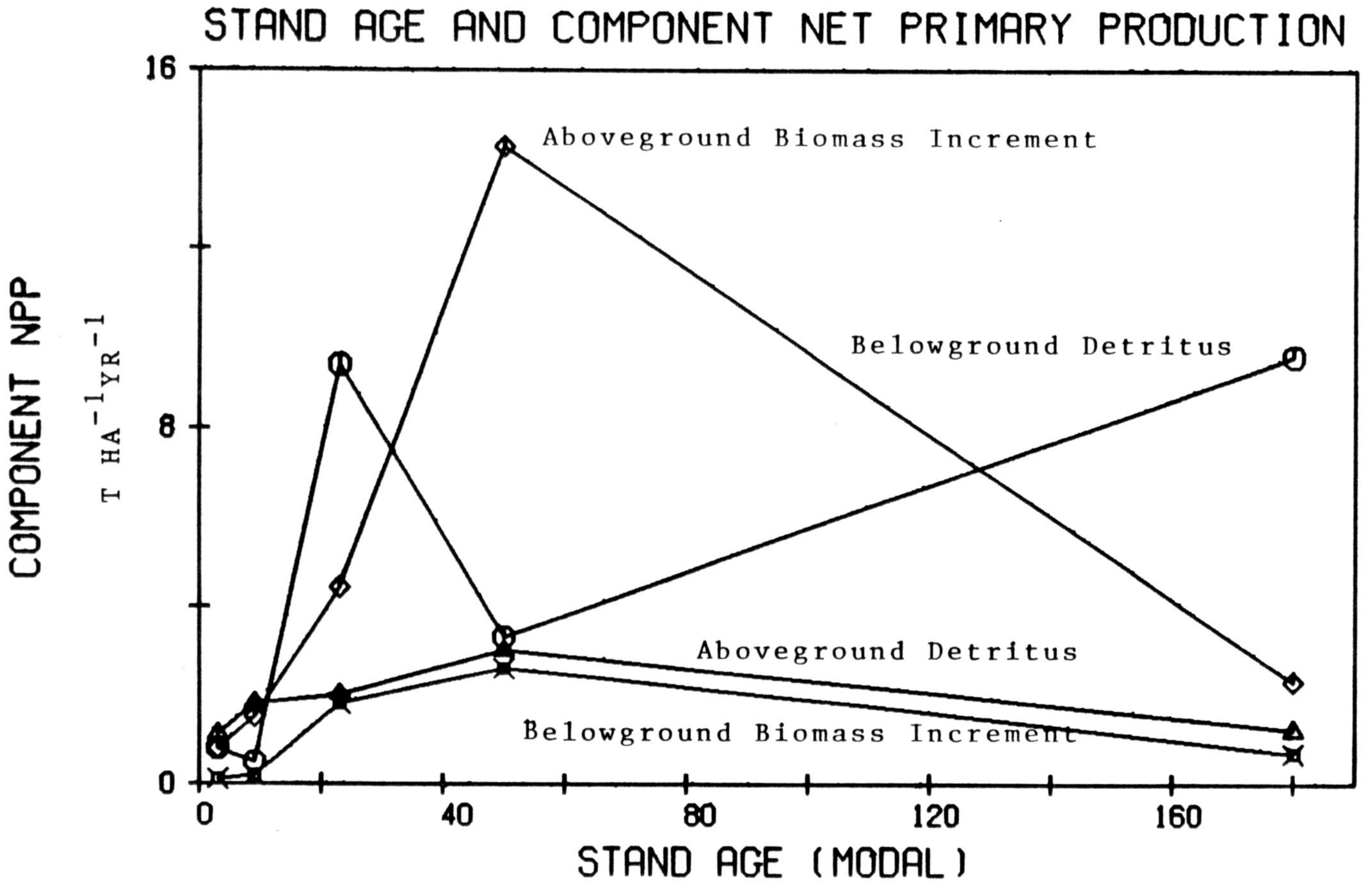

Figure 9. The Distribution of Above- and Belowground Net Primary Production Components with Ecosystem Development

pattern for aboveground biomass increment (stemwood, stembark, and live branches) can be seen. The production of detrital biomass (primarily foliage, dead twigs, and branches) appeared to increase gradually. Foliage biomass and biomass increment peaked in the 50 year-old stand. Production and turnover of fine roots, in contrast, increased abruptly from the 9- to the 23 year-old stand. Associated with the exclusion of the understory in the 50 year-old stand, the fine root component of net production declined. An increase in fine root turnover was noted in the 180 year-old stand in comparison to the 50 year-old stand.

The apparent decline in fine root turnover may be the result of less intensive sampling, as fine root biomass was similar for the 23-, 50-, and 180 year-old stands. In contrast with belowground net production of fine roots, aboveground detritus production approached an equilibrium at 2-3 t ha^{-1} yr^{-1}.

The relationship between net production and foliar biomass showed a strong linear correlation with a coefficient of determination equal to .996 (Figure 10). Although a small (=1 t ha^{-1} yr^{-1}) "b" intercept was noted, the 95% confidence interval includes the origin. Both the highest foliar biomass and the greatest net production were measured in the 50 year-old stand. Foliage biomass and net primary production were nearly identical in the 23- and 180 year-old stands.

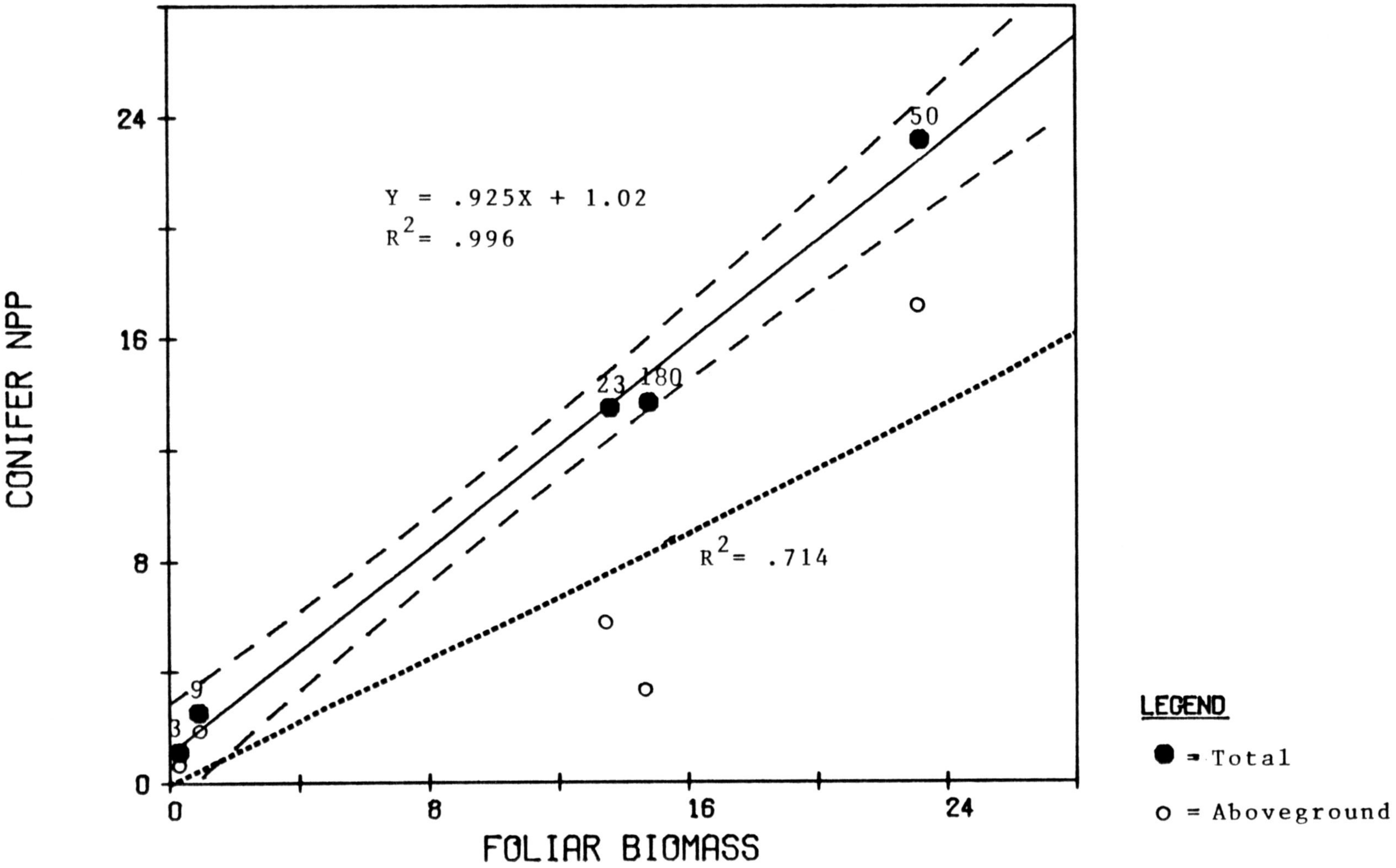

Figure 10. Linear Model of Conifer Foliage Biomass and Conifer Net Primary Production of Five *Abies amabilis* Stands

By comparison, a relatively poor linear correlated (r^2 = .714) for aboveground conifer NPP and foliage biomass.

3.4 Discussion

Production relations along this chronosequence did not strictly conform to the model of community development proposed by Kira and Shidei (1967). The overall pattern of net primary production generally increased with stand age and then declined in the oldest stand. The peak in net production and subsequent decline were paralleled by changes in foliage biomass. Net primary production, as previously stated, is the difference between gross primary production (GPP) and respiration and is expected to decline as ecosystems mature (Margalef, 1968; Woodwell and Whittaker, 1968; Odum, 1969). According to the model presented by Kira and Shidei (1967), gross primary production should be proportional to leaf biomass. As a forest stand matures, leaf biomass is purported to remain near a steady state following canopy closure. Organic matter consumed by respiration is thought to narrow the gap between respiration and GPP as woody biomass increases steadily with age (Kira and Shidei, 1967). This theoretical explanation for the apparent decline in production with increasing ecosystem maturity may be more intuitively appealing than factual. The work of Kira and Shidei is based primarily upon studies conducted in artificially regenerated plantations. The stand's inability to maintain high leaf biomass in the Abies amabilis zone under stresses of heavy snowloads and wind storms may partially explain the decline in NPP and leaf biomass with age. Despite the extreme tolerance of Abies seedlings, advanced regeneration is invariably suppressed. Growth rates in all but the largest storm gaps appear inadequate to fill developing holes left in the slowly thinning canopies.

Large gaps in the canopy with patchy understories are present not only in stands at Findley Lake, but in surrounding stands of the Cedar River Watershed. In general, as one goes upward in elevation from the Abies zone towards the crest of the Washington Cascades, thinner and increasingly patchy canopies become much more prevalent. Continuous forest canopies in the lower Tsuga heterophylla, Abies amabilis, and Tsuga mertensiana zones gradually give way to a mosaic of patchy forest canopies with conifer clumps among shrubby or herbaceous subalpine communities. Finally, on the highest crests, alpine meadow communities prevail (Franklin and Dyrness, 1973).

A supplemental explanation for declining leaf biomass and concomitant net primary production in mature Abies amabilis stands may reside in stand age-size structure. The low stem count and positive skew of the diameter frequency histograms (Figure 5) indicate that even the 180 year-old stand may be still self-thinning (Harper and White, 1970; Mohler, et al., 1980). Sprugel, et al. (1978) found positive skewness until approximately 50 years of age in Abies balsamea stands.

Continued mortality may strongly influence net primary production over time in Abies amabilis stands.

A few studies suggest that aboveground productivity in late successional or near steady state forest communities fail to conform to bioenergetic models. Slowly increasing aboveground net production and leaf biomass has been reported in 600 year-old Pinus albicaulis stands (Forcella and Weaver, 1977). In an "old" Sequoia Sempervirens stand, Westman and Whittaker (1965) found aboveground net primary production to be a modest 14.3 t ha^{-1} yr^{-1}. MacMahon (1980) and his workers have attempted to interpret production along a subalpine sere in light of Odum's (1969) community energetics hypothesis. Tree strata in their oldest (approximately 300 years) stand reportedly have production to respiration ratios greater than one. Leaf production and forest floor biomass continue to increase along MacMahon's (1980) seres, indicating that production and respiration are not in balance in the oldest stand.

The importance of belowground pathways of carbon cycling in forest ecosystems has drawn much attention recently (Harris, et al., 1977; Kimmins and Hawkes, 1978; Persson, 1980; Grier, et al, 1981; Keyes and Grier, 1981). Although data from forest ecosystems is currently limited, increasing evidence indicates that root production and turnover can comprise up to 75% of NPP. Unfortunately, the high variability in results of these labor-intensive investigations continue to plague researchers concerned with the quantification of fine root production and turnover.

In addition to the increasing importance of fine root production and turnover shown by Grier, et al. (1981), one other study has assessed the role of roots in forests with increasing stand age. Larger expenditures for root systems with ecosystem maturity are corroborated in part by Monk (1966) who found that root/shoot ratios increased in late successional species.

Although community biomass steadily increased with age in the present study, the distribution of biomass between conifer and angiosperm species reflects the dynamic nature of stand development in the Abies amabilis zone. Aboveground biomass of angiosperms dropped steadily from clearcutting until crown closure. That proportionately larger amounts of dry matter went into root production in both the 23- and 180 year-old stands may be a reflection of intense root competition and hence lower aboveground stem increment.

Conifer fine root biomass showed a slight decline as maximum leaf biomass was attained and the understory was excluded by stand age 50. A reduction in angiosperm plus conifer fine root biomass and belowground turnover in this 50 year-old stand coincided with accelerated diameter and height growth. The exclusion of angiosperm roots accounted for the greatest portion of the shift from extensively belowground oriented production at a stand age of 23 years to the more commonly recognized aboveground orientation at 50 years. This latter period also corresponds to the time in a stand's life cycle following the majority of self-thinning. Alternatively, accelerated height and diameter growth may be expected as more aboveground growing space is made available by senescing trees. Following the period of rapid aboveground biomass accumulation, there is a shift to increased production belowground, as shown in the 180 year-old stand. More extensive discussion of specific above- and belowground production in the 23- and 180 year-old stands can be found in Grier, et al. (1981). At high elevations, a forests' rapid diameter increment may occur only at certain times in a tree's life cycle; after an adequate root system is established or after competition is reduced.

A current problem remains in presenting a bioenergetic rationale for the apparent decline in NPP with increasing ecosystem maturity. The lack of conformity of this study with the previously characterized drop in productivity with age resides in both the decline in leaf biomass found and the addition of belowground production to the total carbon budget. For comparative purposes, the hypothetical community metabolism model by Odum (1969) and the laboratory microcosm from Cooke (1967) have been redrawn in Figure 11 with actual data from the linear model of the current study (Figure 11c). The overall pattern of community energetics in the Abies amabilis zone takes on a somewhat similar shape to the other models with the inclusion of belowground

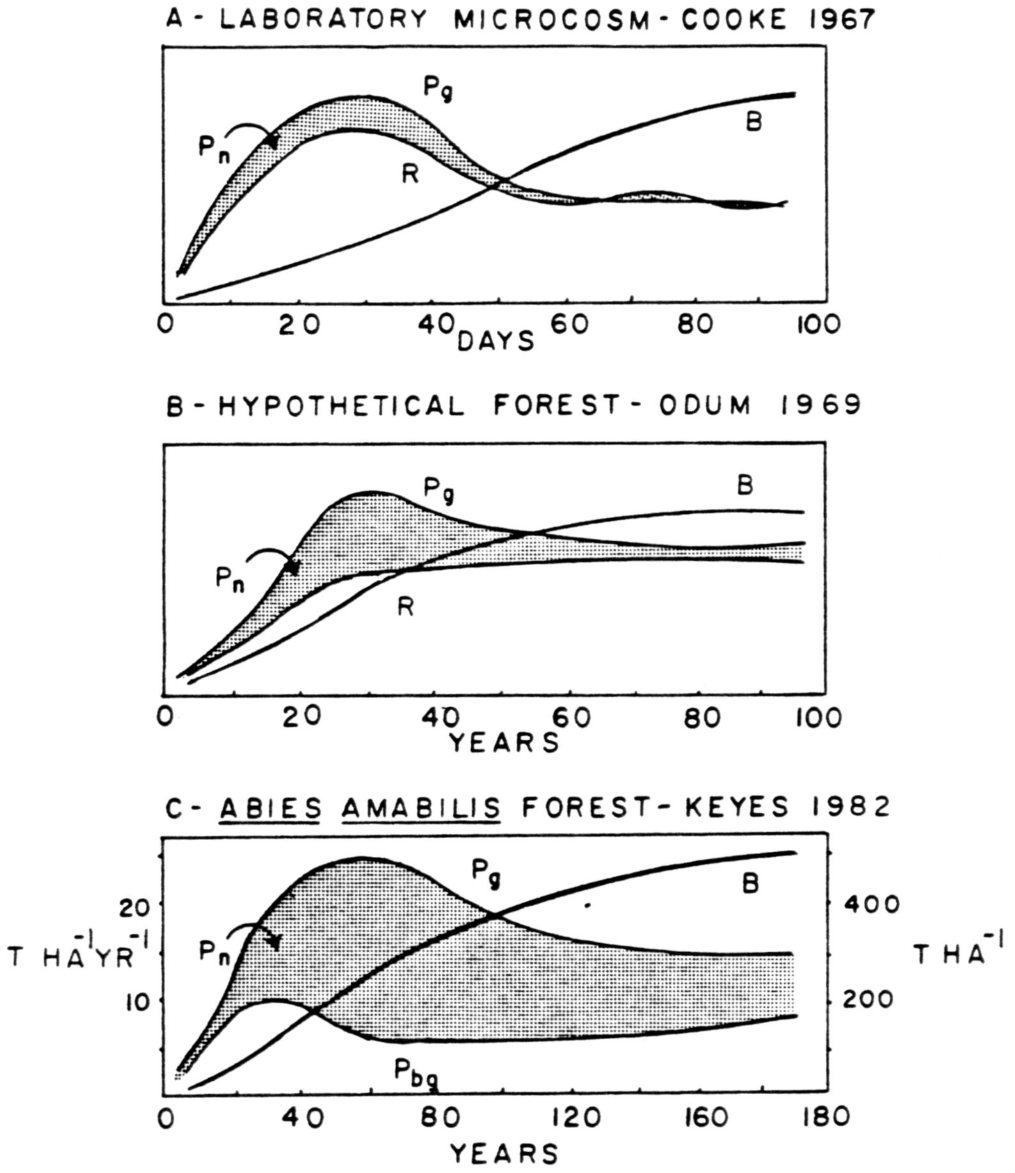

Figure 11. Comparative Community Metabolism Models

production. Changes in respiration need not be invoked to account for trends in primary production if belowground NPP and leaf biomass are incorporated into community metabolism models.

Lack of substantiating data in this and other studies (Kira and Shidei, 1967; Odum, 1969) reflects our current inability to measure NPP either directly or indirectly from the difference between GPP and R_A. Total NPP is not normally measured; rather, aboveground NPP is adjusted by a fixed percentage so as to include belowground production in turnover of the root compartment (Kira, 1975). By using the harvest approach and determining only aboveground NPP, this study would have validated the model proposed by Kira and Shidei (1967) (see Figure 8). However, this model apparently does not reflect conditions in *Abies amabilis* zones when both above- and belowground production budgets are constructed. Certainly, one study in cool temperate forest ecosystems does not prove or disprove the theory of community energetics. However, the exclusion of belowground productivity may well have hampered current theoretical interpretation of production relations as neither GPP nor R_A are measured.

Theoretical problems may reside in assuming that community respiration increases with accumulating woody biomass. Respiration appears to increase with tissue surface area (Whittaker and Woodwell, 1967). They suggest that genera such as *Picea*, *Abies*, *Tsuga*, and *Pseudotsuga* have high surface areas because of numerous small branches and twigs. Since ratios of branch to stem surface area increase with increasing plant size, high rates of respiration would be expected in maturing ecosystems. However, their conclusions were based upon comparisons of one species with another, not from differences which result from increasing plant size among individuals of the same species. In fact, of the 10 species from which data were presented, one of the two conifers in their study (Pinus enchinata) had the lowest stem and bark surface area. They found that trees had higher branch to bole surface areas than shrubs, but these trees were open grown. Open grown "wolf trees" would be expected to have disproportionately higher numbers of branches. With little or no mutual shading, open grown trees commonly have branches extending to or near the ground. This situation may be prevalent at some stages in old field succession, in savanna, and in rain forest biomes which are characterized by multiple layering of leaves supported by a decurrent branching habit.

Forest stands which develop under closed canopy situations may not be characterized by accumulating respiring woody biomass. Conifers are typically excurrent in branching pattern. Many coniferous forests undergo density-dependent mortality and branch pruning unless initial stocking is extremely low (Drew and Flewelling, 1979). The resultant change in distribution from many small branches and stems in young stands to a much smaller number of large branches and stems with increasing maturity runs counter to the notion that respiring surface area increases with ecosystem maturity. The total volume of sapwood is progressively shifted onto fewer stems and branches. In addition, respiration per unit surface area has been shown to decrease with increasing size of the tissue (Hagihara and Hozumi, 1981).

The microclimate is also altered as stands mature and moderate temperatures beneath the canopy and at the soil surface (Edmonds, 1979). As canopy closure progresses, less light reaches the forest floor and stem space. It could be argued that in mature ecosystems, as the canopy ascends in height or as foliar biomass gradually declines, more sunlight becomes incident upon stems. However, more light energy becomes intercepted at greater heights on the stem. Since it has been shown that 50% of stand respiration is from tree boles (Woodwell and Whittaker, 1968), it seems inconsistent that as air temperature declines in the stem space, respiration should increase.

Accumulation of woody biomass does not necessarily imply that respiration increases. The mass of live respiring tissue may remain constant or gradually decline after crown closure. Mature conifer stands may be characterized by high proportions of heartwood accumulations. Heartwood, which consists entirely of dead cells, does not respire. Sapwood basal area, which is directly proportional to leaf biomass (Grier and Waring, 1974), should level off as foliage biomass reaches steady state following crown closure. The only living tissue of the outer, central, and inner sapwood are ray and vertical parenchyma cells (Stewart, 1966). This volume of respiring sapwood, and cambial and phloem cells, may increase slowly on individual trees as self-thinning progresses and suppressed or otherwise weakened trees die. After crown closure, the total volume of respiring tissue may be constant.

Aboveground structural development in Abies amabilis may exert strong control on the overall carbon allocation in maturing stands. Lack of rapid biomass accumulation soon after clearcutting is due in part to the high mortality in the advanced regeneration conifers (typically 1 to 2 meters in height) which extend above the snow pack and are exposed to extremely desiccating conditions resulting from increased radiation loads and wind speeds. The abrupt change in microclimate from that existing in the stem space prior to logging may in part explain this mortality. The more recently established conifer seedlings and deciduous species such as Xerophyllum tenax and Vaccinium are not exposed to such high evaporative demands. If only the plants established after logging had been studied, differences between the 3- and 9 year-old stands would likely have been greater since community biomass and NPP in the 3 year-old stand would have been much lower. There is a strong correlation between size and age of living trees. The static age-diameter matrix (Figure 7) shows that crown position is in part dependent upon age of the tree. This implies that older trees do not have the same potential for achieving dominant status in a community as younger trees of a similar size. In a study of height, age, and growth, Wagner (1980) found that post-logging Abies amabilis saplings had greater current height growth than advanced regeneration of a similar diameter. Abies amabilis advanced regeneration does show satisfactory release up to age 95 (Herring and Etheridge, 1976). The stand densities and hence interspecific competition in this study are much greater. Release of grand fir (Abies grandis) advanced regeneration is most prevalent until age 30 (Fergusson and Adams, 1980). In mature stands, trees of suppressed or intermediate status may be near their compensation point. With little excess carbohydrate reserve on which to draw, these trees may succumb to episodic stresses such as drought or wind and snow breakage. As was previously mentioned, Abies amabilis is an extremely shade tolerant species. This tolerance may manifest itself in slow self-thinning, extending later into a stand's life cycle than in early successional or less tolerant species.

Large gaps in the age and diameter frequency and the age-diameter matrix indicate that establishment and growth are not randomly associated phenomena. Discrete age and size classes are present. It is not known to what extent the current stand structure reflects past disturbances. Modal frequencies in the 180 year-old stand separated by 80 years are comparable to the 60 year intervals between "wave regenerated" Abies balsamea in northeastern North America and "dead-tree-strips" in Abies veitchii stands in Japan (Mohler, et al., 1978; Iwak and Totsuki, 1959). In this study a clearly defined topographic "edge" of mortality in the Abies amabilis zone is absent altogether; yet within all stands, "waves" of regeneration differing by 50 to 85 years can be seen. The ability of Abies amabilis to shift a given amount of fixed carbon to different components such as stem growth or root growth may facilitate the maintenance of the community stability as the stand matures. The understanding of the dynamic process of growth over the lifespan of a forest is practicable only through a detailed analysis of above- and belowground compartments using the chronosequence approach.

3.5 Conclusion

The energetic model of forest succession presented by both Kira and Shidei (1967) and Odum (1969) may conform less to the overall strategy for ecosystem development than the contrasting linear model which was postulated and validated in this study. This former model is both unsubstantiated by the chronosequence of Abies amabilis stands and inconsistent with Odum's tabulated model of succession both from the standpoint of community energetics and overall homeostasis. Declining net production caused by increasing respiration losses reduces the flow of energy through the ecosystem. A reduced amount of net production available to higher trophic levels would thwart rather than promote the development of weblike food chains. If gross primary production and autotrophic respiration balance in late successional or "climax" communities, the individual plants would be near their compensation points. Intuitively, such an ecosystem would be more susceptible to episodic stresses which either decrease gross production or increase respiration such as defoliation, storm damage to the canopy, drought, or fire. Consequently, stability and overall homeostasis might decrease with ecosystem succession in the model proposed by Kira, Shidei, and Odum.

The alternate model of succession presented in this study conforms to the concept of succession presented by Odum (1969) although differing in the bioenergetics. Succession as illustrated in the chronosequence of Abies amabilis ecosystems not only results in the modification of the physical environment by the interception and conversion of solar energy into net primary production, but more significantly, in mature Abies amabilis stands, an increasing amount of energy is apportioned to the turnover of fine root biomass. This may promote the development of the soil physical environment by increasing the flow and cycling of nutrients and possibly enhance the food chain by the maintenance of a symbiosis with mycorrhizal fungi. As ecosystems mature, they shift from aboveground net production to a belowground orientation for subsequent use by further trophic interaction. This notion complies with Odum's concept of symbiotic functioning between organisms which are maintained per unit of energy flow.

CHAPTER IV

SEASONAL ROOT GROWTH PATTERNS IN 23- AND 180 YEAR-OLD *ABIES AMABILIS* ECOSYSTEMS

4.1 General Approach

The bioenergetic importance of incorporating root dynamics in productivity models was addressed in the previous chapter. It was shown that over 50% of net primary production was allocated to production and turnover of fine roots in 23- and 180 year-old *Abies amabilis* stands. These estimates of fine root biomass and production were obtained from soil cores collected at three to eight week intervals (Grier, *et al.*, 1981). However, since seasonal changes in fine root biomass result from differential growth and mortality occurring daily, it is important to monitor more closely the periods of new root growth and the time interval to root death. To provide a more continuous index to seasonal root growth patterns in these two stands *in situ*, rhizotrons were constructed.

In high elevation forests of the Washington Cascades, observation of root activity using the rhizotrons constructed in the field requires special considerations. The duration of the snow cover is normally from seven to nine months with an average depth of two meters by mid-March. Freezing or sub-freezing temperatures can be expected for nine months of the year. Of foremost consideration in constructing the rhizotrons was to insure that the observation windows had an energy balance not appreciably different from ambient soil conditions. Winter and spring access to the observation windows during periods of deep snow accumulation had to be considered before construction of the rhizotrons. The 10 year maximum snowpact load, with the added pressure from downslope creep, was used to calculate the structural strength required.

4.2.1 Rhizotron Construction

Rhizotrons were built in the 23- and 180 year-old Abies amabilis stands. Each rhizotron was situated on similar microrelief in its respective stand and aligned by compass on a southwestern aspect. To minimize the quantity of soil excavated during construction while still allowing a large perimeter for placement of the observation windows, each rhizotron was designed to resemble a "T" shape in plan view. Each rhizotron consisted of three 1 m x 3 m corridors with a total of 12 windows.

During construction, soil was excavated to an average depth of 1.2 m with pick and shovel. To minimize disturbance during excavation, the soil surrounding each observation chamber was first covered with plastic and then overlain with plywood. A 16 cm diameter drainage hole was augered through the bedrock under the southwest (downslope) corner of each pit and lined with flexible drainage hose.

Each rhizotron frame was constructed of 9 cm x 9 cm clear lumber with posts set 76 cm apart (Plate 1). Approximately 60% of this framing was built above the soil surface. A 2.5 m access tower with sloping door was included for primary access during winter months. Removable hatches were constructed over the window viewing areas at the ends of each of the three corridors. Plywood siding (2 cm thick) was nailed to the 9 cm x 9 cm frame and protected from the weather with wood stain. No wood preservative was used on the interior and care was taken to insure that no stain dripped onto the soil surface.

Plexiglas observation windows, 7 mm in thickness, were cut and fitted between the 9 x 9 cm frame posts. To provide close contact between each window and the soil profile directly behind the window, A- and b-horizons were carefully shaved back 5 to 14 cm from the smoothed profile wall. Sieved soil from each horizon, which had been air dried (to prevent smearing), was used in reconstructing each profile. The plexiglas panel was placed 1 to 3 cm from the smoothed soil surface and 2 cm x 2 cm lathes were lightly tacked against each frame while the forest floor, A- and B-horizons were physically reconstructed. The plexiglas was then pressed tightly against the reconstructed profile to prevent soil from sloughing, and the lathes were nailed in place. This procedure was implemented in an attempt to closely simulate the

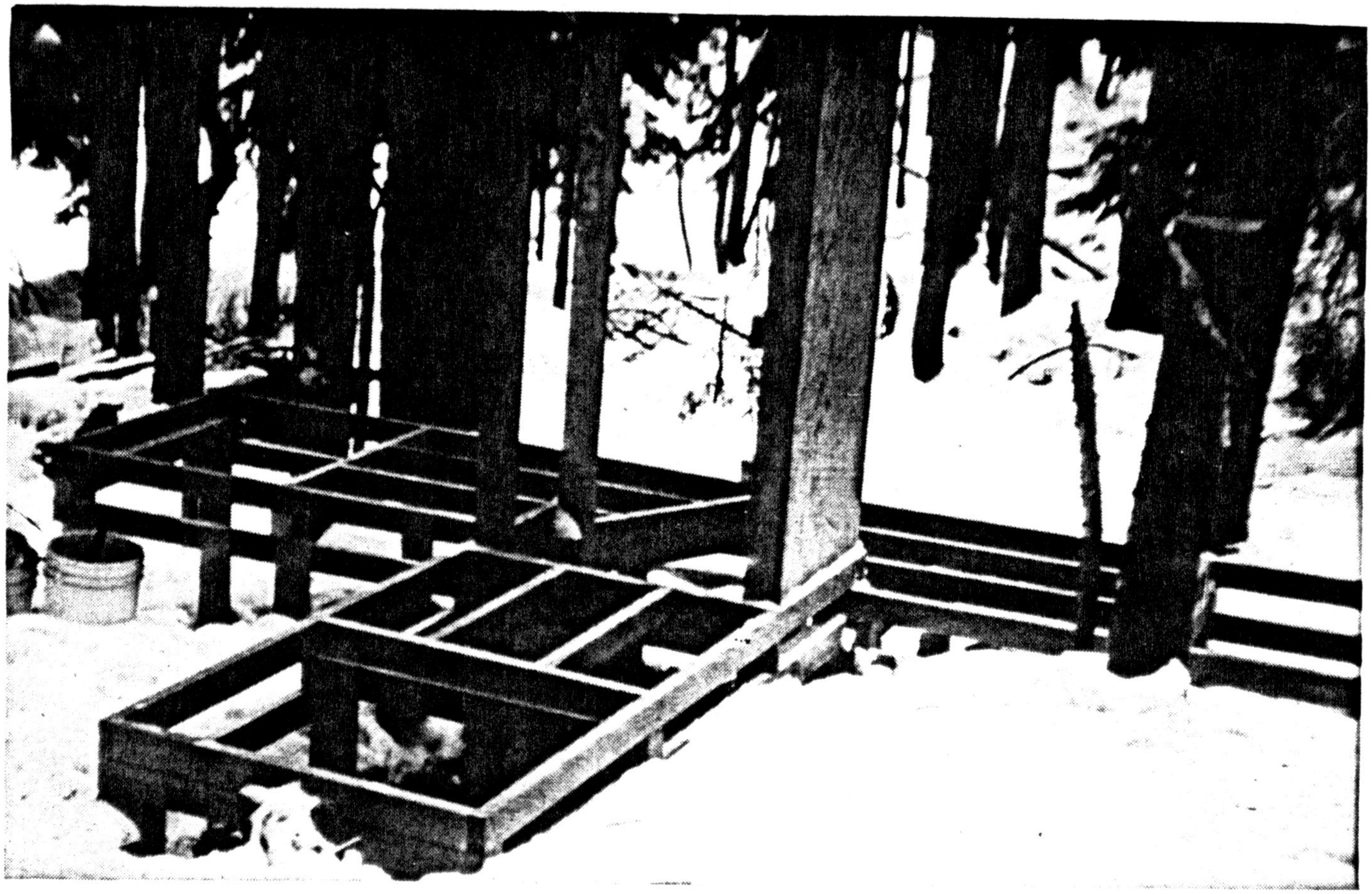

Plate I. Rhizotron Under Construction in 180 Year-Old Abies amabilis Stand original soil density. Below each window in which the forest floor, A- and B-horizons were visible, a second piece of plexiglas was installed for viewing the C-horizon and underlying bedrock. The native soil was shaved back and plexiglas placed 1 to 3 cm from the shaved surface; sieved soil was replaced and windows fastened as with the A- and B-horizons.

To prevent unnatural temperature fluctuations, each rhizotron was extensively insulated (Plate 2). Two sheets of 8 cm rhick styrofoam were cut to fit between the frame posts covering the forest floor, A- and B-horizons. Twelve cm thick spun glass was used to insulate the C-horizon windows and also to cover all of the vertical side walls. Styrofoam was used for overhead insulation. Foam "doors" were also constructed to seal off each of the three corridors. To further reduce heat loss, an insulated interior trap door was placed inside each access tower level with the soil surface.

4.2.2 Data Collection

After the rhizotrons were allowed to equilibrate for four months, root observations were conducted at two to three week intervals. Externally recognizable morphological characteristics were used as a basis for the classification of roots. The major distinctions made were between mycorrhizal and nonmycorrhizal and between angiosperm and conifer roots. Crayons were found to be the most efficient method of

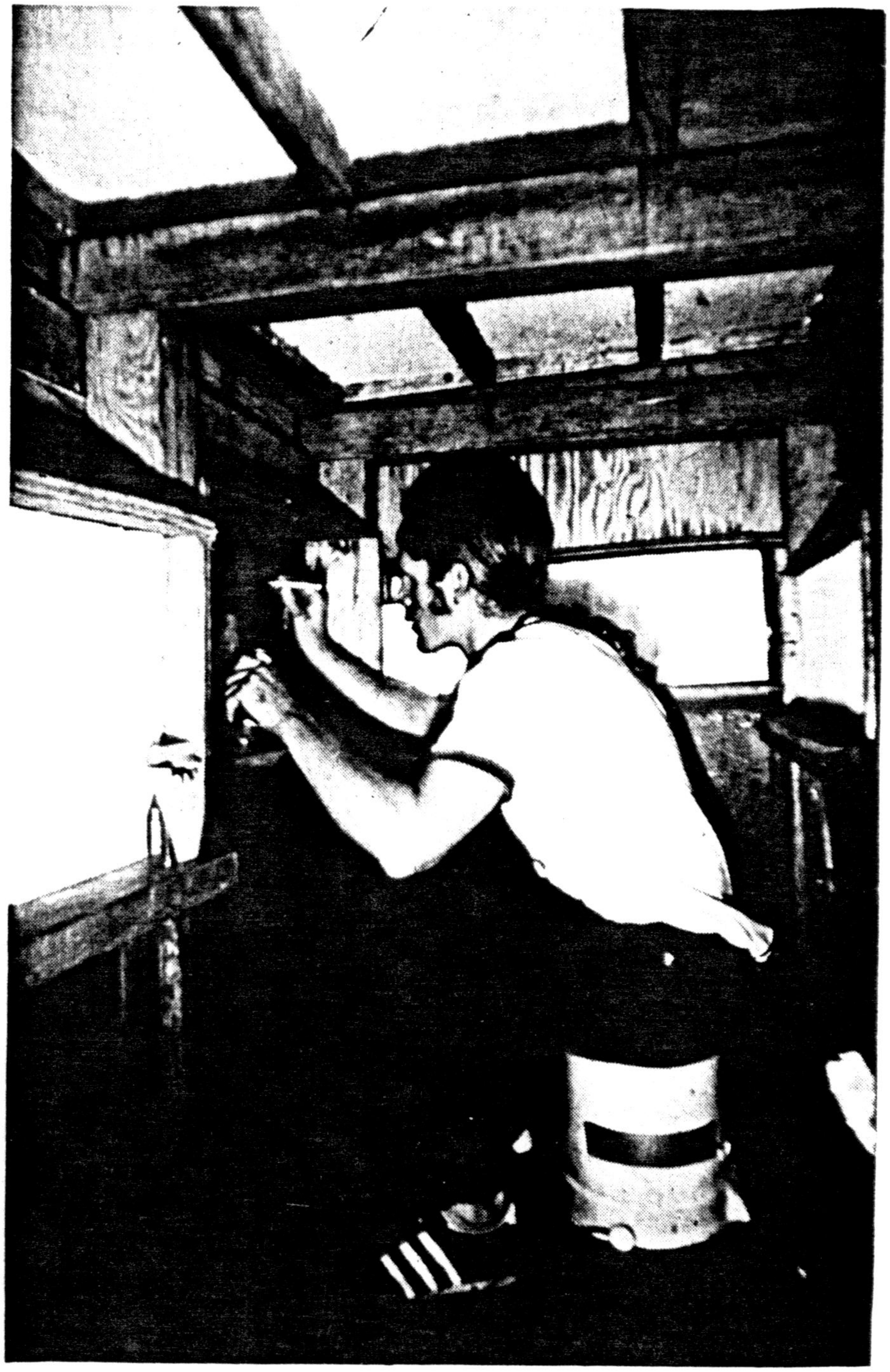

Plate II. Interior View of Rhizotron in 180 Year-Old *Abies amabilis* Stand marking the appearance of new root tips or the elongation of older roots on the frequently moist plexiglas window. Photographic records of root growth were not feasible due to the poor contrast between the roots and the soil.

4.2.3 Soil Temperature and Stem Diameter Measurements--23 year-old stand

Soil temperatures were monitored with 30-day circular recording thermographs installed at a depth of 10 cm in the A-horizon. In the young stand, eight *Abies amabilis* stems near the rhizotron were measured with vernier calipers for diameter growth throughout the summer of 1980. To provide stable and replicable stem measurements, thumbtacks were glued with a rubber sealer on opposite sides of each stem. The heads of the thumbtacks provided a repeatable measurement surface without damage to the thin stembark (Zaerr, 1971).

4.3 Results

4.3.1 General Results

Seasonal patterns in the initiation and elongation of root tips were followed over a 23 month period from November 1978 to October 1980. Root initiations refer to the number of new root tips which appeared on the surface of the plexiglas window at each observation date. While nonmycorrhizal roots exhibited both initiations and elongation, only the frequency (number) of initiations are reported for mycorrhizal root tips since they did not undergo any appreciable elongation after appearing on the rhizotron windows. Nonmycorrhizal root tip initiations were distinguished from the number of actively growing root tips which had been previously initiated; these nonmycorrhizal roots are referred to as previously growing root tips. Primary root growth was determined by first summing nonmycorrhizal root tip initiations and actively growing nonmycorrhizal root tips. This sum was multiplied by the average rate of elongation of actively growing root tips. Since new roots which appeared between observation dates would not have been growing for the entire interval, the elongation rate of actively growing root tips was used rather than the elongation rate of newly initiated root tips. In the 23 year-old stand, both angiosperm and conifer nonmycorrhizal roots were observed in addition to coniferous roots infected by mycorrhizal fungi. Although angiosperms were also present in the understory of the mature stand, no angiosperm roots appeared on windows in this stand.

A parabolic curve-fitting routine was applied in plotting. This technique does not smooth the data points. The seasonal pattern of root growth or rhizograph which emerges passes exactly through every data point.

4.3.2 Mycorrhizal Root Initiations

The pattern of mycorrhizal root tip initiations was similar for the two stands, with fairly inactive periods of two to five months each year. In the young and mature stands the rhizograph for mycorrhizal root tip initiations showed a peak in early spring and variable amounts of summer and fall activity (Figure 12a). In both stands, rapid springtime initiation of mycorrhizal root tips commenced in late April or early May, peaking in mid-May to early June and immediately followed by a decline. A noticeable summer depression was seen in July for both stands, although this period of reduced initiations of mycorrhizal root tips was less pronounced in the young stand. The springtime peak was of longer duration in the mature stand, averaging approximately six weeks as compared to the spring peak of mycorrhizal root tipes in the young stand which averaged slightly less than five weeks.

Summer and fall were the most variable periods in terms of appearance of mycorrhizal root tips in the 180 year-old stand. Whereas abundant mycorrhizal root tips were seen in the young stand through November each year, negligible activity was seen in the summer and fall of 1979 in the mature stand except perhaps in early August. In the mature stand the maximum number of mycorrhizal root tip appearances was recorded in mid-December of 1978, with continued activity over the winter period. Mycorrhizal root tips in this stand were seen with increasing frequency during the fall of 1980. Although an analysis

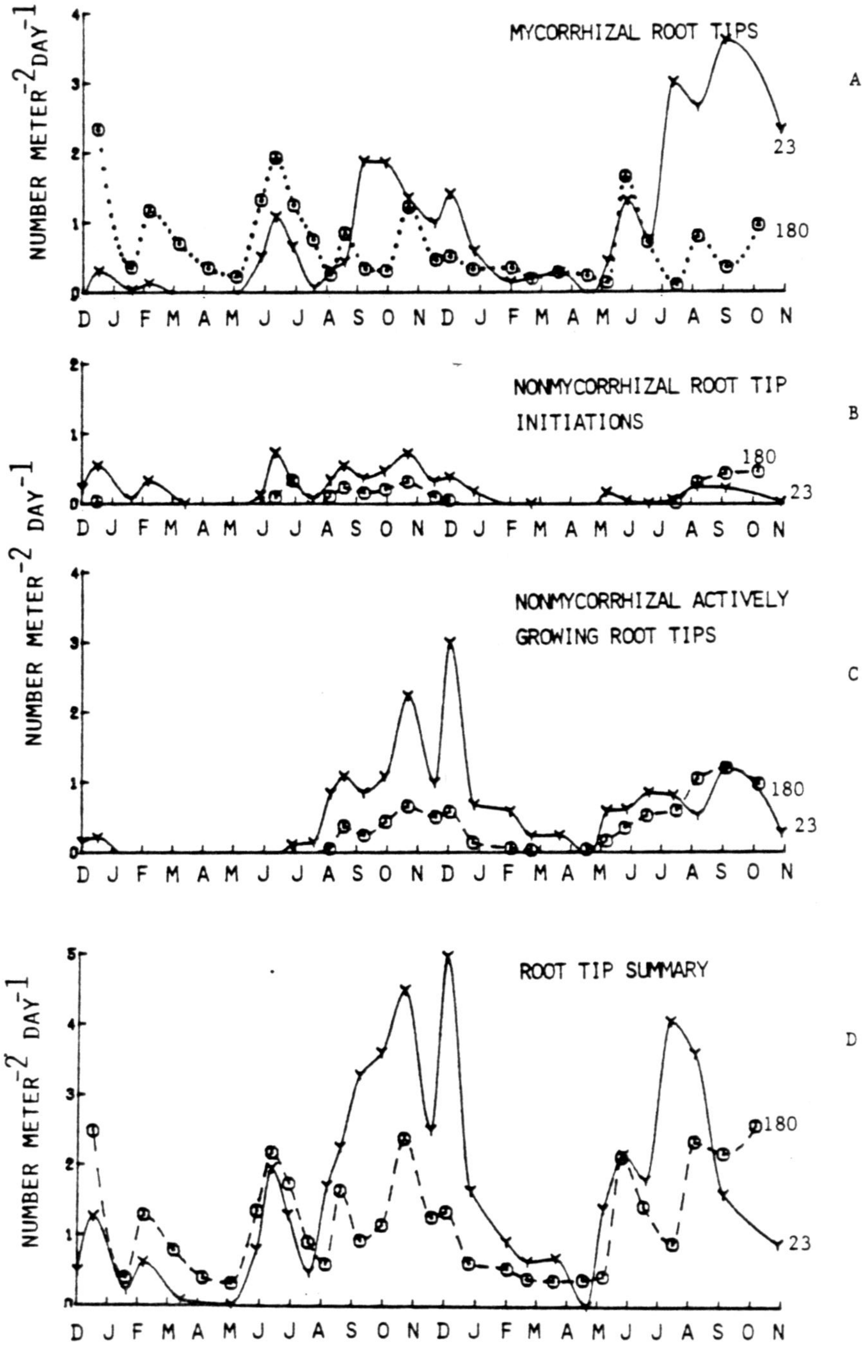

Figure 12. Conifer Rhizographs for Mycorrhizal and Non-mycorrhizal Root Tips in 23- and 180 Year-Old <u>Abies amabilis</u> Stands

of variance showed no statistically significant differences between the two stands, 16% more mycorrhizal root tips were produced in the young stand over the 23 month study period as compared to the mature stand. The largest difference occurred during the mid-summer depression in July, which had followed the spring peak activity.

4.3.3 Nonmycorrhizal Root Growth

4.3.3.1 Conifer Nonmycorrhizal Root Growth

Based on initiation of nonmycorrhizal root tips, it appears that the mature stand has a shorter period of root activity than the young stand. However, as can be seen in Figure 12b, the number of initiations were not nearly as numerous as that observed for the mycorrhizal roots. Both stands showed a sustained period of root initiations from mid-July through November, 1979, with a spring peak evident in early June in the young stand and in late June in the old stand. Fewer root tip initiations occurred in the mature stand than in the young stand in 1979. However, a comparable number were measured in both stands in 1980. Both stands had fewer nonmycorrhizal root tip initiations during 1980 as compared to 1979. A less marked spring peak was detected for the young stand in May, 1979 and there was no apparent spring peak in the mature stand for that year.

Differences in root rhizograph patterns between the two stands was most pronounced for actively growing root tips (Figure 12c). Many of these root tips did not rapidly increase in either stand in 1979 until late July. In contrast, increased numbers of previously growing root tips were found in mid-April of 1980. The number of previously growing root tips in the mature stand appeared to lag behind that of the young stand by approximately four weeks in both years, although activity in both stands peaked in October or November in 1979 and in late August in 1980. Considerably more actively growing root tips were seen in 1979 in the young stand, whereas more were observed in the mature stand during the 1980 growing season.

The timing of the increased total number of root tips was nearly identical for the two stands in 1979. In 1980 spring root growth in the mature stand appeared to lag behind the young stand approximately two weeks (Figure 12d). In the mature stand, the spring peak (mid-June) was followed by a marked decrease in total root initiations for the next two months. From July until about the end of September, an increase in the number of root tips in this stand was witnessed for both years. Total number root of root tips in the mature stand over the two year observation period were only slightly less than in the young stand. More tips which were measured in the 180 year-old stand in the fall of both 1978 and 1980 do not compensate for the much greater late-summer root tip production in the young stand.

4.3.3.2 Angiosperm Root Growth

The period of root tip initiations was found to be shorter for angiosperm than for conifer roots. Angiosperm root tip initiations were markedly reduced in the months of September, October, and November of each year when compared with conifer root tip initiations during the same period (Figure 13a). Angiosperm root tip initiations followed a modal pattern as opposed to the multiple peaks recorded for conifer fibrous root tip initiations. An increase in both nonmycorrhizal conifer and angiosperm root tip initiations was observed each spring. Numbers of new angiosperm and conifer root tip initiations increased in June, 1979 and briefly in April, 1980. However, the increase in the number of angiosperm root initiations began two to three weeks before the increase occurred for coniferous roots.

An active growth period of both angiosperm initiations and angiosperm actively growing root tips was also seen in late February, 1980 (Figure 13b). Both types of root tips were most numerous in late August of each year. In contrast, conifer nonmycorrhizal root tip initiations exhibited a mid-summer depression each August.

The total number of angiosperm root tips which were measured is similar to that of conifers (Figure 13c and 12d). However, the peak period of angiosperm root activity was considerably less as compared to conifer root tips. Moreover, angiosperm root tips are produced earlier in the spring and summer than conifer root tips.

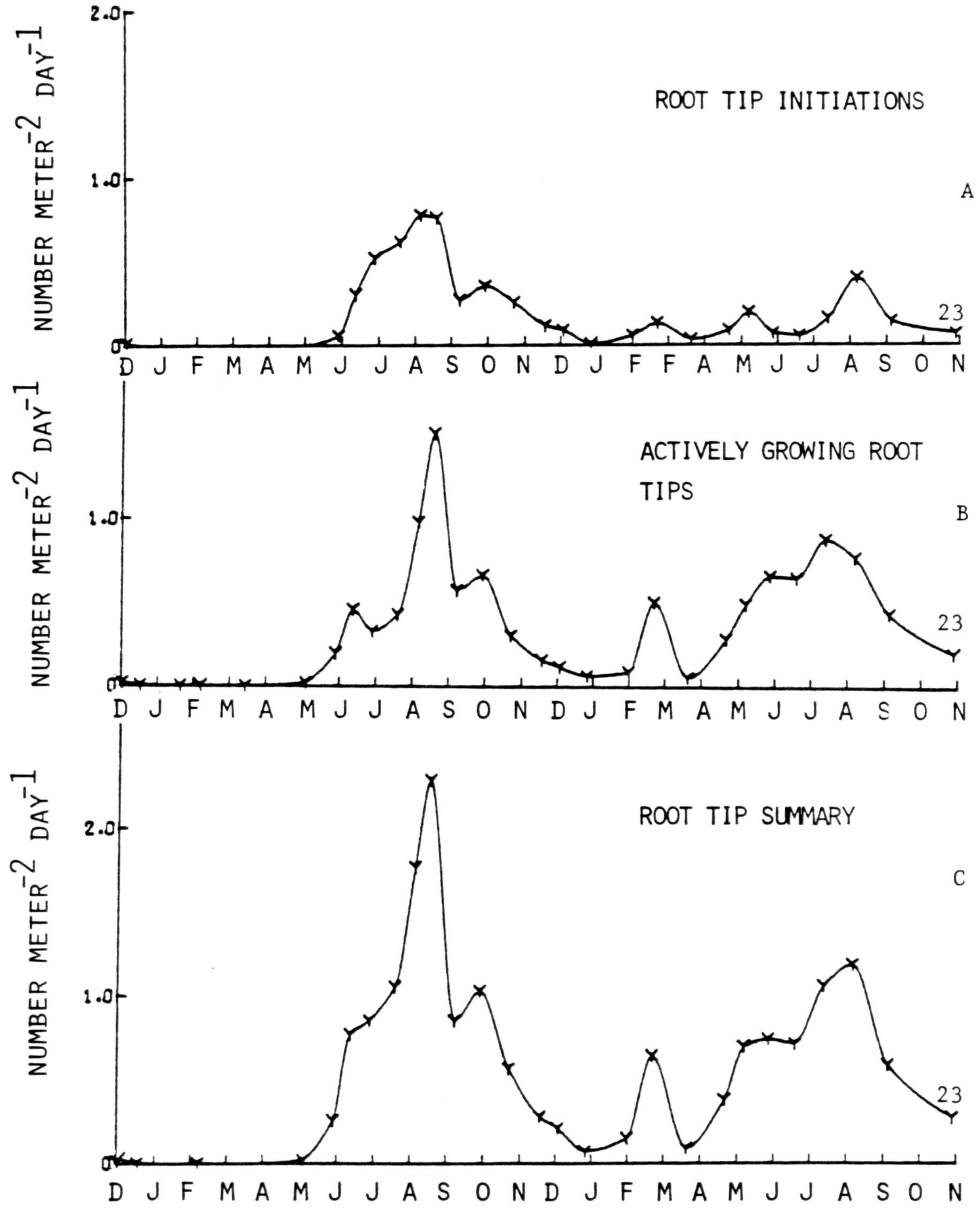

Figure 13. Angiosperm Rhizographs for 23- and 180 Year-old *Abies amabilis* Stands

4.3.3.3 Primary Root Growth

The pattern of conifer primary root growth, as can be seen in Figure 14a, had a similar shape to that of actively growing root tips in Figure 12c. Distinctly different phenological patterns were seen for 1979 and 1980 for both the young and the old stand. In the young stand the peak in primary root growth in 1980 was lower than that measured in 1979. Simiarly, much higher rates of primary root growth were found in the mature stand during the 1980 growing season as compared to 1979. A five month interval of primary root growth occurred in both stands, from the first spring increases in elongation rates until the peak in late summer or early fall. Total primary root growth over the entire observation period was higher in the young stand due to abundant root growth in the summer of 1979 as compared to the mature stand.

Peaks in angiosperm primary root growth for both years occurred in early August, while the peak conifer root growth occurred six and eight weeks later in both 1979 and 1980. There was a small increase in the number of actively growing angiosperm root tips at the end of February, 1980 (Figure 14b). Although nearly imperceptible in Figure 12, this wintertime angiosperm primary root growth can be more fully appreciated in Figure 3 where both the number of root tips and their elongation rate are considered. There was no indication that conifer roots were experiencing a measurable increase in growth during this period.

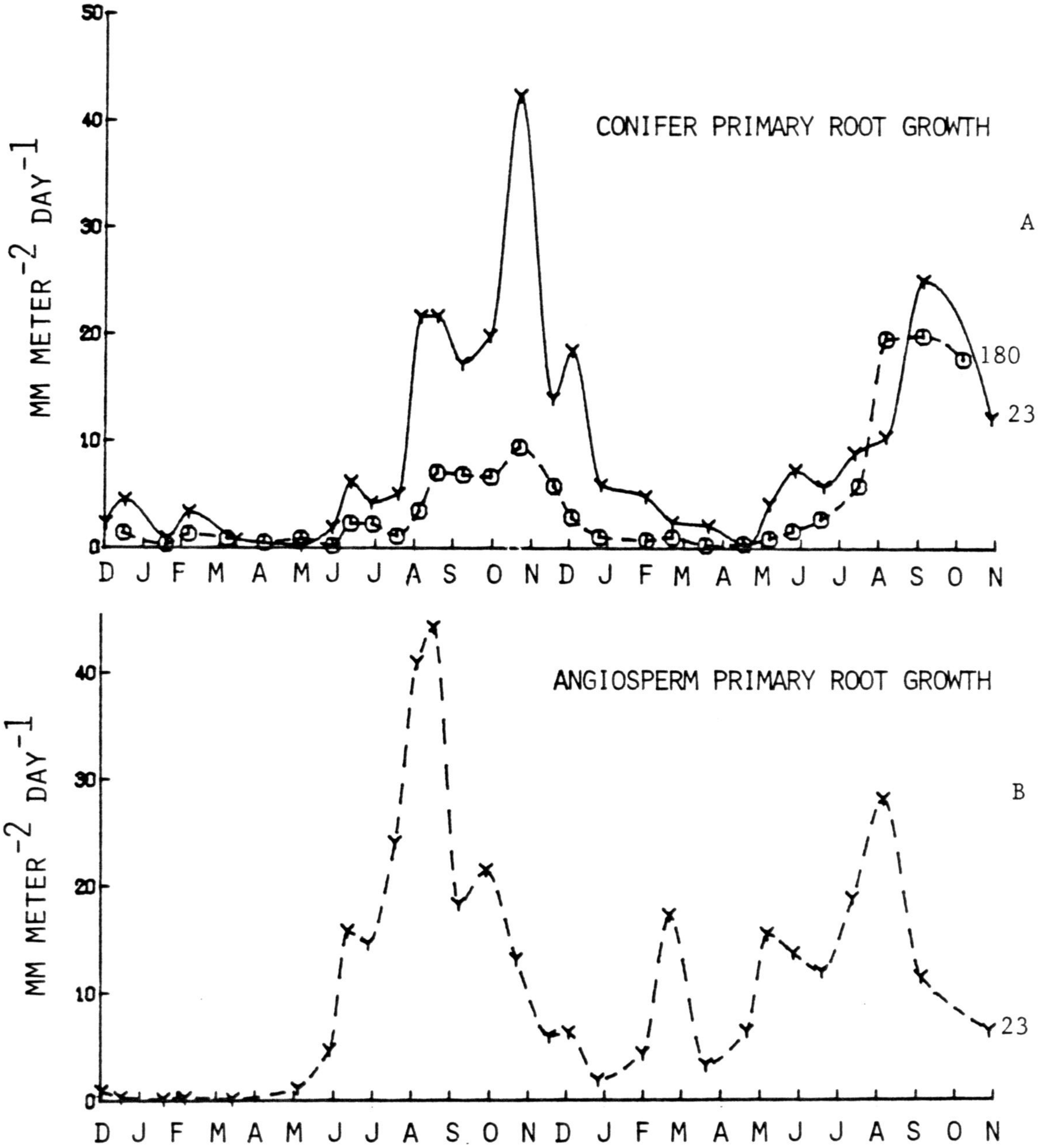

Figure 14. Primary Root Growth in 23- and 180 Year-old *Abies amabilis* Stands

4.3.3.4 Phenology in the 23 year-old stand

A phenological calendar of vegetative growth is shown in Figure 15 for the young stand. The seasonal average of conifer (2 mm) and angiosperm (5 mm) fine root biomass (as measured by soil coring) is compared with the cumulative seasonal average of all root tip initiations (Figures 12d and 13c) and soil temperature. Fine root dynamics are non-synchronous with soil temperatures. The number of fine root tips produced increased sharply two weeks before soil temperature began warming in the spring but declined more slowly than soil temperature through the fall and winter. Fine root biomass increased before root tips increased in the spring. The spring peak in the number of root tips corresponded to a fairly constant period of fine root biomass. Maximum fine root biomass had occurred before the peak in number of root tips and warming of soil temperature. Both estimates of root growth (number of tips and biomass) indicated that the gradual decline in root activity commenced prior to decreasing soil temperatures around mid-August. The number of root tips slowly declined over a period of more than seven months while fall soil temperatures decreased rapidly, reaching a stable 0.5°C three and one-half months following the seasonal maximum. In the spring, aboveground vegetation growth lagged behind root growth by approximately two months; stem diameter growth and bud burst commenced in early June.

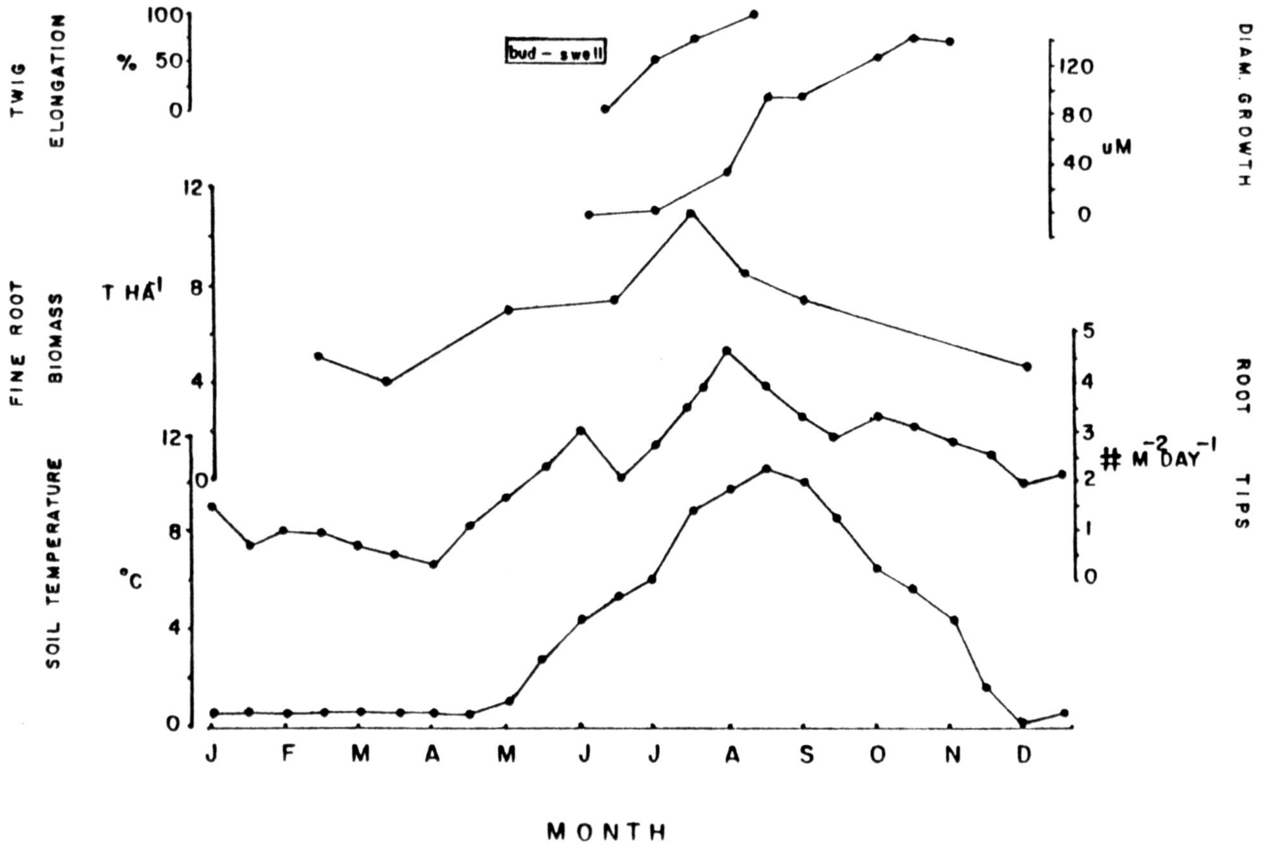

Figure 15. Phenological Calendar of Vegetative Growth for a 23 Year-old *Abies amabilis* Stand

4.4 Discussion

The occurrence of one to three annual peaks of fine root growth indicate that the root compartment in these Abies amabilis stands is extremely labile and does not parallel changes in soil temperature. Increasing amounts of root activity were seen in late April to early May for the two successive years of the study--irrespective of stand age and despite continued existence of snow cover. This early period of root growth followed by sustained root production throughout the fall and winter supports the previously stated hypothesis that existence of the snow pack does not reduce the active period of root growth in Abies amabilis stands. The similar timing of root phenologies in the young and mature Abies amabilis stands and the one to two month longer period of conifer root activity by Abies compared to lowland Pseudotsuga menziesii stands (Keyes and Grier, 1981), indicate that Abies amabilis zone forests have developed a phenological adaptation which allows for the production of roots under very cool soil temperature regimes. Further evidence for an adaptation to cold soil temperatures has been supplied by Kotar (1972). The mean length of the total root system and lateral roots of Abies amabilis were slightly longer after 12 weeks under controlled soil temperatures of 4°C than under 13°C treatment (Kotar, 1972). Vogt, et al. (1980) also found a peak in mycorrhizal root biomass under the winter snow cover at Findley Lake.

The complex root growth patterns seen in these two montane forest stands result at least in part from the distinctly different phenology of mycorrhizal and nonmycorrhizal roots. Differences in production rates of morphologically different root types in young and mature Abies amabilis stands may be a reflection of the production allocation at two different stages in ecosystem development. In the young stand, the ensuing decades will bring dramatic changes in the distribution of exponentially accumulating above- and belowground biomass. The number of stems per hectare will be greatly reduced and, as accelerated height growth continues on surviving individuals, increasing amounts of structural root biomass will be needed to provide support. The fibrous conifer roots seen on the rhizotron windows over a two year period rarely formed mycorrhizal associations, became rapidly lignified, and frequently exhibited secondary growth. The abundance of fibrous roots in the young stand is thought to be the precursor of structural root biomass. The mature stand is probably at or near a steady state in community biomass and growth of structural roots constitute a smaller proportion of net primary production than in the young stand. The development of extensive mycorrhizal root systems has been previously recognized in the mature Abies amabilis stand (Vogt, et al., 1980; Grier, et al., 1981). Turnover of mycorrhizal root tips constitutes approximately 12% of net primary production in the mature stand; over three times that of the young stand (Grier, et al., 1981).

At present it is difficult to assess the correlation between root phenology patterns and the functional role of roots in maturing ecosystems. Within each stand, spatial variability of root growth was high as seen between observation windows. It appears that soil temperatures, in particular the 0°C isotherm, change very slowly in these stands. Differences in timing of root growth in different horizons may have obscured the overall patterns in any horizon. The summing of numbers of root tips from the various horizons, which differ in temperatures, has unfortunately accentuated the natural variability for any observation date in each rhizotron.

Results of this study corroborate those of previous works which indicate that distinctly different phenological patterns of root growth are present in the 23- and 180 year-old stands. The production allocation of morphologically different types of roots may be a reflection of an adaptive response to the changing soil environment which accompanies ecosystem maturation. Vogt, et al. (1981) have shown that the dominance of mycorrhizal and nonmycorrhizal roots in the forest floor and A-horizon of the young stand change with stand age. In the mature stand fine roots are concentrated in the forest floor. This shift in the dominant depth of rooting from the mineral soil of the 23 year-old stand may reflect a more intensive exploitation of the nutrients bound in the accumulating detritus of the 180 year-old stand (Grier, et al., 1981).

The application of different methodologies in root studies has historically complicated interpretation of experimental results. The use of numerous techniques may however simultaneously enhance our ability to examine the dynamic and inaccessible nature of roots. As an area of scientific inquiry, much recent attention has been focused on the rhizosphere (Böhm, 1980). Difficulties in comparing results from this study with fine root biomass estimates in the same stands result in part from the techniques employed. Biomass which is sampled at discrete points in time can portray the seasonal course of dry matter production and turnover. To determine the proportion of belowground allocation to total net primary production, sequential estimations of biomass from soil coring are most commonly used. However, in ecosystems where seasonal fine root biomass does not return to a particular equilibrium, numerous seasons of data collection using this technique are needed to determine that portion of net primary production which occurs belowground. If sample variability is high or if intervals between soil coring are long, fine root production and turnover may be underestimated.

Biomass is essentially an integration of production of new tissue with the mortality of older tissue at any particular point in time. Although rhizotrons are an excellent technique for obtaining phenological data on root tip production, the estimation of root mortality is often difficult or impossible to determine. Root longevity may even be enhanced by observation windows. This problem of mortality assessment is prevalent in the soil coring (harvest) techniques as well. When sorting roots collected by a harvesting technique, the senses of both sight and touch can be used to determine viability, whereas with the glass window method only occular or photographic assessments are possible without large disturbances to the root system.

The seasonal changes in root tip initiations do not necessarily imply that root biomass changes in a similar pattern. Rhizographs indicated that the spring peak in root growth in the 23 year-old stand occurred after the peak in fine root biomass. However, it should be kept in mind that differences in specific gravity of roots and root diameters vary temporally and between species. This could explain some of the discrepancies between root activity estimated from soil cores and that obtained from the rhizotron. Similar to results obtained in this study, Roberts (1976) also found that actual root biomass peaked before increases could be detected on observation windows. However, only two large windows were used in his study and problems with both the installation and maintenance of viewing surfaces were encountered. Although minute seasonal perturbations are masked when data are averaged as in Figure 15, the overall root dynamics illustrated by both soil coring and rhizotron techniques are similar. Rhizographs from Pseudotsuga menziesii stands also paralleled seasonal changes in fine root biomass (Keyes and Grier, 1981). Despite limitations of the rhizotron method, root growth patterns are readily apparent. Soil coring or other root harvesting techniques frequently lack the precision to detect carbon flux from either biomass accumulation or mortality unless both live and dead roots are taken into account (Persson, 1978). Both production rates and mortality would be needed to model fine root dynamics if dry matter estimation had been the goal of this particular study.

Perhaps the largest single problem encountered with rhizotrons is the introduction of foreign material into the solum. Disturbances during rhizotron construction may render a response that is difficult if not impossible to interpret. Such results may reflect the relative ability or necessity of a stand to produce fibrous and mycorrhizal roots following a disturbance. The glass panel can be considered to be a large smooth rock (Rogers, 1939), but may still abnormally increase root densities. The disruption of "normal" rhizosphere activities is inevitable with this technique. However, for comparative purposes, the perturbation on each ecosystem should have been equivalent. Great care was exercised during both the construction and operation phases of this study to minimize the disturbance to the soil environment.

Further research effort is needed to determine how changing patterns of root growth become translated into root production and turnover. Root elongation as measured in this study may not be proportional to biomass accumulation since root mortality has occurred. For example, the spring peak and summer depression shown on the rhizograph are not detectable in fine root biomass (Figure 15). It is not presently known the relative proportions of root growth resulting from current photosynthesis and from stored carbohydrate reserves. Under field conditions, severed roots have been shown to continue to grow at an undiminished rate for ten days (Lyford and Wilson, 1966). Seasonal changes in root growth have been associated with bimodal peaks of labeled ^{14}C translocated to the roots of conifer seedlings in the spring and fall (Ursino, _et al_., 1968; Shiroya, _et al_., 1962). This phenomenon may be less strictly regulated by soil temperature than endogenously controlled. Two peaks in translocated ^{14}C were also reported by Gordon and Larson (1968). They reported high activity of labelled carbon in root tissue just prior to vegetative bud elongation. Translocated ^{14}C in the root systems decreased rapidly as vigorous needle elongation proceeded. Near the end of the rapid needle elongation period, this translocation pattern abruptly shifted from "an upward to a predominantly downward direction." They suggested this renewed growth phase signifies a metabolic state whereby the peak in photosynthetic efficiency of new needles and the reduced export of photosynthate from old to new needles created a "surge" in translocation to the roots. Use of either stored and current fixed carbon may be an effective method for increasing the root surface area beyond the frost-free growing season, particularly if the energy cost associated with the solubilization of starch is low.

4.5 Conclusions

The ability of *Abies amabilis* to maintain or increase its root growth during periods of low soil temperatures may have profound adaptive significance. Because of their slow death and decay rates, the cyclic renewal of structural roots has been suggested to be a long term control mechanism for stabilizing biogeochemical cycles in forests (Harris and Kinnerson, 1973). It was found that *Abies amabilis* has a longer period of rapid root growth than the Ericaceous angiosperms present in the same stands and the peak in root growth of the conifers occurs later in the year. (A longer period of root growth represents a competitive advantage of *Abies amabilis*.)

(The production of new root tissue may be an alternative sink for carbohydrate storage which enhances the ability of *Abies amabilis* to photosynthesize outside the frost-free growing season. Use of belowground carbon storage organs in cool climates has been observed in other plant life forms such as potato and sugar beets. The belowground storage of fixed carbon in the cool yet unfrozen soils of the *Abies amabilis* zone may represent a more conservative pathway than apportioning growth to aboveground tissues which may be subject to higher respiration losses. The formation of mycorrhizal associations may effectively lengthen the growing season for *Abies amabilis* and aid in the absorption of water and nutrients under cool temperature conditions of spring, fall, and winter. This ability to sustain root growth may promote more efficient fixation of carbon under the cool temperate to boreal conditions in which the genus *Abies* attains its dominance.

CHAPTER V

SUMMARY

Temporal changes in ecosystem structure were assessed in Abies amabilis zone ecosystems using a chronosequence approach. Five forest stands were chosen to represent a spatial analog to ecosystem development in the Cedar River watershed of the Washington Cascades.

Field measurements indicated that the heterogeneous structure of these stands was concomitant with discrete size and age classes of Abies amabilis. Bimodal diameter and age frequencies were prevalent. In the mature stand, trees of a particular age and diameter occupied predictable crown classes.

The importance of advanced regeneration in Abies amabilis stands decreased following clearcutting until crown closure in the 50 year-old stand. Biomass and net production of both advanced regeneration conifer and angiosperms initially increased an order of magnitude from the relative suppressed status in the mature stand. Mortality of the sparsely foliated and often damaged conifer saplings was common following clearcutting. The narrowest range in age structure of advanced regeneration Abies amabilis was found in the dense 23 year-old stand.

Post-logging conifers, in particular naturally regenerated *Abies amabilis*, rapidly increased in abundance and biomass following clearcutting. The total conifer stocking levels rose from 38,000 stems per hectare to 53,900 and 110,000 stems per hectare in the 3 year-old, 9 year-old, and 23 year-old stands, respectively. Although aboveground shrub biomass declined from the 3- to the 50 year-old stands, root biomass increased from 2.6 t ha^{-1} in the 3 year-old stand to 4.2 t ha^{-1} in the 23 year-old stand. Both angiosperms and conifers apportioned a higher percentage of their dry matter production to root biomass in maturing ecosystems. Fine root turnover was highest in proportion to fine root biomass in the mature stand.

Foliage biomass generally increased with ecosystem maturity. However, there was a progressive replacement of angiosperm foliage biomass with conifer foliage biomass. *Xerophyllum tenax* constituted the largest proportion of total foliage biomass in the 3- and 9 year-old stands. The 50 year-old stand contained minimal amounts of understory biomass. Conifer foliage biomass declined from 23.2 t ha^{-1} in the 50 year-old stand to 14.8 t ha^{-1} in the 180 year-old stand.

Detritus accumulations reflect the logging history of these stands. Clearcutting of mature trees on the sites which were occupied by the 3-, 9-, and 23 year-old stands removed much of the aboveground biomass. Forest floor biomass (excluding fallen logs) progressively decreased for nine years following clearcutting.

The distribution of aboveground net production changed with increasing ecosystem maturity, with aboveground biomass increment peaking in the 50 year-old stand. Mortality of saplings generally decreased with increasing stand age after the peak in the 9 year-old stand. Leaf litterfall paralleled foliage biomass in all stands. Senescing conifer needles and branchfall were a conspicuous portion of the maximum aboveground net production documented for the 50 year-old stand.

Belowground net primary production was not proportionally distributed. Although biomass increment of coarse roots exhibited a trend similar to that of aboveground biomass increment, a dissimilar pattern of belowground detritus production was noted. The highest rates of fine root turnover were found in the mature stand. Fine root turnover was also high in the 23 year-old stand, partially due to the high turnover of angiosperm roots. Lack of understory, and hence interspecific competition, in the 50 year-old stand may be a contributing factor in the low fine root turnover in this stand.

Consistent with the study hypothesis, net primary production increased in proportion to foliage biomass, peaking in the 50 year-old stand and declining between the 50- and 180 year-old stand. There was a linear correlation between foliage and net primary production, with a coefficient of determination of 99.6%.

Net production of 23.2 t ha^{-1} in the fully stocked 50 year-old stand was comparable with other temperate forest ecosystems.

Energetic models of forest succession presented by Kira and Shidei did not resemble the pattern of net primary production illustrated by this chronosequence of *Abies amabilis* stands. As neither gross production nor respiration can be adequately assessed as ecosystems develop, meticulous care should be taken when net production is estimated. Inadequate assessments of foliage biomass or fine root dynamics may have obscured the theoretical treatment of production patterns in some maturing forest ecosystems.

Seasonal changes in root growth were observed in detail from rhizotrons which were installed in the 23- and 180 year-old *Abies amabilis* stands. Mycorrhizal and nonmycorrhizal roots were monitored in the field for the 23 month period between December, 1978 and November, 1980. In the young stand, angiosperm roots were distinquished from nonmycorrhizal conifer roots.

The duration of mycorrhizal root initiations was similar for both stands. Rapid springtime activity under the snow cover was followed by a noticeable mid-summer depression. This reduction in the number of newly produced mycorrhizal roots was more pronounced in the mature stand. Although regular spring peaks were seen each year, the maximum mycorrhizal root initiations occurred in the winter in the mature stand and in the fall in the young stand.

The total frequency of mycorrhizal root tips was similar for the young and mature stand. Whereas more roots were produced in the mature stand in the first year of the study, fewer were produced during the second year in comparison to the young stand.

The increasing frequency of nonmycorrhizal roots in general lagged behind mycorrhizal roots by two to four weeks in the springtime. Although nonmycorrhizal conifer root initiations began increasing within a week of mycorrhizal root initiations, peak frequency of nonmycorrhizal roots occurred in October to December.

Two or three peaks in the frequency of nonmycorrhizal roots were observed during the first year of the study. In contrast, one or two peaks were observed for the second year of the study.

The frequency of elongating conifer roots had a less distinct summer depression than that of newly initiated roots. The frequency of both elongating roots and newly initiated roots was highly variable in the young stand, particularly in the first year of the study.

The frequency of new and actively growing angiosperm root tips more closely followed a modal pattern, with a peak occurring in August for both years of the study. This peak in the number of actively growing angiosperm root tips occurred one to three months earlier in the growing season than that of Abies amabilis.

The duration angiosperm root growth was comparatively less than that of Abies amabilis. Primary root growth of angiosperms likewise peaked in August, although exhibiting fluctuations in activity. Angiosperm primary root growth slowed in the fall, in contrast with the sustained growth of conifer roots which peaked in October of 1979 and September of 1980.

The cumulative frequency of actively growing root tips indicated that spring growth resumed at the same time in both stands in 1979 and approximately two weeks earlier in the young stand in 1980. More roots were active in the mature stand in the winter of 1978 and the fall of 1980, while fall and winter growth was greater in 1979 in the young stand.

Changes in root growth were not synchronous with toil temperature changes. Increasing frequency of actively growing root tips and fine root biomass increases occurred before soil temperatures warmed in the young stand. Fall and winter root growth was sustained despite the decline in soil temperatures.

The occurrence of from one to three annual peaks in root growth further suggested that root phenology in these two Abies amabilis stands was extremely labile and did not parallel changes in soil temperatures, in accordance with the study hypothesis. Roots were active over a comparatively longer growing season than Pseudotsuga menziesii growing in warmer soils of the Puget Sound lowlands. The complex patterns seen in these two stands result from the different phenology of mycorrhizal and fibrous roots. In addition, annual peaks in angiosperm and conifer root growth differ by one to three months in occurrence.

At present, it is difficult to assess the functional role that these differing phenologies play in maturing ecosystems. Further research is necessary to determine how the seasonal dynamics recorded in this study reflect changing patterns of fine root biomass. However, our present knowledge of fine root dynamics indicates that the energy cost in apportioning dry matter to the belowground compartment is substantial, and this fact should not be overlooked in the development of ecosystem theory.

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APPENDIX A

BIOMASS EQUATIONS AND SUMMARY STATISTICS

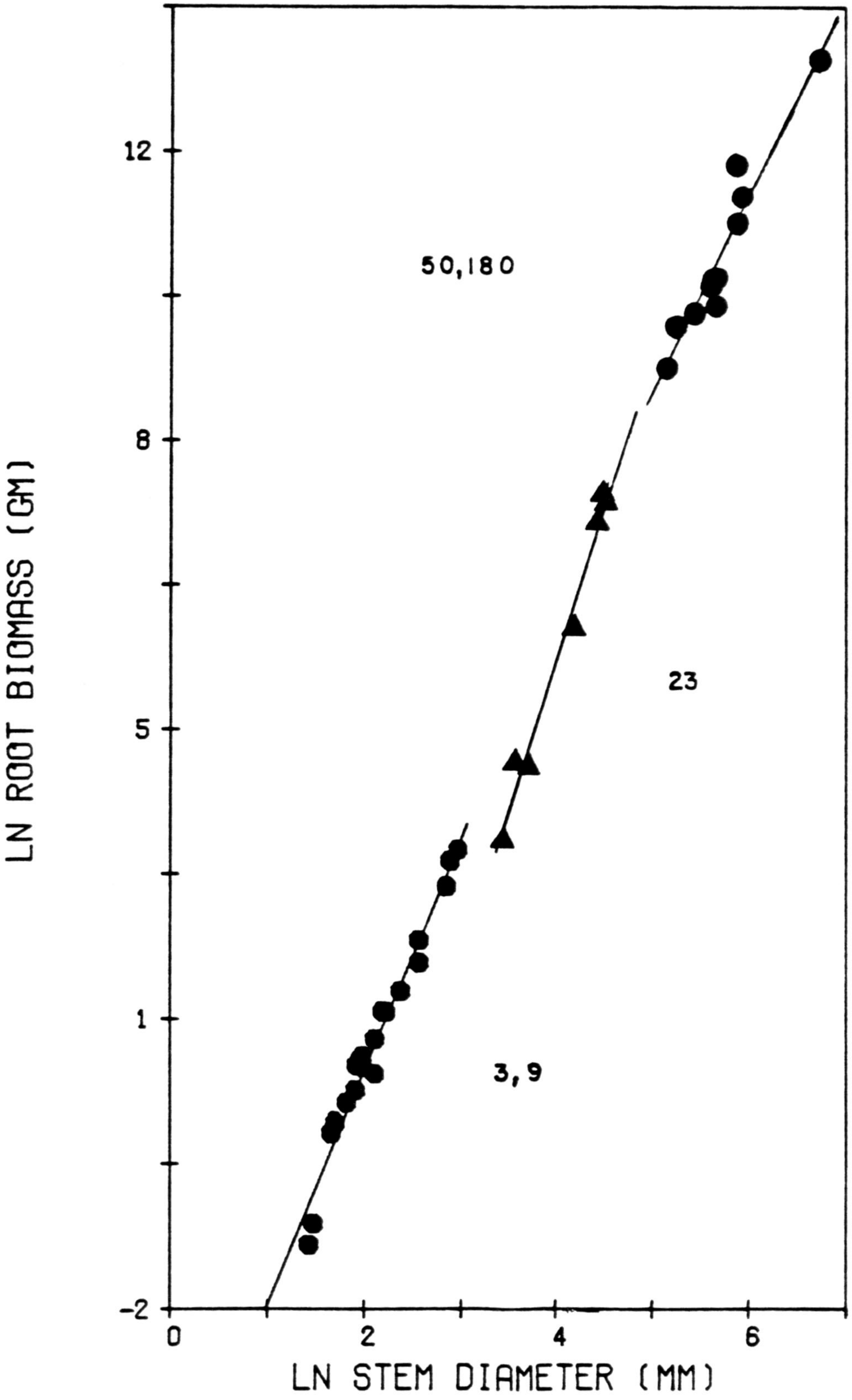
Unless otherwise noted equations are of the form Y (stand) = e^{aX+b} where X = stem diameter (mm) and Y = component biomass (gm).

Y	A	B	R^2	C.V. (%)	N
Branch Foliage (all stands)[a]	2.2747	-1.5600	.9384	8.3	60
Foliage (3-9-)	2.2009	-2.9317	.8138	598.9	31
Foliage (23)	2.6929	-4.0581	.8362	12.8	39
Foliage (50-180)	0.9959	4.2743	.8562	2.7	11
Coarse Root (3-9)	3.0358	-5.4089	.9703	24.3	20
Coarse Root (23)	3.9801	-9.8441	.9846	4.1	7
Coarse Root (50-180)	2.5912	-3.5040	.9116	3.3	11

[a] foliage for branch, x = branch diameter.

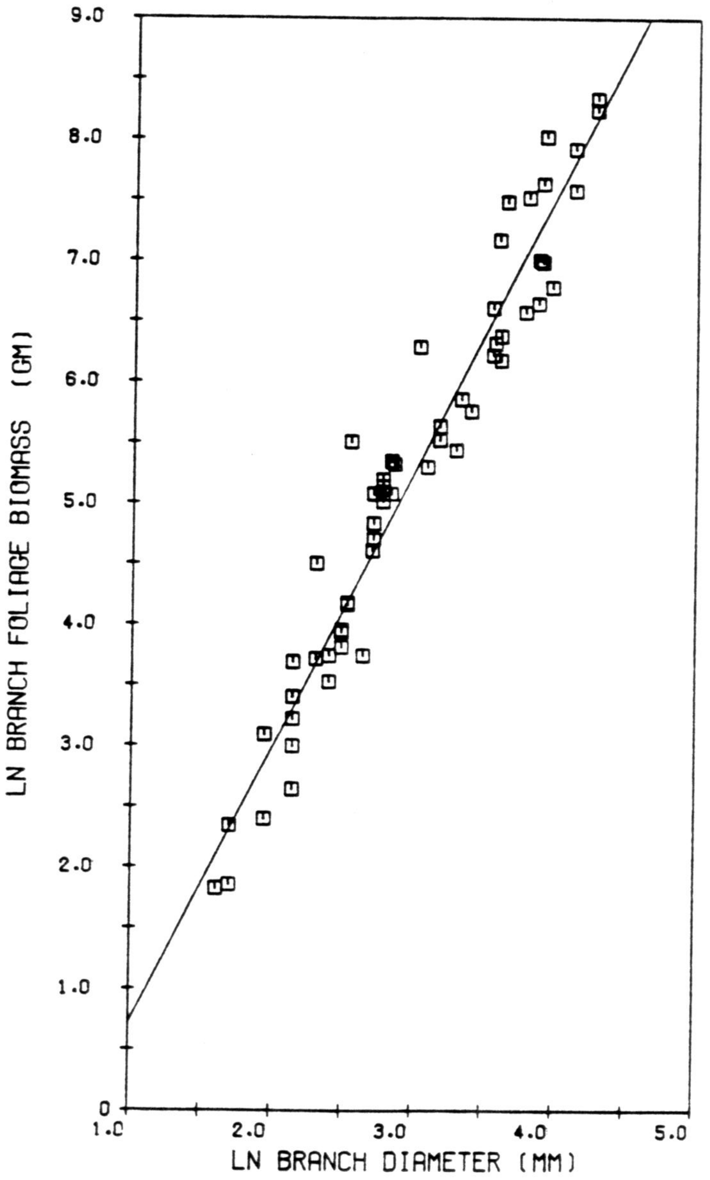
APPENDIX B

COARSE ROOT BIOMASS REGRESSIONS ON STEM DIAMETER



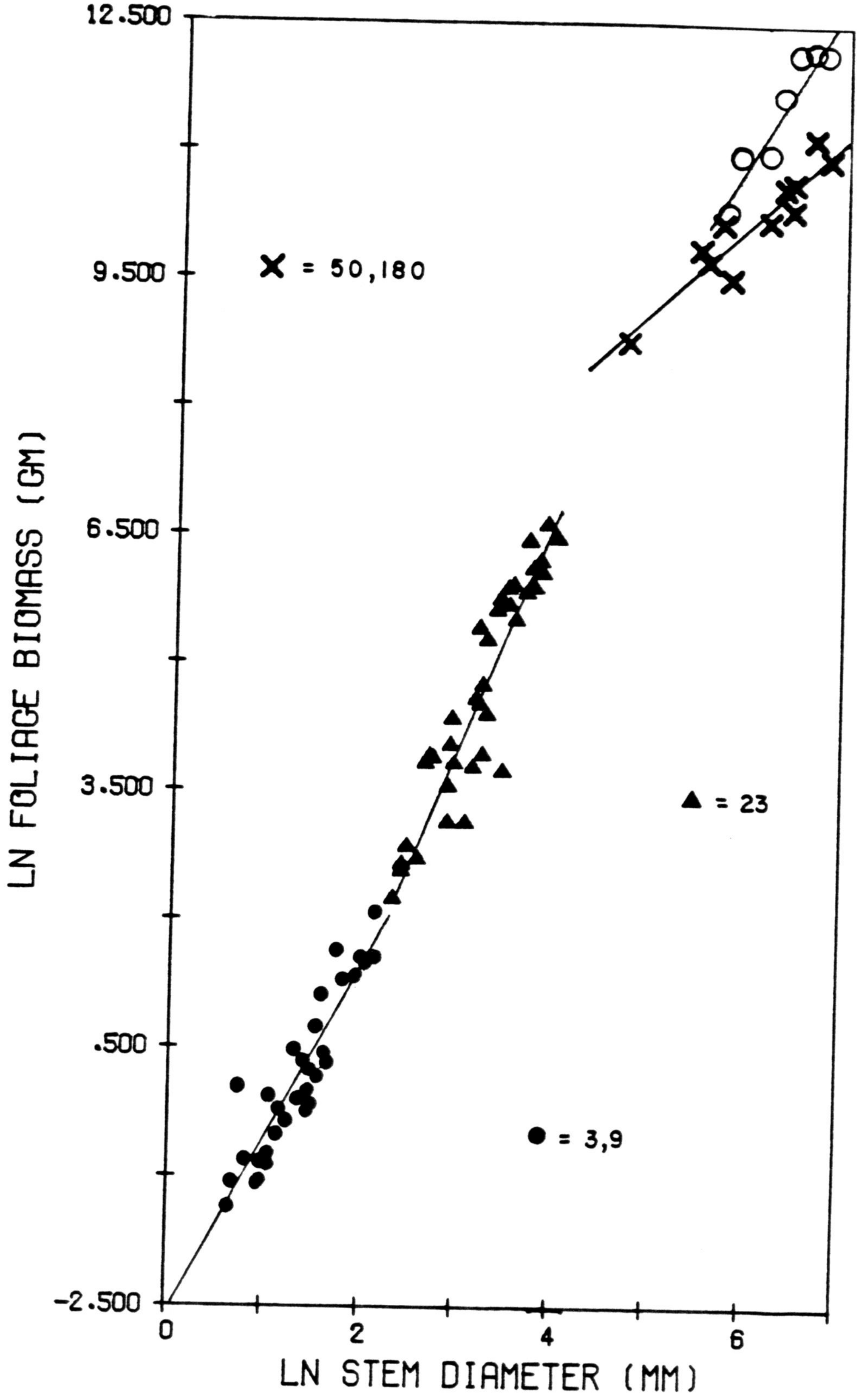
APPENDIX C

FOLIAGE BIOMASS REGRESSION ON BRANCH DIAMETER



APPENDIX D

FOLIAGE BIOMASS REGRESSION ON STEM DIAMETER



CURRICULUM VITAE

NAME:	Michael R. Keyes	
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EDUCATION:	1982	Ph.D., University of Washington, Seattle (Ecology)
	1979	M.S., University of Washington, Seattle (Ecology)
	1976	B.S., University of California, Berkeley (Forestry)
	1972-73	University of California, Santa Barbara
	1971-72	University of California, Riverside
AWARDS:	1975	Walter Mulford Forestry Scholarship
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	1972-73	University of California Grant
	1971-75	American Legion Auxillary Scholarship
	1971-75	California State Scholarship
	1971	Redding Rotary Scholarship

FIELD EXPERIENCE:

1982	Consulting Ecologist. Environmental assessment of private land; predominantly field-oriented. Soils evaluation, land use recommendations. Nautilus Environmental Consultants, Sequim, Washington.
1981	Research Assistant. Report writing for biomass/energy plantation study. Work on hydrological cycle and mineral nutrition.
1981	Spring. Instruction of field ecology course. Design of field exercises in ecological methods. Emphasizing community growth dynamics. Eatonville, Washington.
1978-80	Western Washington. Research on growth and phenology of Pacific Silver Fir stands as related to detritus accumulation. Supported by the National Science Foundation.
1977	Washington and Oregon. Nutrient losses from perturbed forest ecosystems (mineral cycling). Supported by National Science Foundation; unsupported work on masters thesis.

1976	Summer, Southern Oregon. Supervisor of timber falling crew. Field development of wt. scaling techniques. Contract helicopter logging with Evergreen Helicopters, McMinnville, Oregon.
1975	Northern California. Data analysis, forest-type mapping for applicability studies using LANDSAT (ERTS) and SKYLAB imagery. USFS Forest and Range Experiment Station. Remote Sensing Group, Berkeley, California.
1974	Summer-Fall, Montana. Timber and slash inventory, timber stand improvement. USFS Glacier View District, Flathead National Forest, Kalispel, Montana.
1972-73	Summers, Northern California. Recreation aid, brush control crew supervisor. USFS Shasta Lake District, Shasta-Trinity National Forest, Redding, California.
1970-71	Summers, Northern California. Fire-fighting, fire look-out, California Division of Forestry. Tehama-Glenn District, Red Bluff, California.
1969	Summer, Northern California. Rearing of Rainbow and G. Brown trout and trout habitat improvement, Whiskeytown Creek Sportsman Club, Whiskeytown, California.

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