NET PRIMARY PRODUCTION, PRODUCTION ALLOCATION, AND FOLIAGE EFFICIENCY IN SECOND GROWTH DOUGLAS-FIR STANDS WITH DIFFERING SITE QUALITY

By

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ABSTRACT

Several of the current generation of computer models which simulate biomass production in forest ecosystems require a quantitative understanding of the effects of site quality on foliage efficiency (the amount of biomass produced per unit of foliage) and on carbon partitioning between above- and belowground stand components. This study investigated changes in foliage efficiency and carbon allocation in 12 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands for which the site indices ranged from 19.5 to 41.3 m at 50 years. These stands are located on Vancouver Island, British Columbia, Canada.

Regression models for aboveground biomass components were developed from 39 destructively sampled Douglas-fir trees. Foliage biomass was predicted with a model which uses diameter at breast height (dbh) and a competition index as independent variables. This model predicts that stand foliage biomass stabilizes after canopy closure. Diameter and tree mortality data of the 12 Douglas-fir stands were available for 15 to 16 years, and were used to calculate aboveground and coarse root biomass and annual production estimates. In 1985, aboveground biomass in the 12 stands, with ages from 32 to 70 years, ranged from 135 to 573 Mg ha^{-1}. Coarse root biomass was estimated to be equal to 20 - 23% of aboveground biomass. In the period between 1985 and 1987, annual aboveground production (ANPP) in these 12 stands ranged from 4.7 to 16.0 Mg ha^{-1} $year^{-1}$. Coarse root production was estimated to be equal to 13 - 16% of aboveground production.

Fine (0-2 mm) and small (2-5 mm) root biomass and production estimates were derived by analyzing soil cores collected in five of the stands on 5 to 6 sampling dates over a 12 month period. All five stands showed similar seasonal dynamics in live fine root biomass, with the highest values occurring in May and

the lowest values in October. In May 1985, biomass of living fine and small roots ranged from 1.82 to 7.91 Mg ha^{-1} and from 0.59 to 4.10 Mg ha^{-1}, respectively. Three different methods of computing production and mortality were assessed. Different estimates were obtained for annual production and annual mortality in both fine and small roots, because fine root mortality exceeded production during the year which had a very dry summer. Estimates derived using one of the computational methods (decision-matrix) ranged from 1.12 to 5.14 Mg $ha^{-1}year^{-1}$ for fine root production and from 2.15 to 4.89 Mg $ha^{-1}year^{-1}$ for fine root mortality. Small root production and mortality estimates based on this computational method ranged from 0.51 to 2.22 and from 0.88 to 2.13 Mg $ha^{-1}year^{-1}$, respectively.

With increasing site index, a decreasing proportion of total production was allocated to belowground stand components. The site with the lowest site index allocated about 31 to 51% of total net production to belowground components while the site with the highest site index allocated about 23 to 30% belowground. About 56% of the variation in 72 estimates (12 stands and 6 measurement periods) of foliage efficiency based on aboveground production was accounted for by a regression model with foliage biomass and site index as independent variables. This model suggests that there is an optimum foliage biomass at which total aboveground production is maximized and that this optimum foliage biomass increases with increasing site index.

The results of this study emphasize the importance of understanding variation in canopy function and shifts in carbon allocation from above to belowground stand components. Forest ecosystem production simulation models should include an explicit representation of changes in foliage efficiency and carbon allocation patterns to be able to accurately predict the responses of forest ecosystems to changes in environmental conditions and to silvicultural treatments.

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1. GENERAL INTRODUCTION

Until recently, forest production ecology has focussed on aboveground biomass and production because stems are the primary harvestable component of forest ecosystems and because of the difficulties involved in obtaining data on belowground biomass and production. Faced with a changing and uncertain future, it is becoming increasingly important to be able to make accurate predictions about the responses of forest ecosystems to anticipated changes in environmental conditions and management regimes. Such predictions require a sound understanding and quantification of both above- and belowground stand components and of the factors that determine the partitioning of net production between them.

Computer simulation models have become a very important tool for the prediction of forest growth (cf. Ek *et al.* 1988a, 1988b), because they can integrate existing knowledge about complex systems and make projections over time scales which are of interest to foresters. In order to develop, calibrate, and use such models, forest science must provide a quantitative understanding of the major growth determining ecosystem processes.

The central concept underlying many simulation models of forest growth is that foliage biomass or area is multiplied by some measure of foliage production efficiency to obtain an estimate of total photosynthate production. An allocation scheme or hierarchy is then used to partition total production to stand components (McMurtrie and Wolf 1983, Grier *et al.* 1986, Barclay and Hall 1986, Kimmins *et al.* 1986, Mäkelä and Hari 1986, Ford and Bassow 1988). Such an approach to modelling requires a quantitative understanding of the factors which determine foliage biomass, foliage production efficiency, and carbon allocation to above and belowground stand components. Few production studies in forest ecosystems have

investigated belowground production and therefore few have been able to distinguish between the relative contributions of changes in photosynthate production and photosynthate allocation to the observed differences in aboveground production.

In earlier studies, belowground production was often assumed to represent some fixed proportion of aboveground production (Newbould 1967). In 1981, Keyes and Grier reported that the proportion of total production allocated to belowground stand components is affected by site conditions. They found that the difference in total production between a high and low productivity Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand in western Washington was much smaller than the difference in aboveground production, because trees growing on the better site allocated much less photosynthate to fine and small root production (Keyes and Grier 1981). This observed plasticity of resource partitioning in response to environmental conditions has raised questions about the interpretation of the responses of forest ecosystems to silvicultural treatments (Kurz 1989). The increase in aboveground production following nitrogen fertilization, for example, can be due to an increase in photosynthate production, or a shift in carbon allocation away from fine roots, or both (Brix 1983, Brix in press, Friend 1988, Axelsson and Axelsson 1986). With information about aboveground production only, no unequivocal interpretations of observed aboveground responses are possible.

The overall objectives of the research summarized in this dissertation were to answer two questions for coastal second growth Douglas-fir stands growing on Vancouver Island, British Columbia:

1) Does foliage efficiency change with site quality?

2) Does carbon allocation to belowground stand components decrease with increasing site quality?

Specifically, for each of a series of Douglas-fir stands growing on sites covering a range in site quality, the objectives were:

i) to develop regression models, which use diameter and a competition index as independent variables, for the prediction of aboveground biomass components,

ii) to quantify aboveground and coarse root biomass using these and other regression models,

iii) to quantify fine and small root biomass, production, and mortality, and

iv) to quantify foliage biomass and foliage efficiency.

Figure 1.1 gives an overview of the major components of the research reported in this dissertation. Chapter 2 contains a description of the study sites. Each Chapter that reports research results (Chapters 3 to 6) includes introduction, methods, results, and discussion sections. Biomass regression models for foliage and other aboveground biomass components developed from destructively sampled trees are reported in Chapter 3. In Chapter 4, long-term diameter growth and tree mortality data are combined with remeasurement data from this study and used to calculate competition indices and their change over time for all trees on the study plots. Also in Chapter 4, these data and the regression models developed in Chapter 3 are used to compute aboveground and coarse root biomass and production estimates. Chapter 5 reports estimates of fine and small root production and mortality. The results of all previous chapters are combined in Chapter 6 to investigate the effects of site quality on foliage biomass, foliage efficiency, and production allocation. Conclusions are presented in Chapter 7.

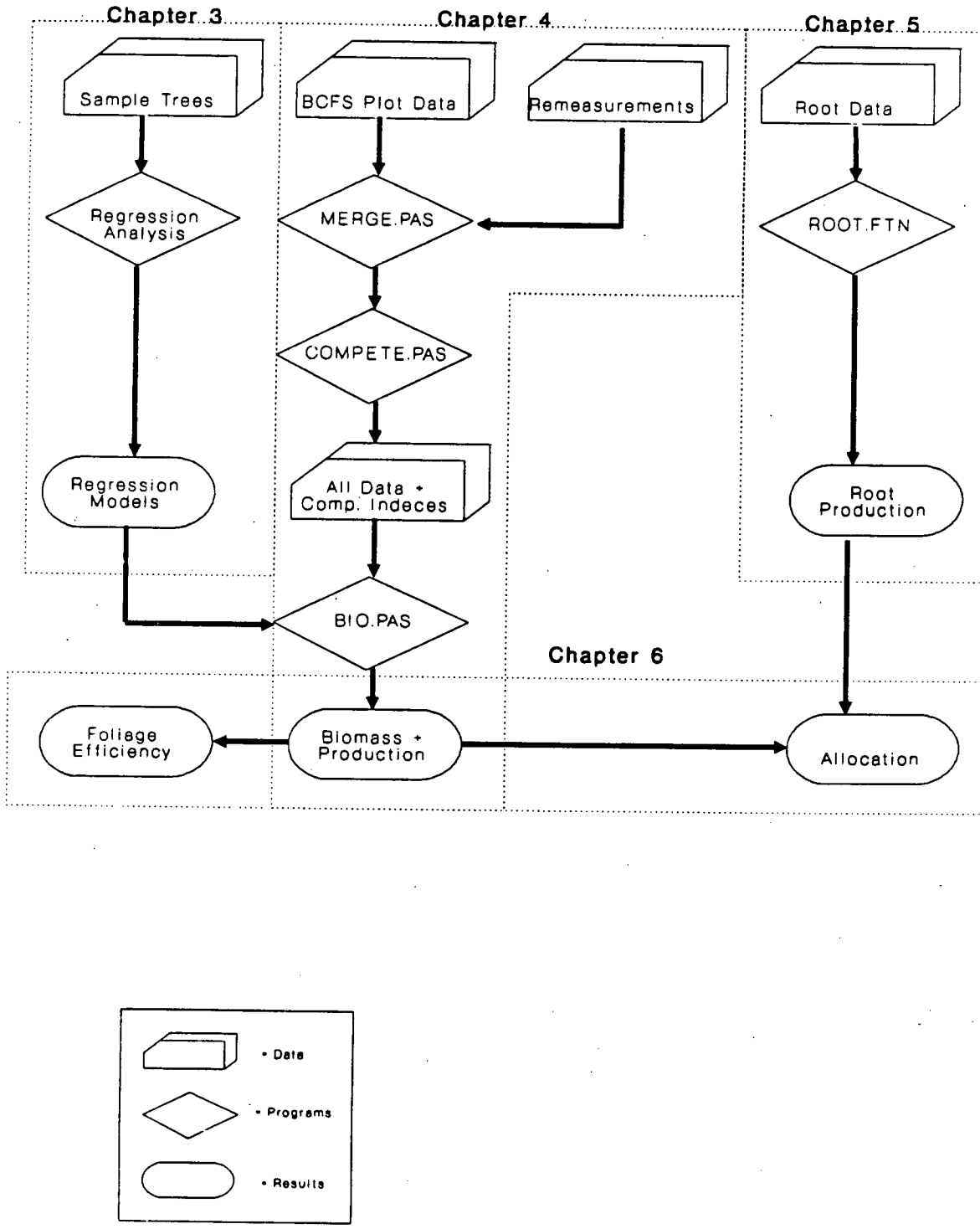

Figure 1.1 A general overview of the major components of this dissertation.

2. DESCRIPTION OF STUDY SITES

This study was conducted in six growth and yield research installations which are part of a network of such installations established by the Forest Productivity Committee, British Columbia Ministry of Forests (Darling and Omule 1989). The six installations of this study are located on the east side of Vancouver Island, British Columbia, Canada (Figure 2.1). Table 2.1 gives the location, elevation, and installation and plot numbers of each of the six study sites. Table 2.2 presents long-term averages of annual precipitation, annual temperature, and temperatures for the coldest and warmest months as measured at nearby climatic stations (Environment Canada 1982).

Five of the six installations are located in the Eastern variant of the Very Dry Maritime Coastal Western Hemlock subzone (CWHxm1) of the British Columbia biogeoclimatic ecosystem classification (Pojar *et al.* 1987, Green *et al.* 1984, Krajina 1969), while the sixth (Installation 72) is in the Western variant of that subzone (CWHxm2) (Table 2.3). Actual soil moisture regimes (Pojar *et al.* 1987, Green *et al.* 1984) range from moderately dry to fresh and actual soil nutrient regimes range from poor to rich (Table 2.3). The parent material in five of the installations is a morainal blanket while in the sixth it is fluvial material (Table 2.4). Soils are either Eluviated Dystric Brunisols or Duric Humoferric Podzols (Agriculture Canada Expert Committee on Soil Survey 1987) that are moderately well to well drained (Table 2.4). Forest floors in all installations are less than 2 cm thick. Mor humus forms were found in five Installations and Installation 72 had a Mull humus form.

Each of the six installations contains up to 18 experimental plots, including the two untreated control plots on which this study is based. Details of site

selection and plot establishment are provided in Darling and Omule (1989). Plots are square (22.36 m x 22.36 m), have an area of 0.05 ha, and are surrounded by a 0.05 ha buffer zone. A distance of at least 12 meters separates the outer edge of the buffer zone from the nearest adjacent buffer zone or road, stream, or other changes in stand structure.

In 1985, Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) accounted for 90% or more of the overstory basal area in nine of the twelve stands (Table 2.5). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was present as a second overstory species. It generally represented less than 4% of total basal area, but in three of the plots western hemlock accounted for 17.7 to 32.4% of total basal area. In four of the five plots in which western redcedar (*Thuja plicata* Donn) was present, it contributed less than 2% of the basal area; in one plot it accounted for 9.1%. In Installation 72, Plot 14, one bigleaf maple (*Acer macrophyllum* Pursh.) contributed 3.8% of the basal area (Table 2.5).

In 1985, Installations ranged in age from 32 to 70 years and were either naturally regenerated, planted, or were planted and additional natural regeneration occurred (Table 2.5). All sites appear to have been burned after logging. Stand densities in 1985 ranged from 3400 to 440 stems per hectare of which 40 to 98 % were Douglas-fir trees. The relative density distribution of stems of other species was fairly similar to the basal area distribution of these species (Table 2.4).

The understory vegetation of the lower site index plots was generally dominated by *Gaultheria shallon* Pursh with some *Mahonia nervosa* (Pursh) Nutt. As site quality improved, the dominance of *Gaultheria shallon* declined and *Mahonia nervosa* became a larger component of the understory. Mosses encountered on the low to medium quality plots were mainly *Kindbergia oregana*

(Sull.) Ochyra and *Hylocomium splendens* (Hedw.) B.S.G., while in the high quality sites *Rhytidiadelphus loreus* (Hedw.) Warnst, *Rhytidiadelphus triquetrus* (Hedw.) Warnst., and *Rhytidiopsis robusta* (Hook.) Broth were dominant.

The understory vegetation of Installation 72 was dominated by *Polystichum munitum* (Kaufl.) Presl and *Achlys triphylla* (Sm.) DC. Frequently encountered herbs were *Tiarella laciniata* Hook., *Tiarella trifoliata* L., and *Trientalis latifolia* Hook. Mosses (*Kindbergia oregana, Hylocomium splendens*) were mostly confinded to decaying logs.

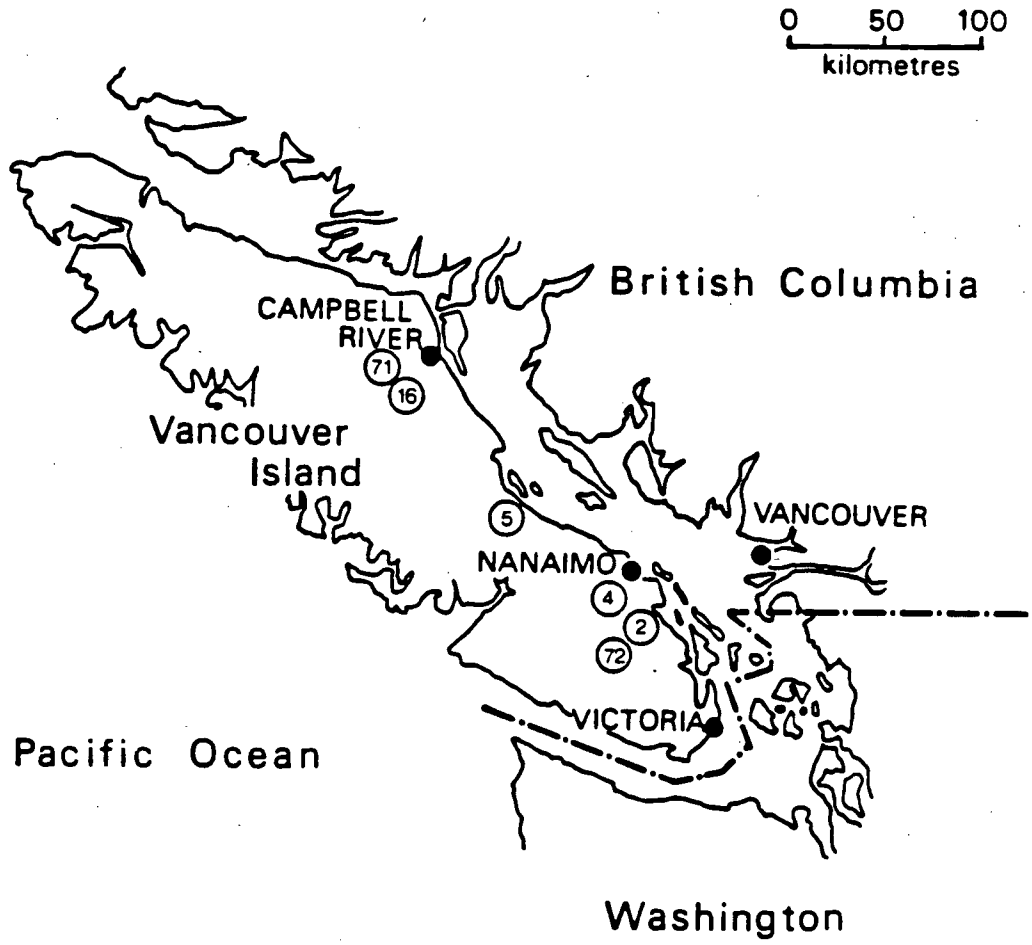

Figure 2.1. The location of the six research installations on eastern Vancouver Island, British Columbia, Canada. Numbers in circles refer to installation numbers (cf. Table 2.1).

Table 2.1. Installation and plot numbers as assigned by the Forest Productivity Committee, nearest town, latitude and longitude, and elevation of the study sites.

Installation	Plots	Location	Latitude	Longitude	Elevation (m)
2	6 11	Chemainus	48°50'N	123°50'W	419
4	1 17	Cassidy	49°05'N	124°01'W	333
5	8 10	Bowser	49°25'N	124°48'W	360
16	2 6	Campbell River	49°58'N	125°30'W	335
71	11 14	Campbell River	50°02'N	125°29'W	244
72	2 14	Cowichan Lake	48°49'N	124°07'W	229

Table 2.2. Mean annual precipitation and temperature at climate stations near the study sites. Data from Canadian Climatic Normals 1951-1980 (Environment Canada 1982).

Inst	Climate Station	Mean annual precipitation (mm)	Mean annual temperature (°C)	Mean Jan. temperature (°C)	Mean July temperature (°C)
2	Nanaimo Airport	1104	9.3	1.8	17.4
4	Nanaimo Airport	1104	9.3	1.8	17.4
5	Mud Bay Fisheries	1714	9.3	1.8	17.4
16	Campbell River Airport	1406	8.2	0.4	16.6
71	Campbell River Airport	1406	8.2	0.4	16.6
72	Cowichan Lake Res. Stn.	2123	9.1	1.4	17.4

Table 2.3. Regional climate (biogeoclimatic variants), soil moisture regime and soil nutrient regime of the six installations according to Smith (1979) but following the more recent terminology of Green *et al.* (1984) and Klinka (pers. comm.). CWHxm = Very Dry Maritime Coastal Western Hemlock subzone, 1 = Eastern variant, 2 = Western variant.

Instal-lation	Biogeoclimatic Variant	Soil Moisture Regime	Soil Nutrient Regime
2	CWHxm1	moderately dry	poor
4	CWHxm1	slightly dry	medium
5	CWHxm1	slightly dry	medium
16	CWHxm1	slightly dry	medium
71	CWHxm1	slightly dry	medium
72	CWHxm2	fresh	rich

Table 2.4. Selected environmental characteristics of the five study sites. Data from Smith (1979).

Inst.	Parent material	Soil classification	Drainage	Texture	Coarse frag. (%)	Humus form[a]
2	morainal blanket	Eluviated Dystric Brunisol	moderately well drained	loam	30	Mor
4	morainal blanket	Eluviated Dystric Brunisol	well drained	sandy loam	56	Mor
5	fluvial	Duric Humo-Ferric Podzol	well drained	sandy loam	65	Mor
16	morainal blanket	Duric Humo-Ferric Podzol	moderately well drained	sandy loam	45	Mor
71	morainal blanket	Eluviated Dystric Brunisol	well drained	sandy loam	33	Mor
72	morainal blanket	Duric Humo-Ferric Podzol	moderately well drained	sandy loam	48	Mull

[a] Forest floor thickness in all plots is less than 2 cm.

Table 2.5. Stand age, stand origin, site index (SI) (Bruce 1981), stand density, and basal area (BA) distribution in 1985 for the 12 study plots.

					Stand Density		Basal Area[b]					
Inst	Plot	Origin[a]	Age (yr)	SI (m@50)	(st. ha^{-1})	%DF	(m^2ha^{-1})	%DF	%WH	%RC	%WP	%BM
2	6	N	42	27.7	3000	40.0	53.4	66.5	32.4	1.0	-	-
2	11	N	41	19.5	2840	71.8	33.6	80.3	17.7	1.9	-	-
4	1	C	44	29.1	1840	97.8	45.3	99.7	0.3	-	-	-
4	17	C	48	25.7	1640	86.6	37.4	94.8	3.2	-	1.9	-
5	8	P	40	26.8	3400	53.5	58.7	76.0	23.9	0.1	-	-
5	10	P	39	29.5	1420	87.3	47.4	96.9	3.1	-	-	-
16	2	P	32	29.4	2000	98.0	41.3	98.6	0.2	1.2	-	-
16	6	P	32	32.4	2520	80.2	45.1	90.4	0.5	9.1	-	-
71	11	P	41	24.6	1880	97.9	45.3	99.5	0.5	-	-	-
71	14	P	41	23.3	2460	97.6	46.0	99.1	0.9	-	-	-
72	2	C	70	41.3	440	90.9	69.1	97.0	3.0	-	-	-
72	14	C	70	41.0	480	95.8	75.3	96.2	-	-	-	3.8

[a] Stand origin: N= natural, P=plantation, C=combination. (from Darling and Omule 1989).

[b] DF = Douglas-fir, WH = western hemlock, RC = western redcedar, WP = western white pine, BM = bigleaf maple.

3. BIOMASS REGRESSION EQUATIONS

3.1 INTRODUCTION

Biomass regression equations are widely used in both forest science and management (Satoo and Madgwick 1982, Cannell 1982). Such equations typically relate a variable which is difficult to measure, such as foliage biomass, to one or more other variables which are easier to measure, such as diameter at breast height (dbh). Regression models that describe relationships between stem biomass components and stem diameter typically have very high coefficients of determination (R^2), which indicates that the independent variable accounts for most of the observed variation in the dependent variable. In contrast, models which relate crown biomass components to stem characteristics (e.g. foliage biomass to dbh) have much lower R^2 values, indicating that factors other than those accounted for by the independent variable influence the relationship.

Regression equations are often developed for predictive purposes. A sample of a population is measured in detail and the observed relationships are employed to calculate the variables of interest for the entire population. This works well if the population from which the regression models were developed and the population to which they are applied for prediction are similar. There are, however, many examples in forestry where models derived in one study have been used in other studies without ensuring that the allometric relationships described by those models are indeed similar in the two populations. Part of the problem is that it is often unclear what factors influence the allometric relationships. Thus, the criteria by which to judge whether two stands can be described by the same regression models are often not available.

One approach to dealing with between-stand variation has been to develop regional regression models that are based on sample trees from a large number of stands (Gholz *et al.* 1979, Standish *et al.* 1985). Such models average the variation between stands, but their predictions for individual stands may be substantially in error (Marshall and Waring 1986).

A second approach is to incorporate into the regression equation additional independent variables which account for some of the remaining sources of variability. For example, Baskerville (1983) found that stand age accounts for some of the between-stand variation in foliage biomass regression models developed for balsam fir (*Abies balsamea* (L.) Mill.). The pipe model theory (Shinozaki *et al.* 1964a, b) suggests that a functional relationship exists between the cross sectional area of the water-conducting sapwood and the amount of foliage which can be supported by this sapwood. Several studies have since shown that sapwood basal area can be used to predict foliage biomass (Grier and Waring 1974, Snell and Brown 1978, Whitehead 1978). More recent studies have found that factors such as sapwood permeability (Whitehead *et al.* 1984) and mean annual sapwood ring width (Albrektson 1984) can account for additional variation in the foliage area-sapwood area relationship.

Although the use of sapwood basal area as an independent variable in regression models may account for some of the between-stand variation, this variable is not always measurable, particularly in permanent sample plots where the need for repeated diameter measurements often precludes the use of increment corers. Other variables which have been shown to account for some of the residual variation in canopy biomass regression models, such as crown length or stem diameter at the base of the live crown, are difficult to measure on large numbers of trees.

Brown (1978) investigated the suitability of stand density, determined with a prism plot, as an independent variable in biomass regression models and found that it reduced the residual variation somewhat for some conifer species. A competition index might be superior to stand density in reducing the residual variation in biomass regression models, because it integrates the cumulative competitive influence of the trees surrounding a subject tree. Competition indices are based on various computational methods that typically use either the distance and relative size of competing trees or the crown area overlap. For detailed reviews see Noone and Bell (1980) and Daniels *et al.* (1986). Traditionally, these indices have been used in growth and yield studies to predict growth rates of trees following thinning (Smith and Bell 1983). None of the published regression models includes a competition index as independent variable, although stand maps are frequently available for research installations and competition indices can be computed from such data. In this study, four competition indices were tested for their contribution to regression models that predict the biomass of crown and stem components.

The first objective of the research reported in this chapter was to provide regression equations for the prediction of foliage, branchwood, stemwood, and stembark biomass for my study areas. The second objective was to investigate the contribution of several competition indices to these regression models. It was hypothesized that competition indices, which measure the growing conditions experienced by individual trees, will significantly improve biomass regression equations, especially those for canopy biomass components.

It was hoped that by adding these indices, the generality of the regression models, and their value to other studies, might be increased. One of the criteria for the development of these new models was that their independent variables should be easily measurable. This excluded the use of sapwood basal area because it can

only be measured by taking increment cores which may not be desirable in permanent sample plots where diameters will be measured repeatedly.

3.2 REVIEW OF EXISTING MODELS

3.2.1 Foliage biomass regression models for Douglas-fir

Investigations into the relationships between foliage biomass and other tree variables in Douglas-fir date as far back as Burger (1935) and Kittredge (1944). While these relationships were merely statistical, Shinozaki *et al.* (1964 a,b) proposed a functional relationship between foliage biomass and the cross-sectional area of the water-conducting tissue supporting the foliage. This pipe model theory has become the basis for many investigations which relate foliage biomass to sapwood basal area. In Douglas-fir, as in many other tree species, sapwood basal area has often, though not always, been found to be superior to dbh as a predictor of foliage biomass (Grier and Waring 1974, Snell and Brown 1978, Brix and Mitchell 1983).

Table 3.1 lists 32 published models for the prediction of Douglas-fir foliage biomass. The relationship between foliage biomass and the independent variable, dbh or basal area (BA), varies greatly (Figure 3.1, Table 3.2). For example, the predicted foliage biomass for a tree of 25 cm dbh ranges from 9.0 kg (Model 10) to 26.4 kg (Model 1), an almost threefold difference (294%). Regression coefficients of the 10 models presented in Figure 3.1 are listed in Table 3.2. Some of the regression lines in Figure 3.1 are extrapolated beyond the range of diameters from which the models were derived, but the above numeric example is within the range of diameters of Models 1 and 10.

Table 3.1. Regression models for calculating foliage biomass of Douglas-fir.

n = number of sample trees, ln = logarithm base e, log = logarithm base 10, d.b.l.c.= diameter at base of live crown, cw = crown width, BA = basal area, SA = sapwood area

Independent Variable	n		Range of dbh (cm)	Source
log dbh	22		6-46	Kittredge 1944
dbh	29			Ahmed 1956
log dbh	5			Swank 1960
log dbh	35		6-46	Heilman 1961
dbh cw^2	23		2-120	Kurucz 1969
log dbh	10		2-23	Dice 1970
log dbh	104	a	x=11.6	Dice 1970
log dbh	8		9-111	Woodard 1974
SA	36			Grier and Waring 1974
log dbh				Gholz *et al.* 1976
ln dbh	29		2-163	Grier and Logan 1977
ln dbh	5		34-53	Kay 1978
ln d.b.l.c.	5		34-53	Kay 1978
ln dbh	18		1-11	Snell and Brown 1978
ln SA	18		1-11	Snell and Brown 1978
log dbh	123	a	2-162	Gholz *et al.* 1979
dbh^2ht	171	a	2-162	Shaw 1979
SA	14			Granier 1981
SA b.l.c.	13			Granier 1981
BA	15			Granier 1981
SA	96	b	5-25	Brix and Mitchell 1983
BA u. bark	96	b	5-25	Brix and Mitchell 1983
ln dbh	8	c	6-29	Feller *et al.* 1983
ln dbh	10		5-56	Feller *et al.* 1983
ln height	10			Feller *et al.* 1983
ln height	16			Feller *et al.* 1983
log dbh	26	d	9-30	Grier *et al.* 1984
dbh^2ht	49		4.5-66.0	Standish *et al.* 1985
dbh	12		10-25	Borghetti *et al.* 1986
SA	12		10-25	Borghetti *et al.* 1986
ln dbh	40			Espinosa Bancalari and Perry 1987
lndbh	18		1.4-13.4	Helgerson *et al.* 1988

[a] This study compiles data previously published elsewhere.
[b] 24 trees in each of 4 treatments.
[c] Old (height > 2.5m) and young (< 2.5m) stands on good and poor sites separated.
[d] 13 trees in a control and fertilizer treatment.

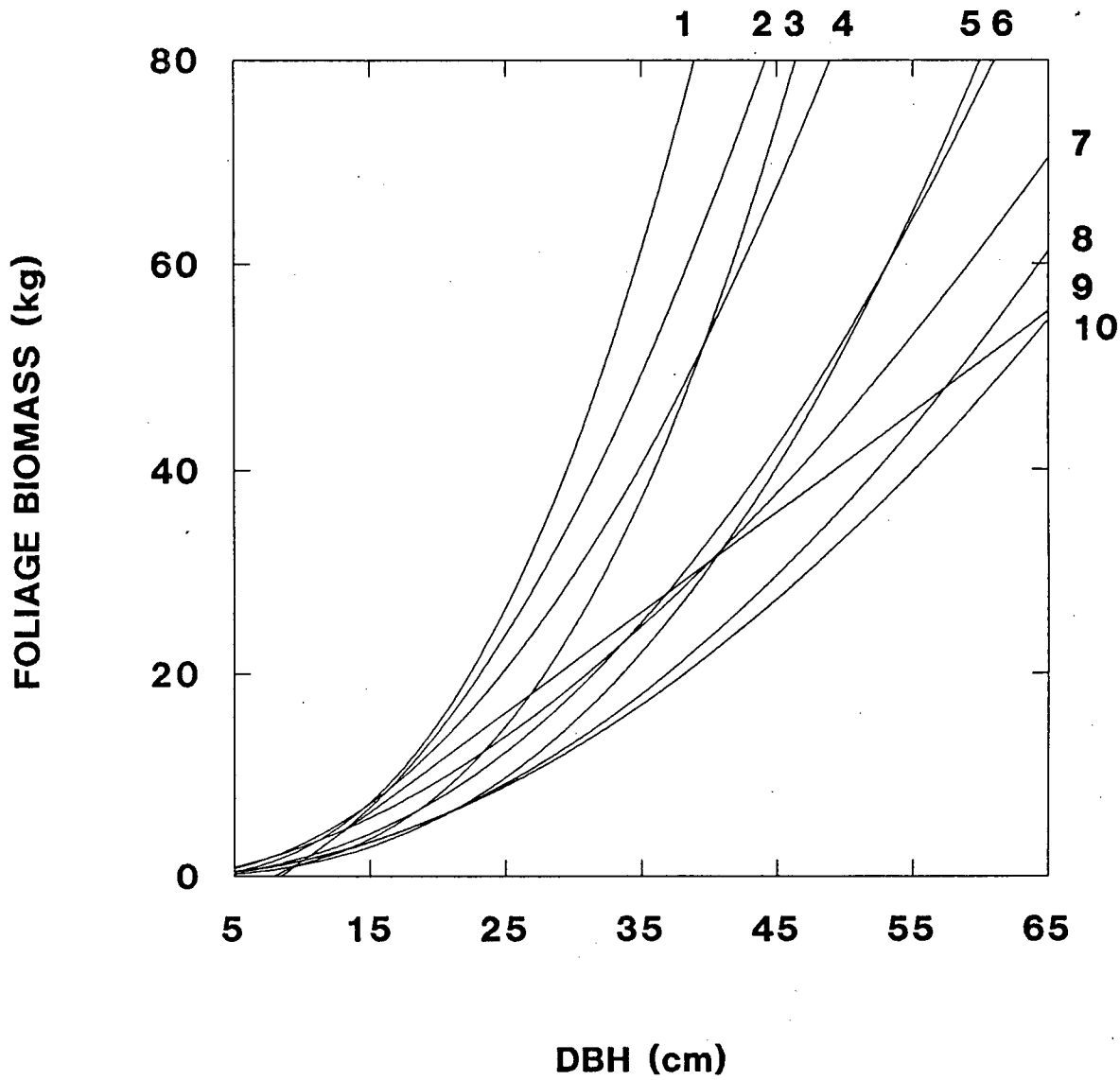

Figure 3.1. Foliage biomass as predicted by 10 regression models which use dbh or basal area as the independent variable. Details of the models are listed in Table 3.2.

The relationship between foliage biomass and sapwood area (SA) is equally variable (Figure 3.2) for six regression models (Table 3.3). For example, a tree of 250 cm^2 SA is predicted by Model 6 to have 10.0 kg and by Model 1 to have 20.2 kg of foliage biomass, a twofold difference.

All models in Table 3.1 include, as the independent variable, one or several measures of dimensions of individual trees, but do not account for any additional sources of variability in the relationship between that variable and foliage mass. Factors which may affect this allometric relationship include stand density, and nutrient and moisture availability (Grier *et al.* 1986, Brix and Mitchell 1983).

Estimating foliage mass for an individual stand using regression models from a different stand, or with combined regional models (e.g. Gholz *et al.*, 1979), may yield large errors (Grier *et al.*, 1984, Marshall and Waring 1986). Madgwick (1983) identifies the need to determine additional variables which may affect the relationship between crown weight and individual stem dimensions. As pointed out by Madgwick (1983), a new approach is required which identifies sources of variability not accounted for in the models listed in Table 3.1. Competition indices may account for some of the residual variability as they describe the competitive status of a tree relative to its neighbours.

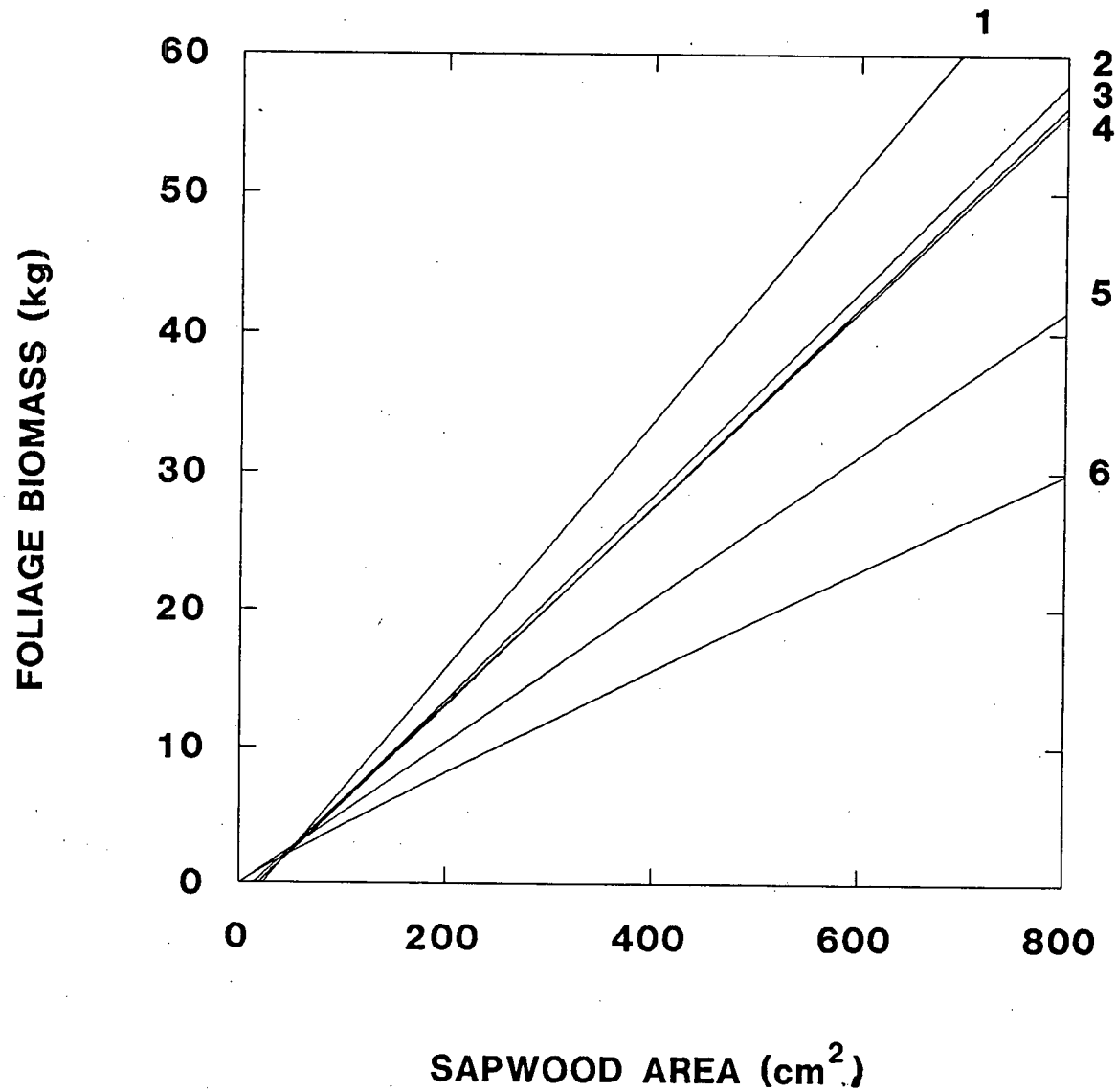

Figure 3.2. Foliage biomass as predicted by 6 regression models which use sapwood area as the independent variable. Details of the models are listed in Table 3.3.

Table 3.2. Ten regression models for the prediction of foliage biomass (FOL) of Douglas-fir with dbh or basal area (BA) as independent variable. ln = logarithm base e, log = logarithm base 10. Standard error of estimate (SEE) is in logarithmic units.

Model			R^2	SEE	Source	Number[a]
lnFOL (kg)	=	-4.791+2.502*lndbh	0.92	0.160	Grier *et al.* 1984	1
FOL (kg)	=	-2.688+0.054*BA	0.74		Granier 1981	2
lnFOL (kg)	=	-6.093+2.723*lndbh	0.93	0.240	Espinosa Bancalari and Perry 1987	3
lnFOL (g)	=	3.329+2.031*lndbh	0.94	0.348	Helgerson *et al.* 1988	4
logFOL (g)	=	0.643+2.396*logdbh	0.87	0.194	Dice 1970[b]	5
logFOL (g)	=	1.159+2.097*logdbh	0.82	0.279	Dice 1970[c]	6
lnFOL (kg)	=	-2.846+1.701*lndbh	0.86	0.695	Gholz *et al.* 1979	7
lnFOL (kg)	=	-4.151+1.982*lndbh	0.96	0.176	Grier & Logan 1977	8
FOL (kg)	=	-8.296+0.979*dbh	0.92		Borghetti *et al.* 1986	9
lnFOL (kg)	=	-3.890+1.890*lndbh	0.88		Gholz *et al.* 1976	10

[a] refers to labels in Figure 3.1
[b] Cedar River data set
[c] combined data set

Table 3.3. Six regression models for the prediction of foliage biomass (FOL) of Douglas-fir with sapwood area (SA) as independent variable. ln = logarithm base e, log = logarithm base 10. SEE is in logarithmic units.

Model			R^2	SEE	Source	Number[a]
FOL (kg)	=	-2.020+0.089*SA	0.85		Brix & Mitchell 1983[c]	1
FOL (kg)	=	-1.365+0.074*SA	0.92		Granier 1981	2
FOL (kg)	=	-1.340+0.072*SA	0.97		Grier & Waring 1974	3
FOL (kg)	=	-1.004+0.071*SA	0.86		Borghetti *et al.* 1986	4
FOL (kg)	=	-0.030+0.052*SA	0.78		Brix & Mitchell 1983[b]	5
lnFOL (g)	=	3.996+0.938*lnSA	0.96	0.274	Snell & Brown 1978	6

[a] refers to labels in Figure 3.2
[b] control plot data
[c] all data

3.2.2 Branchwood biomass regression models for Douglas-fir

Six regression models for the prediction of branchwood biomass in Douglas-fir are summarized in Table 3.4 and plotted in Figure 3.3. Model 1 (Helgerson *et al.* 1988) was derived from a data set that included young trees with a maximum of 13.4 cm dbh. The plotted line for Model 1 in Figure 3.3 is clearly an extrapolation beyond the range of the original data, but even at 13 cm dbh this model differs greatly from the other five models.

As with foliage biomass models, there are no criteria by which to judge which model will yield the best biomass prediction for a specific stand. Note that predictions from the regional model (Table 3.4, Model 4, Gholz *et al.* 1979) are approximately in the middle of the range (Figure 3.3).

3.2.3 Stem component biomass regression models for Douglas-fir

Stemwood and stembark biomass are treated as two separate biomass components. Both components are highly correlated with dbh and the range of biomass predictions is much narrower than in the crown biomass components. Table 3.5 lists 6 biomass regression equations for stemwood biomass which are plotted in Figure 3.4. Table 3.6 and Figure 3.5 present six stembark biomass prediction models. Note that both the predicted stemwood and stembark biomass of the regional models (Tables 3.5 and 3.6, Model 1, Gholz *et al.* 1979) are the highest of the range of models presented in Figures 3.4 and 3.5.

Table 3.4. Six regression models for the prediction of branchwood biomass (BRA) of Douglas-fir with dbh as independent variable. ln = logarithm base e, log = logarithm base 10. SEE is in logarithmic units.

Model		R^2	SEE	Source	Number[a]
lnBRA (g)	= 2.856+2.503*lndbh	0.94	0.440	Helgerson *et al.* 1988	1
lnBRA (g)	= ln(1.64)+2.96*lndbh	0.81	0.073	Barclay *et al.* 1986[b]	2
lnBRA (kg)	= -4.456+2.469*lndbh	0.86	0.200	Grier *et al.* 1984	3
lnBRA (kg)	= -3.694+2.138*lndbh	0.92	0.631	Gholz *et al.* 1979	4
logBRA (g)	= 0.945+2.388*logdbh	0.90	0.230	Dice 1970[c]	5
logBRA (g)	= 1.112+2.162*logdbh	0.90	0.156	Dice 1970[d]	6

[a] refers to labels in Figure 3.3
[b] control plot data
[c] combined data
[d] Cedar River data

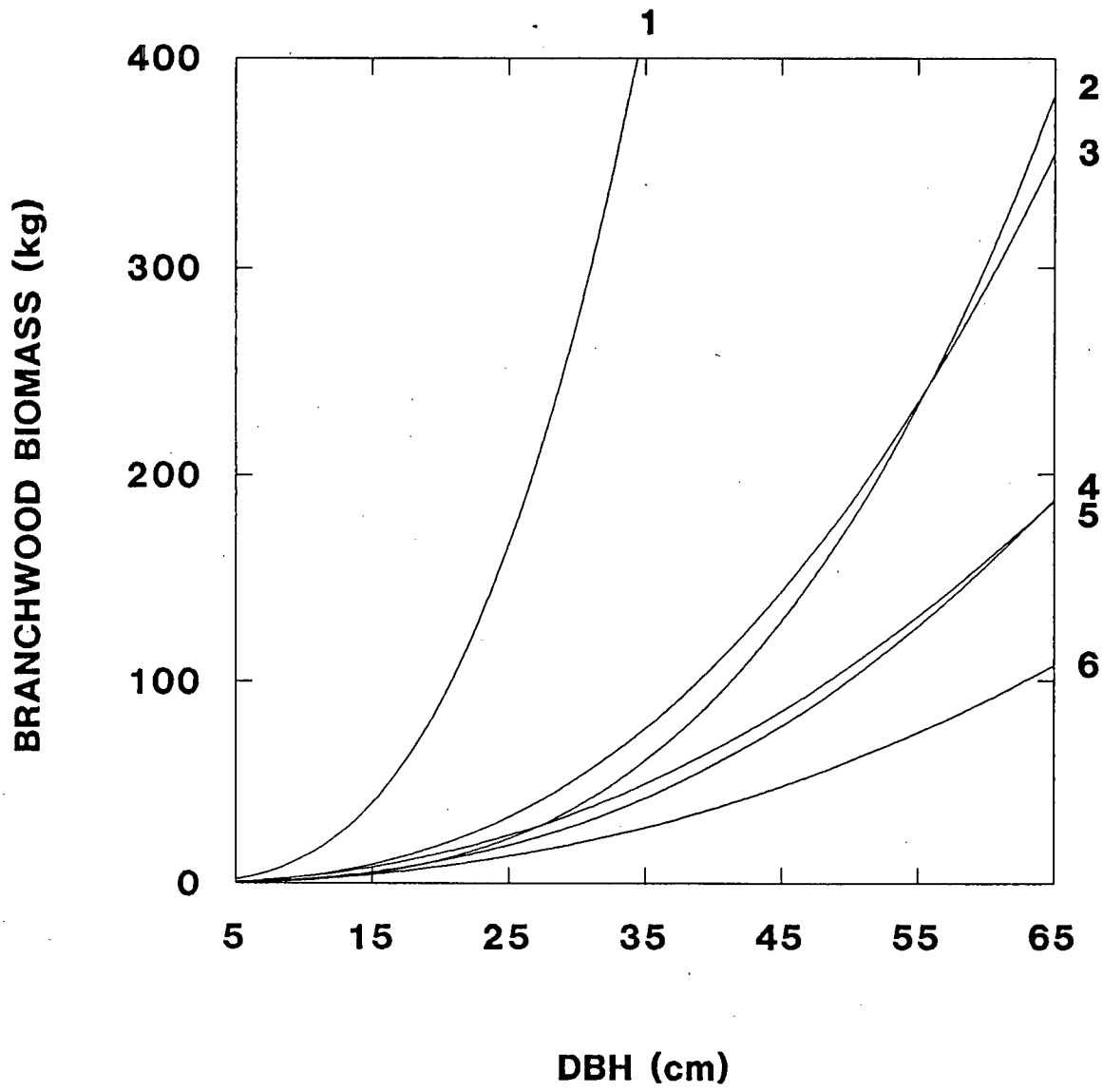

Figure 3.3. Branchwood biomass as predicted by 6 regression models which use dbh as the independent variable. Details of the models are listed in Table 3.4.

Table 3.5. Six regression models for the prediction of stemwood biomass (STW) of Douglas-fir with dbh as independent variable. ln = logarithm base e, log = logarithm base 10. SEE is in logarithmic units.

Model		R^2	SEE	Source	Number[a]
lnSTW (kg)	= -3.040+2.595*lndbh	0.99	0.310	Gholz *et al.* 1979	1
logSTW (g)	= 1.636+2.609*logdbh	0.98	0.064	Dice 1970[b]	2
lnSTW (g)	= -4.747+2.967*lndbh	0.98	0.097	Dice 1970[c]	3
logSTW (kg)	= 1.857+2.444*logdbh	0.89	0.320	Espinosa Bancalari and Perry 1987	4
lnSTW (kg)	= -2.603+2.367*lndbh	0.97	0.080	Grier *et al.* 1984	5
lnSTW (g)	= ln(99.61)+2.28*lndbh	0.98	0.025	Barclay *et al.* 1986[d]	6

[a] refers to labels in Figure 3.4
[b] combined data
[c] Cedar River data
[d] control plot data

Table 3.6. Six regression models for the prediction of stembark biomass (STB) of Douglas-fir with dbh as independent variable. ln = logarithm base e, log = logarithm base 10. SEE is in logarithmic units.

Model		R^2	SEE	Source	Number[a]
lnSTB (kg)	= -4.310+2.430*lndbh	0.99	0.322	Gholz *et al.* 1979	1
lnSTB (kg)	= -5.610+2.701*lndbh	0.85	0.340	Espinosa Bancalari and Perry 1987	2
lnSTB (kg)	= -4.906+2.530*lndbh	0.94	0.130	Grier *et al.* 1984	3
logSTB (g)	= 1.169+2.328*logdbh	0.98	0.027	Dice 1970[b]	4
lnSTB (g)	=ln(16.31)+2.30*lndbh	0.98	0.027	Barclay *et al.* 1986[c]	5
logSTB (g)	= 1.347+2.165*logdbh	0.97	0.115	Dice 1970[d]	6

[a] refers to labels in Figure 3.5
[b] combined data
[c] control plot data
[d] Cedar River data

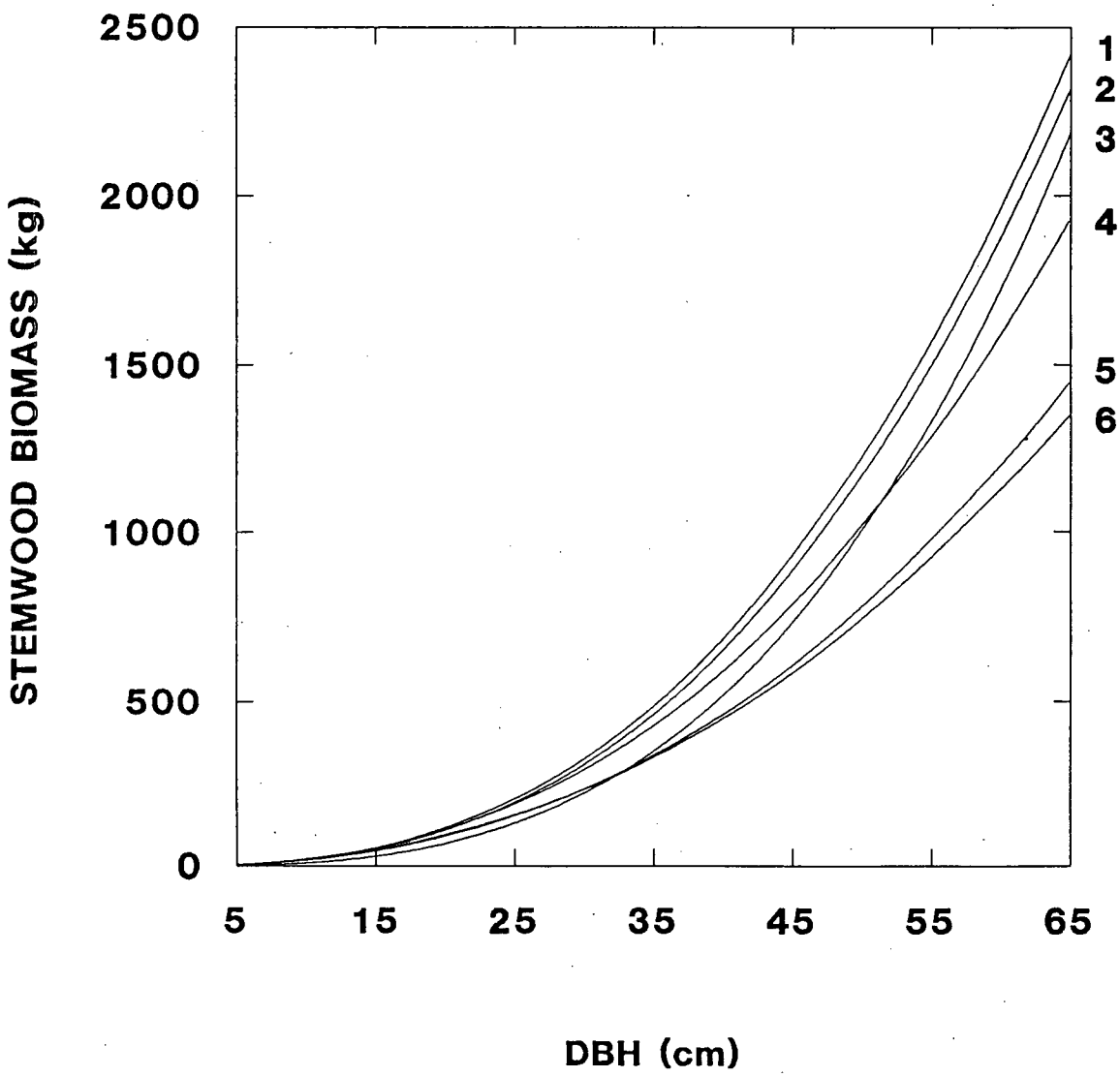

Figure 3.4. Stemwood biomass as predicted by 6 regression models which use dbh as the independent variable. Details of the models are listed in Table 3.5.

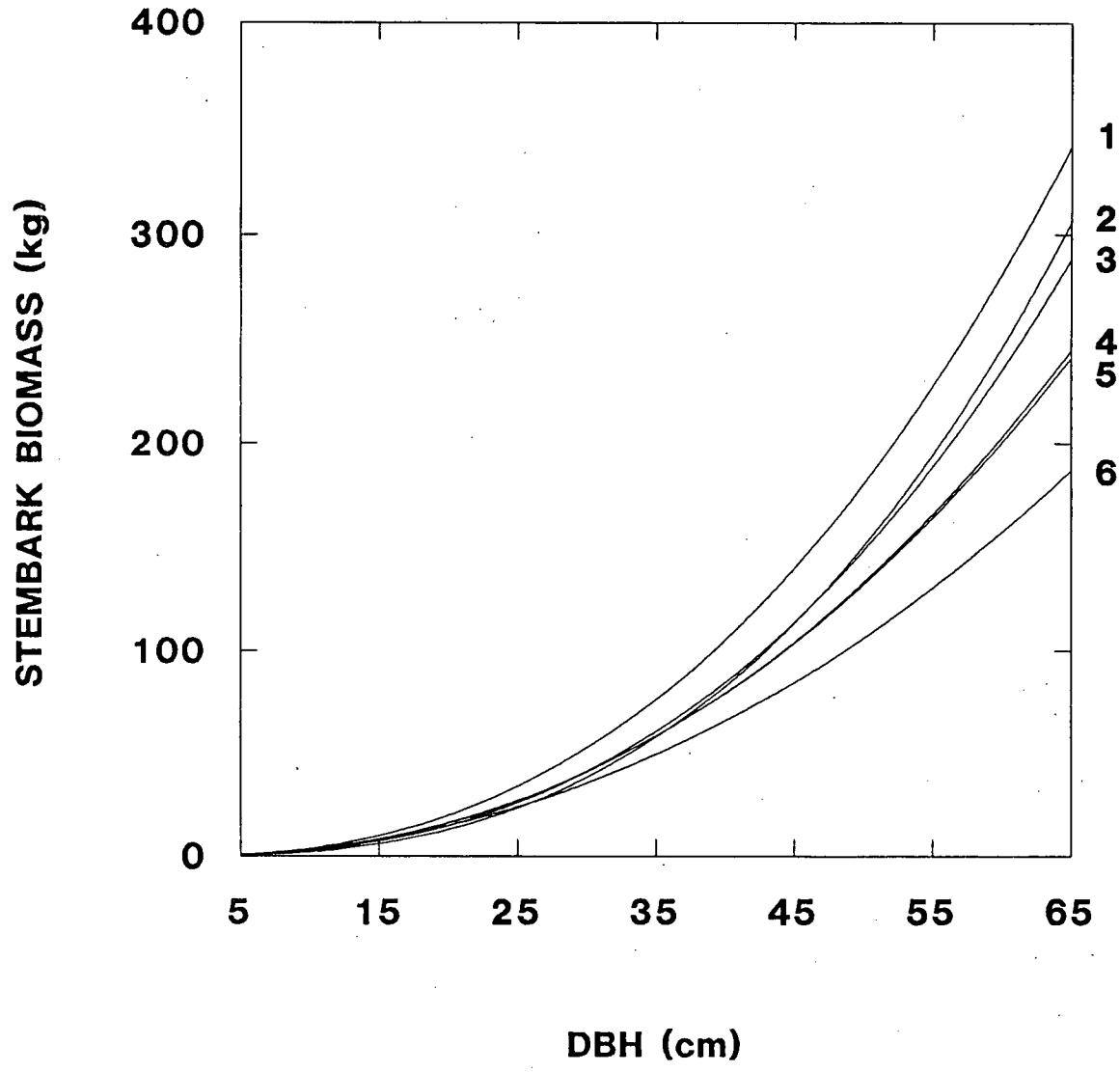

Figure 3.5. Stembark biomass as predicted by 6 regression models which use dbh as the independent variable. Details of the models are listed in Table 3.6.

3.3 MATERIALS AND METHODS

3.3.1 Site Description

The six research installations in which non-destructive measurements were made are described in detail in Chapter 2.

Stand characteristics of the 6 auxiliary plots used for destructive sampling, and statistics of the sample trees from those plots are summarized in Table 3.7.

3.3.2 Biomass Sampling

Destructive sampling of trees inside the control plots of the Productivity Committee Installations was not permissible. In each Installation, one temporary auxiliary plot (20 x 20 m) was therefore established in a section which was representative of the stand conditions in the control plots. All trees were numbered and dbh (1.3 m) measurements taken. Based upon a stratified random sampling scheme (by dbh-class), 6 to 8 trees in each auxiliary plot were selected for biomass sampling. Each tree was felled and processed within one day to minimize potential needle weight loss due to respiration (Forrest 1966). In total, 39 trees were sampled.

Prior to felling of the sample trees, the distance and direction (compass bearing) to, and the dbh of, each of the neighbouring trees were determined. After felling a sample tree, total height, length of the live crown, and distance from the top of the stem for each live whorl were determined.

Table 3.7. Stand characteristics of the six auxiliary plots (0.04 ha) in which trees were destructively sampled. %DF = percent of total represented by Douglas-fir. Statistics are based on 1984 data.

	Basal area		Density		Age[a]	Height[a]	Sample
Inst.	(m^2ha^{-1})	%DF	(st. ha^{-1})	%DF	(years)	(m)	size
2	35.5	92	1850	87	34	17.4	7
4	54.3	96	1975	87	40	21.7	6
5	22.8	81	1425	63	30	16.1	8
16	39.8	99	2125	99	24	17.4	6
71	43.8	99	2100	98	34	18.2	6
72	80.1	96	625	72	67	44.2	6

[a] mean of sample trees.

For every whorl, each living branch was cut from the stem, weighed and its length was measured to the nearest cm. Branch diameter near the base was determined to the nearest mm as the mean of two orthogonal caliper measurements. The condition of each branch was recorded to indicate whether sections were lost during the felling or whether other abnormalities were observed. One branch selected at random from all branches of every third whorl was processed further. Within each whorl the number and combined weight of all dead branches, as well as all non-nodal branches, were also recorded.

The selected branches from every third whorl, counting from the top down, were clipped into sections by age class. All sections for which an age determination was not possible were combined in an "unidentified" age-class. The samples of twig sections and foliage, as well as all remaining branchwood, were taken to the laboratory and weighed the same day.

A subsample of approximately 25g (or the entire sample if its freshweight was less than 25g) was randomly selected from each needle age-class and dried in a forced air drying oven at 105° C for 24 hours. Later, these subsamples were manually separated into needles and twigs, redried at 105° C for 24 hours, and the component weights determined to the nearest 0.1 gram.

The stems were cut into 6 to 13 sections (depending on tree size) and the length of each section was determined. At the bottom of each section a disk was cut. Each disk was measured along four orthogonal radii to obtain: radius, thickness of bark and sapwood, and increment over the last 5 years. The number of annual rings in the sapwood and the total age of each disk were also recorded. Subsamples of sapwood, heartwood, and bark were collected from approximately every second disk for the determination of specific density (Forest Products Laboratory 1952).

Biomass values for stemwood, stembark, and total stem (wood plus bark) were obtained by calculating the volume of each component in each stem section and multiplying it by the appropriate specific density. Volumes were calculated using Smalian's formula (Husch *et al.* 1982). Specific densities for sapwood, heartwood and bark were obtained from stem disks cut at each section, or by linear interpolation between adjacent disks. The biomass of each section was summed to obtain stem totals.

3.3.3 Competition Indices

In this study, four competition indices were tested for their contribution to regression models that predict the biomass of crown and stem components. The four indices are the Competitive Influence Zone Overlap (CIO) (Bella 1971), the Competitive Stress Index (CSI) (Arney 1973), the Diameter-Distance Competition Index (DCI) (Hegyi 1974), and the Growing Space Index (GSI) (Lin 1974).

Competitive Stress Index (CSI) (Arney 1973):

Arney's (1973) Competitive Stress Index (CSI) is based on the observation that in open-grown trees of a particular species, there is a high correlation between stem diameter (dbh) and crown width. This relationship for open-grown trees is used to compute the hypothetical crown width for the subject tree and each of its competitors. The sum of the area of overlap of these hypothetical crowns is defined as CSI which is computed as:

$$CSI = (((\sum_{i=1}^{n} O_{ij}) + A_j)/ A_j) * 100 \qquad [3.1]$$

where O_{ij} = area of zone overlap (m^2), A_j = influence zone of the subject tree (m^2), and n = number of competitors.

The crown width in this study was computed from Arney's (1973) model for the combined data sets of western Oregon and B.C. which include 290 open-grown trees. For this study the model has been converted to metric units.

Competitive Influence Zone Overlap (CIO) (Bella 1971):

Bella's (1971) Competitive Influence Zone Overlap (CIO) sums the hypothetical overlap between the influence zones of the subject tree and its competitors. The influence zone is defined as a zone with three times the diameter of the crown width of the open-grown tree. Crown width is computed from the same regression equation as described above. This competition index also accounts for the diameter ratio of the competing trees and the subject tree. The equation to compute the CIO is:

$$CIO = \sum_{i=1}^{n} ((O_{ij}/A_j) * (D_j/D_i)^{1.2}) \qquad [3.2]$$

where O_{ij} = area of zone overlap (m^2), A_j = influence zone of the subject tree (m^2), D_i = diameter of the i^{th} competing tree (cm), D_j = diameter of the j^{th} subject tree (cm), and n = number of competitors.

Diameter-Distance Competition Index (DCI) (Hegyi 1974):

Hegyi (1974) included all competitors within a set radius around the subject tree, without specifying the radius used. The formula to compute the DCI is:

$$DCI = \sum_{i=1}^{n} \left(\frac{D_i}{D_j} * \frac{1}{DIS_{ij}} \right) \qquad [3.3]$$

where D_i = dbh of the i^{th} competing tree (cm), D_j = dbh of the j^{th} subject tree (cm), and DIS_{ij} = distance between i^{th} competitor and j^{th} subject tree (m).

Growing Space Index (GSI) (Lin 1974):

Lin's Growing Space Index (GSI) considers only the cumulative influence of one tree in each of four quadrants surrounding the subject tree. The decision whether a neighbouring tree exerts a competitive influence is based on the angle (Θ) between two lines which, at breast height, connect the centre of the subject tree with the outside of the stem of the competing tree. This angle is a function of both the distance between subject tree and competitor and the dbh of the competitor. In each quadrant, the tree with the largest Θ is the competing tree. Each quadrant is initially assigned a growing space of 25 which is reduced depending on Θ. If $\Theta \leq 2.15^{o}$, no competition occurs (GSI_i=25) or if $\Theta \geq 5.25^{o}$, maximum competition occurs (GSI_i=0). For $2.15^{o} > \Theta \leq 5.25^{o}$:

$$GSI_i = 25 - (\Theta - 2.15) * 8.0645 * \frac{D_j + D_i}{2 * D_j} \qquad [3.4]$$

where D_i = diameter of the i^{th} competing tree (cm), and D_j = diameter of the j^{th} subject tree (cm).

The sum of the GSI_i for the four quadrants is:

$$GSI = \sum_{i=1}^{4} GSI_i \qquad [3.5]$$

which by definition yields $0 \leq GSI \leq 100$.

3.3.4 Statistical analysis

Numerical analyses were performed with MIDAS (Fox and Guire 1976) and SYSTAT (Wilkinson 1988b). Logarithmic transformations were applied to variables when scatter diagrams indicated that such transformations would yield linear models. Such logarithmic transformations also reduce heteroscedasticity, i.e. the increase of the variance of Y at any X in proportion to the value of X is reduced or eliminated (Zar 1984:286). The systematic bias introduced by such transformations (Baskerville 1972) is reduced by applying a correction factor ($\exp(SEE^2/2)$) (Sprugel 1983) whenever equations are converted to their anti-log form.

3.3.5 Data from the Shawnigan Lake study

The Biology of Forest Growth study (Crown and Brett, 1975) at Shawnigan Lake, Vancouver Island, is the source of an independent data set which was used to test the foliage biomass regression models developed for this study. The Shawnigan Lake study is investigating the effects of thinning and fertilization on growth of Douglas-fir. Data from four treatments were used:

T0F0 - control plots

T2F0 - 2/3 of basal area removed at time of thinning

T0F2 - 448 kg/ha N applied

T2F2 - combined thinning and fertilizer treatment.

Details of the experimental design and the site are described by Crown and Brett (1975) and by Barclay and Brix (1985). The destructive sampling of trees for biomass equations is described in Brix and Mitchell (1983) and in Barclay *et al.* (1986).

In addition to the information published previously, distance and bearing to the nearest competitors and their diameters have been recorded for 76 of the 96 trees used by Brix and Mitchell (1983). This information was made available by Dr. Holger Brix (Forestry Canada, Victoria). Based on these data, competition indices for the 76 sample trees have been computed using the same methods as described above.

3.4 RESULTS

3.4.1 Foliage biomass for individual branches

In total, 3149 branches were measured for diameter, length, branch freshweight, whorl number and height in the crown. Of these, 230 branches were further separated into needles and twigs by age-class for the determination of dry weights.

Regression equations were developed[1] which predict foliage and branchwood biomass for individual branches. The highest R^2 values were obtained when the

[1] Morello, R. (1986). Regression models for predicting foliage and branchwood biomass per branch in Douglas-fir. B.Sc. Thesis, University of British Columbia, Vancouver, BC. 91 pp.

models included branch freshweight and whorl number (counting from the top down) as independent variables. Not all branches were intact after felling the trees, and freshweight, as measured after felling, was therefore not always representative. Branches which had sections missing after felling had been coded appropriately. Foliage and branchwood biomass of such branches were calculated from a second regression model which used branch diameter and whorl number as independent variables. Complete measurements, including branch freshweight, were available for 2594 branches, 82.4% of the total.

Table 3.8 lists regression models for each of the six Installations and for the combined data set. Foliage dryweight per branch is predicted from the model

$$\ln FOL = b_0 + b_1 * \ln BFWT + b_2 * WHORLN^2 \qquad [3.6]$$

where lnFOL is the natural logarithm of foliage dryweight (g), lnBFWT is the natural logarithm of branch freshweight (g), and WHORLN is the number of the whorl. In Table 3.9, similar statistics are shown for the second model type which predicts foliage biomass per branch from branch diameter and whorl number:

$$\ln FOL = b_0 + b_1 * \ln DIA + b_2 * WHORLN^3, \qquad [3.7]$$

where lnDIA is the natural logarithm of branch diameter (cm) and other variables are as in model 3.6.

F-tests showed that, in each model type, some of the installation-specific equations are significantly different ($p=0.05$) from others and that therefore a combined model is not applicable in either case. Installation-specific regression models were therefore applied to the data from each installation to calculate foliage biomass for all branches of the sample trees.

Table 3.8. Regression models to predict foliage biomass per branch (g) from branch freshweight (g) and whorl number (Model 3.6). SEE is in logarithmic units.

Inst	R^2	SEE	n	b_0	b_1	b_2
2	.947	.286	47	-2.3074	1.1756	-0.0019196
4	.973	.227	36	-1.5759	1.0528	-0.0015907
5	.975	.187	44	-1.7268	1.0780	-0.0018445
16	.965	.192	28	-1.6962	1.0882	-0.0046709
71	.966	.200	33	-1.8342	1.0979	-0.0023376
72	.977	.191	42	-1.1793	0.9616	-0.0015755
ALL	.959	.248	230	-1.6081	1.0478	-0.0018554

Table 3.9. Regression models to predict foliage biomass per branch (g) from branch diameter (cm) and whorl number (Model 3.7). SEE is in logarithmic units.

Inst	R^2	SEE	n	b_0	b_1	b_2
2	.820	.527	47	3.5214	2.7813	-0.0000970
4	.873	.489	36	3.5602	2.7313	-0.0000913
5	.905	.365	44	3.4714	2.6966	-0.0001275
16	.865	.375	28	3.4855	3.0913	-0.0004972
71	.857	.407	33	3.5167	2.7843	-0.0001641
72	.904	.390	42	3.4121	2.4674	-0.0000764
ALL	.856	.390	230	3.4568	2.6099	-0.0000969

3.4.2 Branchwood biomass for individual branches

Regression models for the prediction of branchwood biomass were developed from the data set described in the previous section. The independent variables branch freshweight and whorl number yielded the highest R^2 values and the lowest SEE in the model:

$$\ln(BRA) = b_0 + b_1*\ln(BFWT) + b_2*WHORLN, \quad [3.8]$$

where BRA = branchwood dryweight (g), BFWT = branch freshweight (g), and WHORLN is the number of the whorl. A second model was developed to be used for the prediction of branchwood biomass of those branches for which branch freshweight did not represent the condition of the branch prior to felling. The model which best predicted branchwood biomass was

$$\ln(BRA) = b_0 + b_1*\ln(DIA) + b_2*WHORLN, \quad [3.9]$$

where DIA = branch diameter (cm) and other variables as in model 3.8. Tables 3.10 and 3.11 list the regression equations for each of the six Installations and for the combined data set, for models 3.8 and 3.9, respectively.

Some of the installation-specific equations of model 3.8 differed from others, as determined by F-tests (p=0.05). Model 3.9 had no significant differences between the equations. For both models, installation-specific equations were used to predict branchwood biomass.

3.4.3 Foliage biomass regression models

Summary statistics for dbh, height, biomass, and the four competition indices for the 39 sample trees are presented in Table 3.12. Models 3.6 and 3.8, with specific regression coefficients for each installation, were applied to 82.4% of

Table 3.10. Regression models to predict branchwood biomass per branch (g) from branch freshweight (g) and whorl number (Model 3.8). SEE is in logarithmic units.

Inst	R^2	SEE	n	b_0	b_1	b_2
2	.975	.225	47	-2.8292	0.98751	0.62063
4	.990	.156	36	-2.3409	0.94293	0.54197
5	.980	.193	44	-2.3733	0.99359	0.44686
16	.989	.117	28	-1.6902	0.81482	0.68041
71	.976	.202	33	-2.2889	0.91410	0.60983
72	.992	.149	42	-2.1937	0.97060	0.46828
ALL	.981	.202	230	-2.3911	0.96853	0.52261

Table 3.11. Regression models to predict branchwood biomass per branch (g) from branch diameter (cm) and whorl number (Model 3.9). SEE is in logarithmic units.

Inst	R^2	SEE	n	b_0	b_1	b_2
2	.952	.308	47	2.0114	2.3645	0.65479
4	.945	.374	36	2.1687	2.3794	0.60136
5	.966	.250	44	2.2397	2.4279	0.53269
16	.975	.181	28	2.5696	2.5075	0.41756
71	.966	.242	33	2.6310	2.5585	0.35416
72	.980	.233	42	2.2517	2.4453	0.53480
ALL	.966	.274	230	2.3024	2.4678	0.52487

the 3149 branches to calculate foliage and branchwood biomass for each branch, respectively. For the 17.6% of the branches of which sections were missing, models 3.7 and 3.9 were applied. For each tree, foliage biomass was summed to obtain total foliage biomass and total branchwood biomass per tree.

The contribution of each competition index (CI) was highly significant ($p<0.001$) (Table 3.13) when included in the simple model:

$$\ln FOL = b_0 + b_1 * \ln dbh + b_2 * CI, \quad [3.10]$$

where lnFOL is the natural logarithm (base-e) of foliage biomass (g) and lndbh is the logarithm of the diameter at breast height (dbh, in cm). When dbh was added to the model so that:

$$\ln FOL = b_0 + b_1 * \ln dbh + b_2 * dbh + b_3 * CI \quad [3.11]$$

the contribution of the competition indices remained significant ($p<0.05$). Dbh, however, did not contribute significantly to models 3.22 and 3.23 (Table 3.13).

When computing predicted values from regression models based on logarithmic transformations, a correction factor was applied as suggested by Baskerville (1972) and Sprugel (1983):

$$Predicted = \exp(model) * \exp(SEE^2/2), \quad [3.12]$$

where model is the regression equation in its logarithmic form and SEE is the standard error of estimate of this model.

In regression models based on logarithmic transformation of the dependent variable, the coefficient of determination (R^2) and the standard error of estimate (SEE) are affected by the transformation. When the models are transformed back into the original units, the coefficient of determination and the SEE can be calculated from a new linear model

$$Actual = b_0 + b_1 * Predicted. \quad [3.13]$$

Table 3.12. Mean, standard deviation (S.D.), and range of tree measurements, biomass data, and competition indices for the 39 sample trees.

Variable	Mean	S.D.	Min.	Max.
Tree measurements				
dbh (cm)	22.6	13.4	6.8	59.2
height (m)	22.0	10.4	8.1	48.4
age (years at b.h)	37.6	13.5	24.0	67.0
Biomass (kg)				
Total stem[a]	322.1	554.1	12.9	2140.4
Stemwood	277.7	481.3	11.2	1816.2
Stembark	44.4	73.7	1.7	324.2
Foliage	8.97	9.38	0.31	35.69
Branchwood	16.47	34.69	0.43	91.22
Competition Indices[b]				
GSI	24.8	19.25	0.0	65.2
CSI	437.1	111.93	253.1	784.8
CIO	9.2	7.41	2.1	33.0
DCI	4.0	2.82	0.8	13.5

[a] stemwood plus stembark
[b] see Methods for explanation

Table 3.14 shows R^2 and SEE for the significant models (3.14 to 3.22) in anti-log form. Models 3.20 and 3.21 rank first and second with respect to highest R^2 and lowest SEE. Model 3.19 is the best model which does not include a competition index. The three regression equations are:

$$\text{lnFOL} = -0.2681+3.4051*\text{lndbh}-0.0587*\text{dbh} \quad [3.19]$$

$$\text{lnFOL} = 0.3081+2.9902*\text{lndbh}-0.0411*\text{dbh}+0.0104*\text{GSI} \quad [3.20]$$

$$\text{lnFOL} = 2.1452+2.8449*\text{lndbh}-0.0456*\text{dbh}-0.0024*\text{CSI} \quad [3.21]$$

Additional statistics are listed in Tables 3.13 and 3.14. The regression coefficients of the competition indices in models 3.20 and 3.21 have opposing signs because of the way the indices are computed: intense competition is expressed by a low GSI value and by a high CSI value.

Figure 3.6 shows a plot of model 3.19. The surfaces described by models 3.20 and 3.21 are plotted in Figures 3.7 and 3.8. The combinations of dbh and competition index in the data set are displayed in the lower sections of Figures 3.7 and 3.8. Note that some regions of the regression surfaces are not defined by the sample trees, e.g. large open-grown trees are absent. Such regions should therefore be regarded as tentative extrapolations of the model. Large, open grown trees do not occur in the data sets to which the model will later be applied.

Bias of regression models is another valuable criterion by which to judge their performance. Here, percent bias is expressed as the mean residual (actual - predicted) divided by the mean actual value multiplied by 100:

$$\text{Percent Bias} = 100 * \left(\left(\sum_{i=1}^{n} (y_i - \hat{y}_i)/n \right) / \left(\left(\sum_{i=1}^{n} (y_i)/n \right) \right) \right) \quad [3.24]$$

where $\hat{y}_i$ = predicted value, y_i = actual value, and n = number of sample trees.

Table 3.15 shows percent bias for each of 6 diameter classes and for the combined data set for models 3.19, 3.20, and 3.21 and, for comparative purposes, for a regional model (Gholz *et al.* 1979) frequently used to predict foliage biomass. Bias for the combined data set is less than 1% for the 3 models that were derived from this data set. In contrast, the model from the literature has an average bias of -55.2%, i.e. the model greatly overestimated foliage biomass of the sample trees. Models 3.19, 3.20, and 3.21 consistently overestimated foliage biomass of trees in the 10-15 cm diameter class. Model 3.20 has little bias (<8%) for all diameter classes except the 10-15 cm dbh class where bias is -29.9%. The regional model always overestimated foliage biomass. It had a bias of -233.4% and -99.9% for the smallest and largest dbh classes, respectively.

In models 3.19, 3.20, and 3.21 over- and under-estimation alternate in successive diameter classes, indicating that there is no lack-of-fit in these three models. The regional model's bias suggests that lack-of-fit is a problem.

The models' bias in predicting foliage biomass of the sample trees from the 6 Installations is summarized in Table 3.16. The bias of model 3.20 ranges from -15.1 to 14.4%. The ranges of models 3.19 and 3.21 are somewhat larger. Such bias will introduce some error in the predictions of foliage biomass on a stand basis, but these biases are much lower than those that result from the application of the regional model from the literature (Table 3.16).

The only way to reduce the biases further is by using 6 separate regression equations for the 6 Installations. It seemed preferable, however, to select one model that adequately describes the entire data set (n=39) rather than 6 plot specific models, each based on a much smaller and inadequate sample size (n=6 to 8). While site specific equations may reduce bias in predicting foliage biomass of the small number of sample trees from each site, they may result in increased error

Table 3.13. Statistics of ten models predicting Douglas-fir foliage biomass (grams, n=39), CI = Competition Index. R^2 is based on log-transformed data. SEE is in logarithmic units.

Model	R^2	SEE	Significance (p)				
			Const.	lndbh	dbh	CI	No.
C+lndbh	0.843	0.4889	<.001	<.001			[3.14]
C+lndbh+GSI	0.890	0.4150	<.001	<.001		<.001	[3.15]
C+lndbh+CSI	0.894	0.4078	<.001	<.001		<.001	[3.16]
C+lndbh+CIO	0.896	0.4035	<.001	<.001		<.001	[3.17]
C+lndbh+DCI	0.894	0.4075	<.001	<.001		<.001	[3.18]
C+lndbh+dbh	0.884	0.4262	.756	<.001	.001	-	[3.19]
C+lndbh+dbh+GSI	0.907	0.3861	.702	<.001	.015	.005	[3.20]
C+lndbh+dbh+CSI	0.917	0.3655	.035	<.001	.003	<.001	[3.21]
C+lndbh+dbh+CIO	0.889	0.4024	.075	.002	.282	.026	[3.22]
C+lndbh+dbh+DCI	0.904	0.3924	.048	<.001	.059	.010	[3.23]

Table 3.14. Eight models predicting Douglas-fir foliage biomass. The significant models from Table 3.13 predicted foliage biomass and linear regression of the form ACTUAL = b_0+b_1*PREDICTED are calculated. R^2 is based on non-transformed data and SEE is in actual (non-logarithmic) units.

Model	R^2	SEE	b_0	b_1	No.
C+lndbh	0.687	5320.3	2988.8	0.575	[3.14]
C+lndbh+GSI	0.797	4283.7	2058.6	0.702	[3.15]
C+lndbh+CSI	0.704	5171.2	2699.7	0.636	[3.16]
C+lndbh+CIO	0.787	4385.8	1012.4	0.868	[3.17]
C+lndbh+DCI	0.755	4706.8	1432.9	0.806	[3.18]
C+lndbh+dbh	0.756	4691.4	301.0	0.962	[3.19]
C+lndbh+dbh+GSI	0.867	3467.0	-185.0	1.013	[3.20]
C+lndbh+dbh+CSI	0.814	4098.5	33.7	1.001	[3.21]

Table 3.15. Percent bias (calculated as mean residual divided by mean actual foliage biomass, times 100) for 3 foliage biomass models from this study and one regional model (RM, Gholz *et al.* 1979) for the combined data set and stratified by diameter class.

			%Bias of Model			
DBH	n	Actual	3.19	3.20	3.21	RM
5-65	39	8971.2	-0.8	-0.9	0.5	-55.7
5-10	6	672.1	-14.8	-1.7	-0.8	-233.4
10-15	6	2063.7	-20.0	-29.9	-24.1	-122.6
15-20	8	5470.7	4.6	6.7	3.9	-39.4
20-25	8	7946.9	-7.0	-5.3	-7.5	-39.4
25-35	6	17259.6	15.1	7.6	13.8	-5.2
35-60	5	24513.0	-10.5	-5.6	-5.4	-99.9

Table 3.16. Percent bias (calculated as mean residual divided by mean actual foliage biomass, times 100) for 3 foliage biomass models from this study and one regional model (RM, Gholz *et al.* 1979) for the combined data set and stratified by Installation.

			%Bias of Model			
Inst	n	Actual	3.19	3.20	3.21	RM
ALL	39	8971.2	-0.8	-0.9	0.5	-55.7
2	7	10103.1	29.7	14.4	18.2	5.4
4	6	9436.5	13.7	6.4	14.6	-15.2
5	8	4376.3	-0.9	9.2	4.0	50.7
16	6	5099.8	-0.7	0.7	-0.8	-45.3
71	6	5172.2	-14.6	-15.1	-13.6	-59.8
72	6	20982.5	-21.0	-12.6	-13.1	-111.2

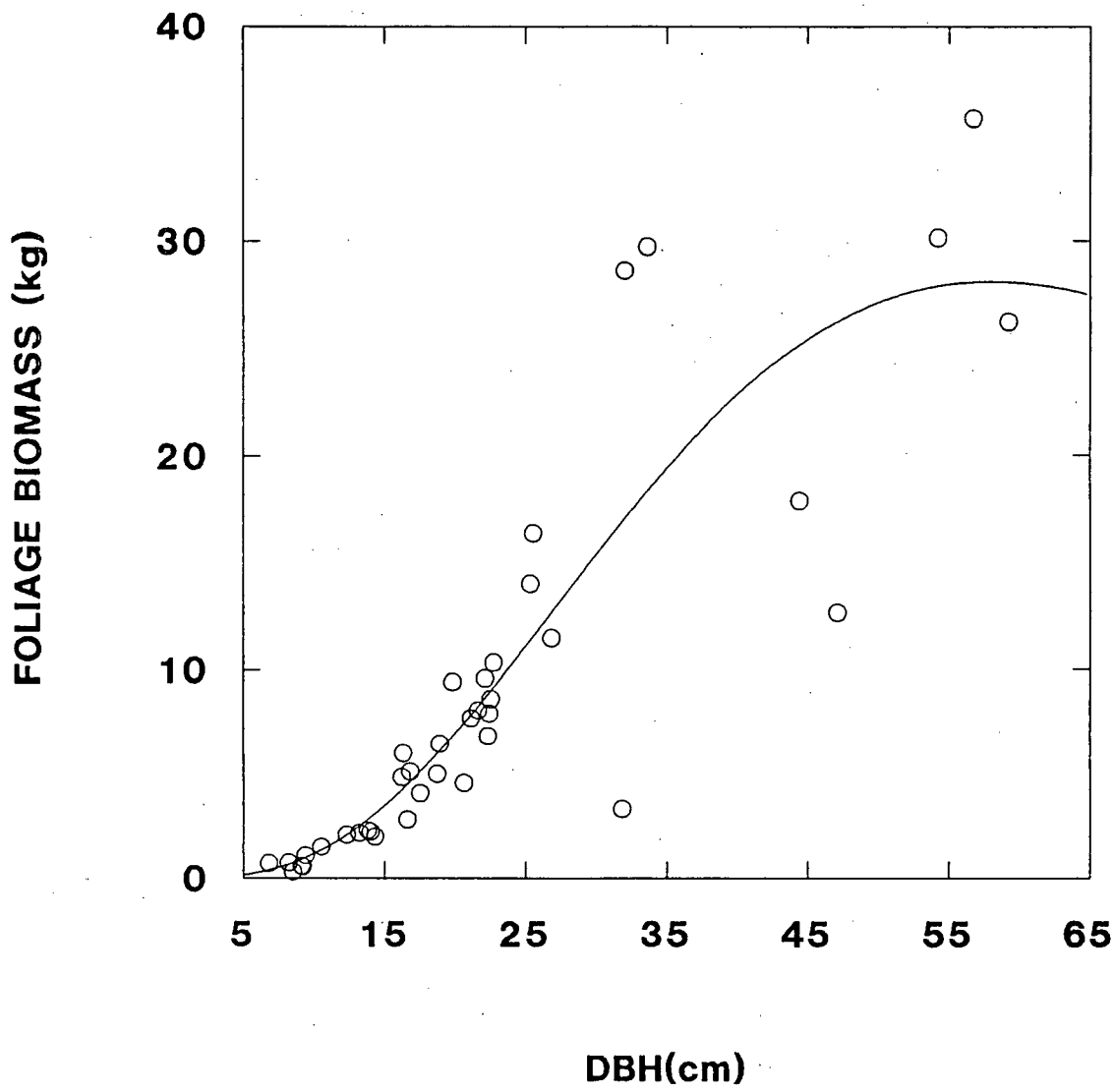

Figure 3.6. Foliage biomass as predicted by Model 3.19. See text for more details.

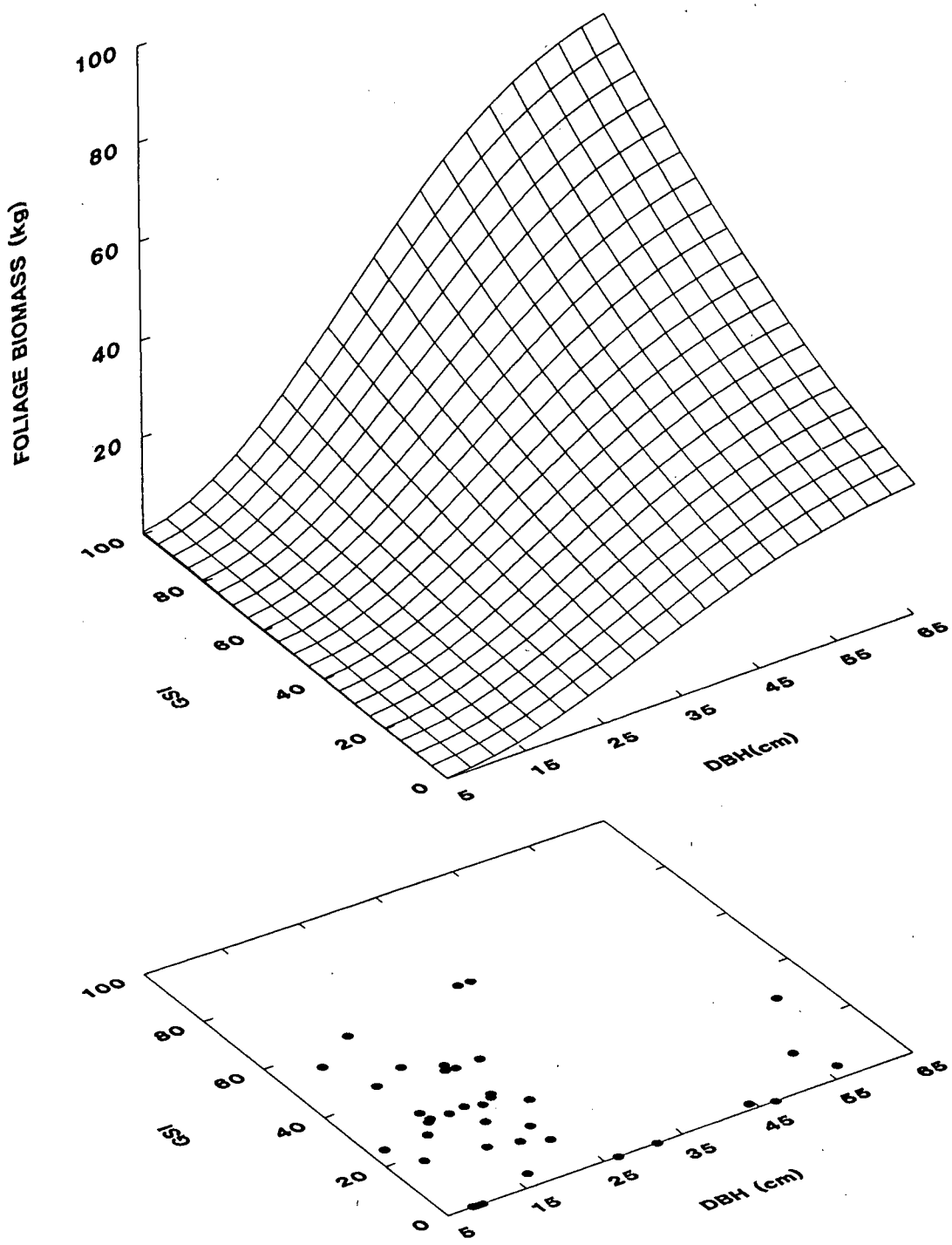

Figure 3.7. Foliage biomass as predicted by Model 3.20. See text for more details.

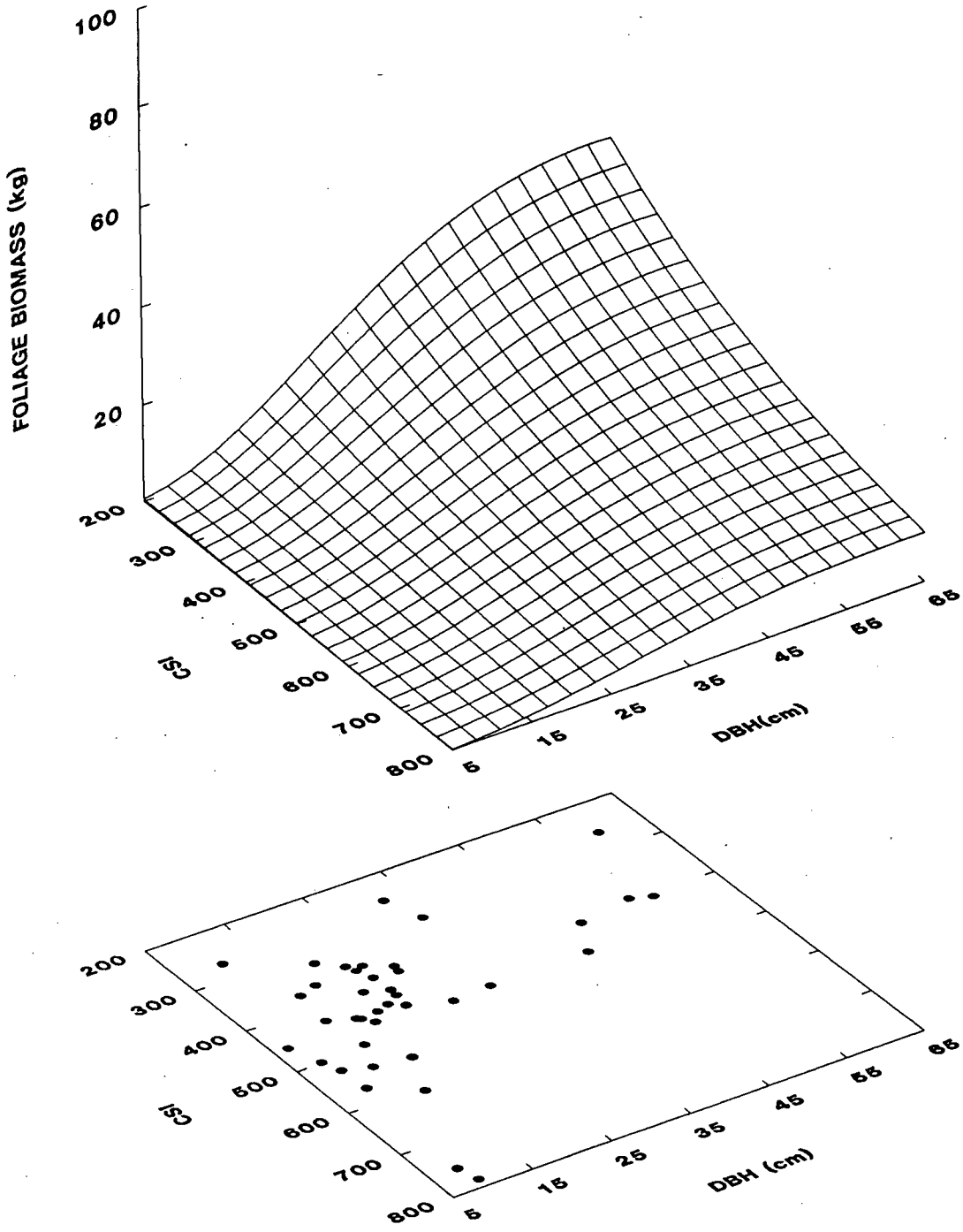

Figure 3.8. Foliage biomass as predicted by Model 3.21. See text for more details.

when predicting foliage biomass of trees from different sites. The 6 plots from which the sample trees were collected are in the vicinity of, but not identical to, the plots for which the predictions will be made. The general models, some of which incorporate a competition index, will therefore be used for biomass prediction.

3.4.4 A test of the models on an independent data set

Brix and Mitchell (1983) used 96 trees for the development of foliage biomass regression equations. The auxiliary data required to compute competition indices were available for 76 of these trees. Five regression models were used to predict foliage biomass of the 76 trees: models 3.19, 3.20 and 3.21 of this study, the regional model of Gholz *et al.* (1979), and the model of Brix and Mitchell (1983) that predicts foliage biomass from basal area under bark which was derived from the combined data set (n=96).

Table 3.17 shows the coefficients of determination (R^2) and the standard error of estimate (SEE) for each of the five models in non-logarithmic units. As before, these were derived from two computational steps. The predicted values were derived from the five regression models described above. Then the regression between actual and predicted values (Equation 3.13) was computed. The R^2 value of the latter expresses the proportion of the variation in the actual data that is accounted for by the predicted data.

The five models accounted for 82.4 to 85.2% of the variation in the Shawnigan Lake data set (Table 3.17). Model 3.21, which uses lndbh, dbh and CSI as independent variables, has the highest R^2 value. Note, however, that the slopes

(b_1) of the regression lines differ greatly from one, which indicates that systematic bias in the prediction of foliage biomass occurs.

All five models tended to underestimate foliage biomass (Table 3.18). The amount of bias varied with treatment and with model. Figure 3.9 shows predicted versus actual foliage biomass for each of the four treatments as predicted by model 3.20. The discrepancy was largest for the T2F2 treatment (34.7% bias), in which trees differed most from the untreated trees, and the bias was smallest for the control plots (T0F0, bias = 12.1%).

Finally, the question was addressed whether competition indices would also contribute significantly to regression models derived from the Shawnigan Lake data set. Models of the form

$$\text{lnfol} = b_0 + b_1*\text{lndbh} + b_3*\text{CI}, \qquad [3.10]$$

where CI is one of the four competition indices, were calculated. Table 3.19 lists five models and the significance of each of the regression coefficients. Three of the four competition indices contributed significantly to the regression model, the exception being CIO (p=0.061).

Table 3.17. Five models for the prediction of foliage biomass for Douglas-fir applied to the Shawnigan Lake data set. The models have the form ACTUAL = b_0+b_1*PREDICTED. R^2 is based on non-transformed data and SEE is in actual (non-logarithmic) units.

No.	Model	R^2	SEE	b_0	b_1
[3.19]	C+lndbh+dbh	0.839	2593.1	-759.6	2.158
[3.20]	C+lndbh+dbh+GSI	0.824	2707.2	289.2	1.327
[3.21]	C+lndbh+dbh+CSI	0.852	2485.7	-1198.2	1.436
[-]	Gholz *et al.* 1979	0.834	2633.3	-4228.6	1.949
[-]	Brix & Mitchell 1983	0.837	2606.4	-733.9	0.890

Table 3.18. Percent bias (calculated as mean residual divided by mean actual foliage biomass, times 100) for 5 models for the prediction of foliage biomass for the combined data set and stratified by treatment.

			%Bias of model				
Treatment	n	Actual	3.19	3.20	3.21	Gholz[a]	B&M 83[b]
T0F0	16	4312.4	34.5	12.1	5.3	-12.2	21.4
T2F0	22	9958.8	50.4	20.6	16.5	26.7	8.7
T0F2	14	7078.8	40.0	22.9	13.2	8.4	-15.1
T2F2	24	14892.1	55.6	34.7	30.8	39.0	11.6
ALL	76	9797.4	50.1	26.9	21.9	26.5	4.1

[a] Gholz *et al.* 1979
[b] Brix and Mitchell 1983

Table 3.19. Contribution of four competition indices to the prediction of foliage biomass of Douglas-fir trees (n=76) from four treatments of the Shawnigan Lake experiment. CI = Competition Index. R^2 is based on log-transformed data and SEE is in logarithmic units.

Model	R^2	SEE	Significance (p)		
			Const.	lndbh	CI
C+lndbh	0.877	0.276	.005	<.001	
C+lndbh+GSI	0.914	0.265	.001	<.001	.008
C+lndbh+CSI	0.928	0.243	<.001	<.001	<.001
C+lndbh+CIO	0.910	0.271	.877	<.001	.061
C+lndbh+DCI	0.926	0.246	<.001	<.001	<.001

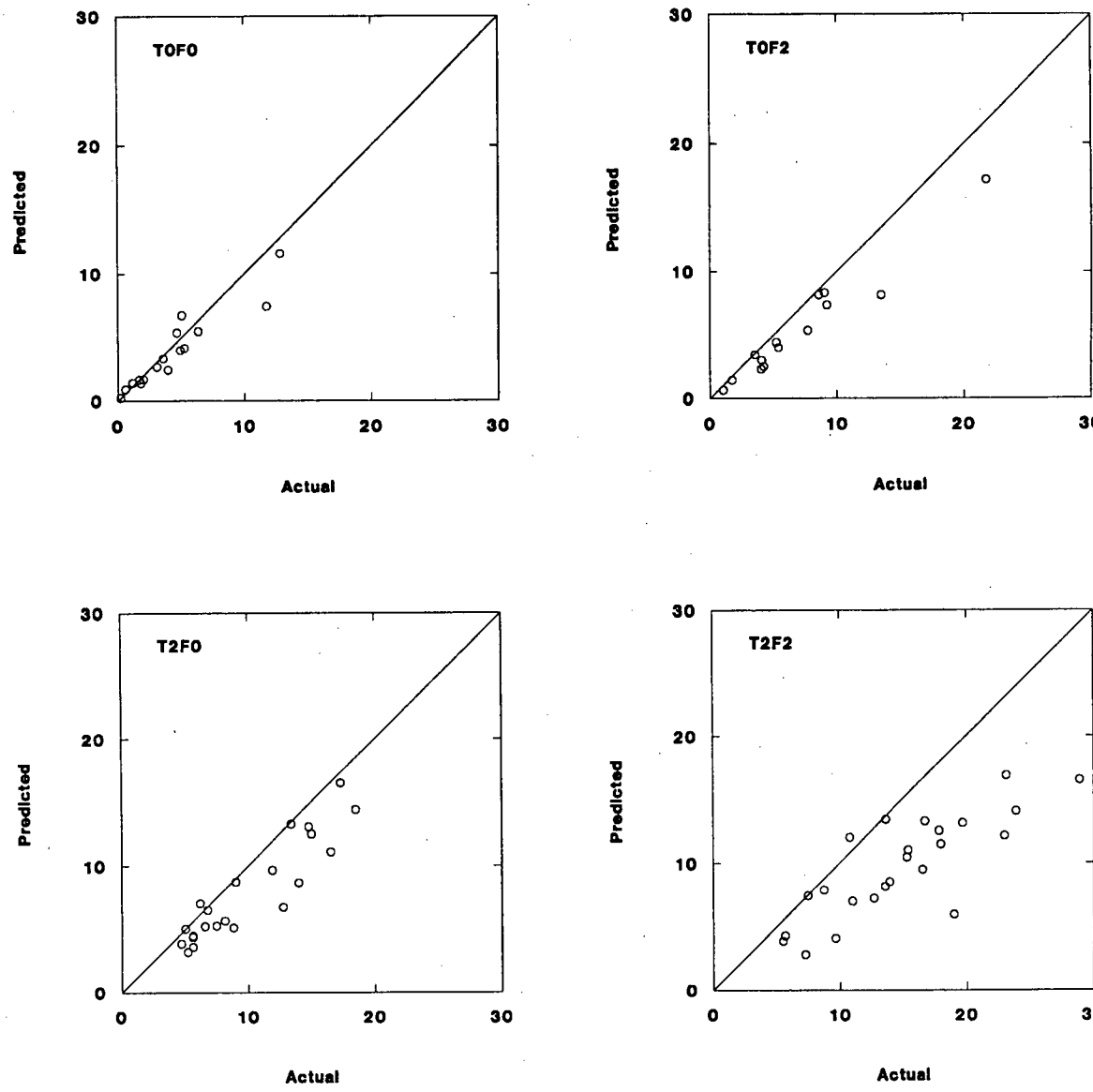

Figure 3.9. Comparison of actual and predicted foliage biomass of 76 Douglas-fir trees in 4 treatments of the Shawnigan Lake experiment. Predictions are based on model 3.20 from this study. T0F0 = control, T0F2 = fertilized, T2F0 = thinned, and T2F2 = thinned and fertilized.

3.4.5 Branchwood biomass regression models

Three of the four competition indices contributed significantly to the model

$$\ln BRA = b_0 + b_1 * \ln dbh + b_2 * CI \quad [3.25]$$

where lnBRA is the logarithm (base-e) of branchwood biomass, lndbh is the logarithm of the diameter at breast height (dbh, in cm), and CI is the competition index (Table 3.20). CIO was the only competition index that was not significant. Adding dbh as additional independent variable did not contribute significantly (p=0.05) to the models. As with the foliage biomass models, the branchwood models were converted to the anti-log form with the appropriate correction factors. The regression equations between actual and predicted values (see Equation 3.10) are summarized in Table 3.21. Model 3.27 yielded the highest R^2 and the lowest SEE.

Percent bias, as defined above, was lowest for model 3.27, averaging -2.0%. Percent bias for diameter classes and for the six installations for each of the 4 models and for the regional model of Gholz *et al.* (1979) is listed in Tables 3.22 and 3.23. The two models selected for computation of branchwood biomass are model 3.27, which includes a competition index, and model 3.26, which is the best model without a competition index. The coefficients of these two models are:

$$\ln BRA = 1.9036 + 2.3522 + \ln dbh \quad [3.26]$$

$$\ln BRA = 1.7018 + 2.3471 * \ln dbh + 0.0087 * GSI \quad [3.27]$$

Figures 3.10 and 3.11 present the two equations graphically. Note that the combination of dbh and competition index in the data set does not cover the entire range displayed in the graphs (Figure 3.11). Therefore, the predicted branchwood biomass for large trees with little competition must be regarded as a tentative extrapolation of the model. Such trees, however, do not occur in the data sets to which the models will be applied for prediction purposes.

Table 3.20. Statistics of five models to predict branchwood biomass (grams) for Douglas-fir (n=39), CI = Competition Index. R^2 is based on log-transformed data and SEE is in logarithmic units.

Model	R^2	SEE	Significance (p)			No.
			Const.	lndbh	CI	
C+lndbh	0.922	0.3804	<.001	<.001		[3.26]
C+lndbh+GSI	0.938	0.3446	<.001	<.001	.005	[3.27]
C+lndbh+CSI	0.947	0.3193	<.001	<.001	<.001	[3.28]
C+lndbh+CIO	0.929	0.3679	<.001	<.001	.067	[3.29]
C+lndbh+DCI	0.938	0.3433	<.001	<.001	.004	[3.30]

Table 3.21. Four models to predict branchwood biomass for Douglas-fir. The significant models from Table 3.20 predicted branchwood biomass and linear regression of the form ACTUAL = b_0+b_1*PREDICTED are calculated. R^2 is based on non-transformed data and SEE is in actual (non-logarithmic) units.

Model	R^2	SEE	b_0	b_1	No.
C+lndbh	0.888	7967.1	1815.2	0.833	[3.26]
C+lndbh+GSI	0.922	6640.4	804.2	0.932	[3.27]
C+lndbh+CSI	0.885	8053.9	1511.3	0.891	[3.28]
C+lndbh+DCI	0.900	7526.1	208.6	0.997	[3.29]

Table 3.22. Percent bias (calculated as mean residual divided by mean actual branchwood biomass, times 100) for 2 branchwood biomass models from this study and one regional model (RM, Gholz *et al.* 1979) for the combined data set and stratified by diameter class.

			%Bias of model		
DBH	n	Actual	3.26	3.27	RM
ALL	39	16472.5	-6.8	-2.0	-69.9
5-10	6	1001.1	-13.5	4.3	-146.3
10-15	6	2611.1	-17.4	-26.3	-132.7
15-20	8	6548.6	5.5	3.7	-75.9
20-25	8	10542.9	2.4	-1.3	-73.7
25-35	6	25639.0	19.8	10.2	-33.6
35-60	5	66038.0	-22.8	-7.8	-80.5

Table 3.23. Percent bias (calculated as mean residual divided by mean actual branchwood biomass, times 100) for 2 branchwood biomass models from this study and one regional model (RM, Gholz *et al.* 1979) for the combined data set and stratified by Installation.

			%Bias of model		
INST	n	Actual	3.26	3.27	RM
ALL	39	16472.5	-6.8	-2.0	-69.9
2	7	14307.4	34.7	19.5	-13.7
4	6	12611.2	12.3	1.7	-50.7
5	8	5537.5	2.8	7.8	-79.8
16	6	6997.8	11.3	8.7	-62.9
71	6	6692.6	-9.0	-14.0	-96.6
72	6	56694.6	-26.4	-10.4	-87.2

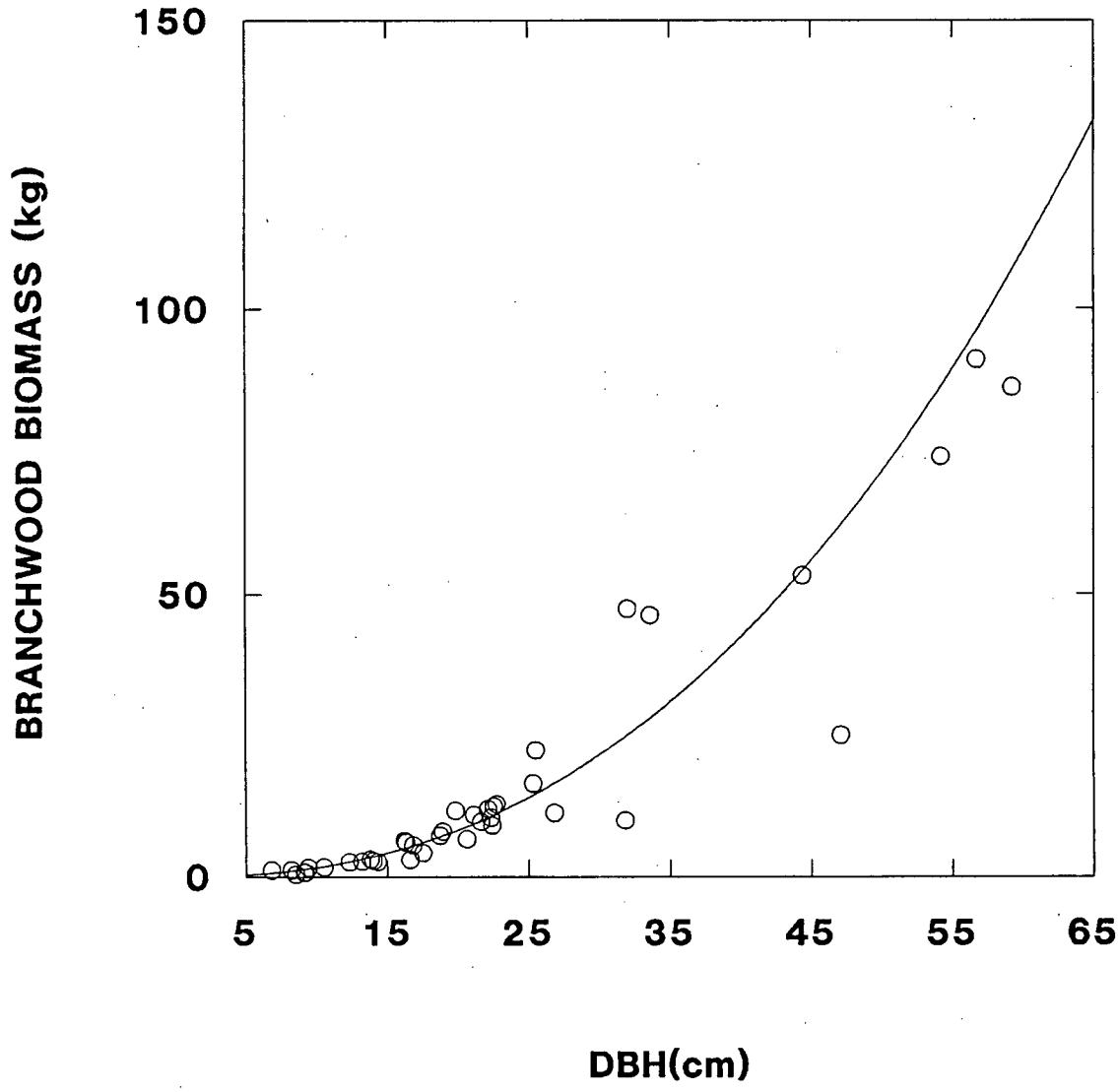

Figure 3.10. Branchwood biomass as predicted by Model 3.26. See text for more details.

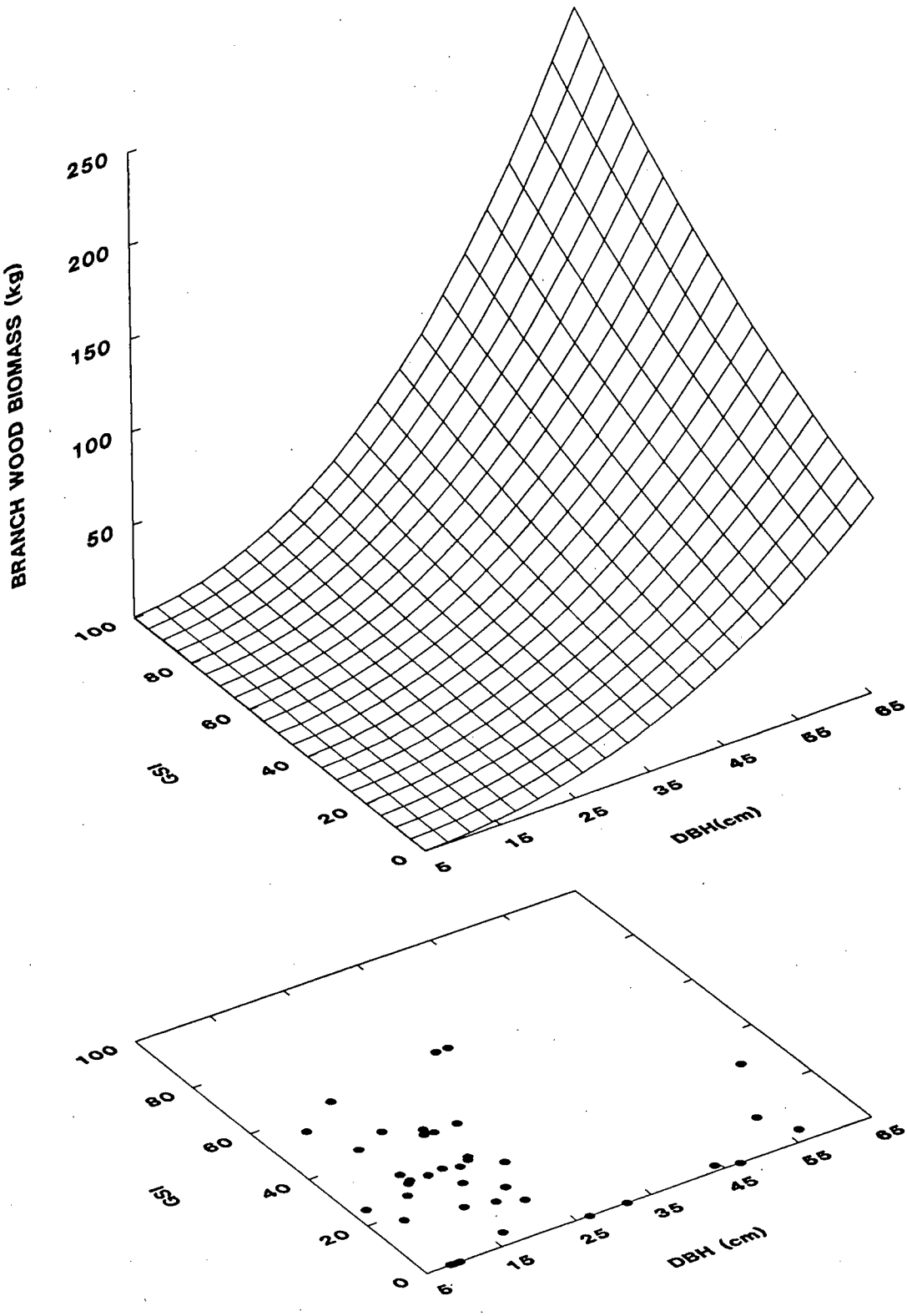

Figure 3.11. Branchwood biomass as predicted by Model 3.27. See text for more details.

3.4.6 Regression models for stem biomass components

Separate regression models have been developed for each of the three stem biomass components: stemwood, stembark, and total stem (wood plus bark). The contribution of the competition indices to the regression models varied with the biomass component. In models for the prediction of stemwood or total stem biomass which use lndbh as independent variable, three of the four CIs contributed significantly, the exception being CSI (Table 3.24). Adding dbh to the models rendered all CIs except GSI insignificant. In stembark models, only CIO contributed significantly (Table 3.24). Coefficients of determination (R^2) ranged from 0.976 to 0.989 for logarithmically transformed data.

The regressions between actual values and those predicted from the significant models of Table 3.24 express the performance of the predictive models in non-logarithmic units (Table 3.25). For the prediction of stemwood biomass, model 3.37 yielded the highest R^2 value, a low SEE, an intercept (b_0) near zero, and a slope (b_1) near 1.0. Of the two models which do not use a CI as an independent variable, model 3.36 is preferable because b_0 is closer to zero and b_1 is closer to 1.0. With similar arguments, models 3.46 and 3.47 are identified as the best predictive models for total stem biomass. For the prediction of stembark, models 3.38 and 3.39 are selected as the best models with and without CI, respectively. The relationships between predicted values obtained from the regional models of Gholz *et al.* (1979) and actual values are very similar to those obtained with regression models from this study (Table 3.25).

Two models each for the prediction of stemwood (models 3.36 and 3.37) and stembark (models 3.39 and 3.40) biomass were selected as the best models:

$$\ln SW = -1.2850+1.7980*\ln dbh-0.0267*dbh \qquad [3.36]$$

$$\ln SW = -1.4995+1.9524*\ln dbh+0.0202*dbh-0.0039*GSI \qquad [3.37]$$

$$\ln SB = -4.8505+2.5563*\ln dbh+0.0136*CIO \quad [3.39]$$

$$\ln SB = -3.4709+1.9925*\ln dbh+0.0185*dbh \quad [3.40]$$

where lnSW = logarithm stemwood biomass (kg) and lnSB = logarithm stembark biomass (kg). Additional statistics are listed in Tables 3.24 and 3.25.

These four models and the regional models of Gholz *et al.* (1979) were further analyzed for their bias (see Equation 3.24). Percent bias ranged from -1.7 to -0.6% and from -2.4 to 2.3% for the stemwood and stembark regression models, respectively (Table 3.26). Percent bias in separate diameter classes was somewhat larger for the models from this study but was considerably larger in the regional model. Stratifying the data set by Installation showed that the bias of the stemwood models was small for five Installations (-3.1 to 7.4%), but in Installation 2 it was -25.2 and -15.7% for models 3.36 and 3.37, respectively (Table 3.27).

Percent bias of the stembark models for all data combined was small (-2.4 to 0.8%) (Table 3.27). For the six Installations, percent bias ranged from -11.6 to 7.0% and was largest in Installation 5. The regional model had a small bias when averaged over all data, but it had a much larger bias in predicting stemwood biomass (-38.6% in Installation 2) and stembark biomass (-18.3% in Installation 5) of individual installations.

Table 3.24. Statistics of regression models to predict stem biomass components (kg) for Douglas-fir (n=39), CI = Competition Index. R^2 is based on log-transformed data and SEE is in logarithmic units.

Model	R^2	SEE	Significance (p) Const.	lndbh	dbh	CI	No.
STEMWOOD BIOMASS							
C+lndbh	0.978	0.2028	<.001	<.001			[3.31]
C+lndbh+GSI	0.984	0.1746	<.001	<.001		<.001	[3.32]
C+lndbh+CSI	0.980	0.1951	<.001	<.001		.055	[3.33]
C+lndbh+CIO	0.987	0.1588	<.001	<.001		<.001	[3.34]
C+lndbh+DCI	0.982	0.1864	<.001	<.001		.008	[3.35]
C+lndbh+dbh	0.985	0.1703	<.001	<.001	<.001		[3.36]
C+lndbh+dbh+GSI	0.987	0.1568	<.001	<.001	.004	.010	[3.37]
STEMBARK BIOMASS							
C+lndbh	0.976	0.2109	<.001	<.001			[3.38]
C+lndbh+CIO	0.979	0.2014	<.001	<.001		.039	[3.39]
C+lndbh+dbh	0.979	0.1983	<.001	<.001	.021		[3.40]
TOTAL STEM BIOMASS							
C+lndbh	0.981	0.1887	<.001	<.001			[3.41]
C+lndbh+GSI	0.985	0.1661	<.001	<.001		.002	[3.42]
C+lndbh+CSI	0.982	0.1849	<.001	<.001		.120	[3.43]
C+lndbh+CIO	0.989	0.1464	<.001	<.001		<.001	[3.44]
C+lndbh+DCI	0.984	0.1763	<.001	<.001		.016	[3.45]
C+lndbh+dbh	0.987	0.1557	<.001	<.001	<.001		[3.46]
C+lndbh+dbh+GSI	0.989	0.1464	<.001	<.001	.002	.022	[3.47]

Table 3.25. Seven models to predict stemwood biomass for Douglas-fir. The significant models from Table 3.24 and a regional model predicted stemwood biomass and linear regression of the form ACTUAL = b_0+b_1*PREDICTED are calculated. R^2 is based on non-transformed data and SEE is in actual (non-logarithmic) units.

Model	R^2	SEE	b_0	b_1	No.
STEMWOOD BIOMASS					
C+lndbh	0.981	67.0	-30.6	1.216	[3.31]
C+lndbh+GSI	0.982	66.1	-20.4	1.139	[3.32]
C+lndbh+CSI	0.985	59.9	-27.8	1.190	[3.33]
C+lndbh+CIO	0.984	62.7	-10.8	1.065	[3.34]
C+lndbh+DCI	0.985	59.7	-18.4	1.129	[3.35]
C+lndbh+dbh	0.979	70.9	8.2	0.961	[3.36]
C+lndbh+dbh+GSI	0.985	59.9	3.8	0.980	[3.37]
Gholz *et al.* 1979	0.983	63.7	-10.5	1.021	[ ]
STEMBARK BIOMASS					
C+lndbh	0.983	9.9	-2.8	1.113	[3.38]
C+lndbh+CIO	0.980	10.6	-1.0	1.031	[3.39]
C+lndbh+dbh	0.983	9.8	1.4	0.946	[3.40]
Gholz *et al.* 1979	0.983	9.9	-2.7	1.086	[ ]
TOTAL STEM BIOMASS					
C+lndbh	0.984	70.9	-33.9	1.205	[3.41]
C+lndbh+GSI	0.984	72.5	-23.3	1.138	[3.42]
C+lndbh+CIO	0.986	67.9	-12.0	1.062	[3.43]
C+lndbh+DCI	0.987	63.9	-21.6	1.130	[3.45]
C+lndbh+dbh	0.983	74.8	9.6	0.960	[3.46]
C+lndbh+dbh+GSI	0.987	65.6	5.5	0.975	[3.47]

Table 3.26. Percent bias (calculated as mean residual divided by mean actual biomass, times 100) for stemwood and stembark biomass as calculated with 2 models from this study and one regional model (RM, Gholz *et al.* 1979) for the combined data set and stratified by diameter class.

DBH (cm)	n	Stemwood				Stembark			
		Act. (kg)	3.36	3.37	RM	Act. (kg)	3.40	3.39	RM
			% Bias				% Bias		
5-65	39	278.9	-1.0	-0.6	-1.7	44.5	0.8	-2.4	2.3
5-10	6	18.0	6.4	2.9	29.2	2.6	-5.1	-3.6	3.9
10-15	6	37.9	-7.3	-3.4	-0.5	6.8	1.6	-0.5	-3.0
15-20	8	80.1	1.8	1.0	-3.1	13.1	-3.4	-2.8	-10.3
20-25	8	128.3	-1.4	-1.5	-12.7	22.0	-3.4	-1.7	-10.7
25-35	6	268.4	-1.4	0.9	-16.0	47.9	-1.9	2.9	-4.2
35-60	5	1453.1	-1.0	-1.0	2.7	222.2	2.6	-3.9	7.4

Table 3.27. Percent bias (calculated as mean residual divided by mean actual biomass, times 100) for stemwood and stembark biomass as calculated from 2 models from this study and one regional model (RM, Gholz *et al.* 1979) for the combined data set and stratified by Installation.

Inst	n	Stemwood				Stembark			
		Act. (kg)	3.36	3.37	RM	Act. (kg)	3.40	3.39	RM
			% Bias				% Bias		
ALL	39	278.9	-1.0	-0.6	-1.7	44.5	0.8	-2.4	2.3
2	7	97.3	-25.2	-15.7	-38.6	21.4	1.0	2.6	-4.4
4	6	145.8	0.0	2.7	-11.3	26.1	1.9	4.7	-1.8
5	8	70.4	1.6	-1.8	-3.2	10.6	-11.6	-11.0	-18.3
16	6	76.9	-3.1	-3.1	-9.6	12.5	-8.5	-8.5	-16.4
71	6	100.0	6.6	7.4	-1.2	16.3	0.7	1.7	-5.8
72	6	1283.0	0.4	-0.1	3.2	195.3	2.1	-3.3	7.1

3.5 DISCUSSION

In the 45 years since Kittredge (1944) published the first paper on foliage biomass regression equations, over 30 additional models for the prediction of foliage biomass of Douglas-fir have been published (c.f. Table 3.1). Collectively, they have identified a great variability in the relationships between dbh and foliage biomass.

Some researchers found that sapwood basal area is a superior predictor of foliage biomass, but the relationship described by this variable appears to be affected by additional factors (Figure 3.2). Sapwood basal area can only be determined from increment cores or through destructive sampling. These measurements are often not available, however, especially in permanent sampling plots where the swelling of the stem following increment core sampling may not be desirable. In some projects, sapwood basal area has been predicted from a second regression equation established from sampling trees. This second model, however, represents an additional source of error.

Despite the large number of existing regression models, a researcher who wants to predict foliage biomass is facing a difficult task. Given the existing variability between regression models, what criteria should be used to select and judge a model?

Existing models for the prediction of foliage biomass typically use one or more variables which describe stem characteristics, such as dbh, height, or sapwood basal area. The size of the crown and the amount of foliage of a tree are also influenced by the amount of competition a tree is experiencing. The "social" position within a stand can be quantified by a competition index (CI). Four competition indices have been tested in this study for their contribution to regression models for the prediction of foliage and branchwood biomass of Douglas-

fir. Each of these competition indices contributed highly significantly to the regression equations (Table 3.13 and 3.20).

The regression coefficients associated with the competition indices in foliage and branchwood regression models have values that are ecologically meaningful: the coefficients are positive in models which include GSI, a CI that increases from 0 to 100 with decreasing competition. The coefficients are negative in models that use the other three CIs, all of which decrease with less competition. In both cases, the models predict that trees with less competition will have more foliage and branchwood biomass.

Competition indices will account for the between and within stand variability in crown biomass allometric relationships that is attributable to variations in stand density. Competition indices can be computed from stand maps which are often available for research plots. Furthermore, repeated measurements of dbh and recording of tree mortality are sufficient to compute the changes in CI over time. Other variables occasionally used in regression models, such as height, sapwood basal area, or length of the live crown, are more difficult and more expensive to measure. In addition, these measurements would have to be taken repeatedly, if a prediction of biomass trends over time is desired.

Competition indices by themselves may not be able to account for the changing allometric relationships following fertilization (Grier *et al.* 1986, Brix and Mitchell 1983, Barclay *et al.* 1986). In stands that have recently been thinned, a CI will express competition based on present stand density but tree crowns and foliage biomass may not have had the time to fully occupy the newly available space. This must be considered when using these equations to predict foliage and branchwood biomass.

Foliage biomass regression models developed in this study were applied to predict foliage biomass of 76 sample trees in 4 treatments at the Shawnigan Lake research project. The 3 models (3.19, 3.20, and 3.21) accounted for 83.9%, 82.4%, and 85.2% of the variation in this independent data set. Model 3.21 accounted for a greater proportion of the variation in the data than either the regional model (Gholz *et al.* 1979) or the model developed from the combined data of the Shawnigan Lake study (Brix and Mitchell 1983).

All three models developed in this study consistently underpredicted foliage biomass. The two models which include a CI underpredicted foliage biomass of the trees in the unthinned and unfertilized control plots with 12.1% (Model 3.20) and 5.3% bias (Model 3.21). The model without CI had 34.5% bias (Model 3.19). Bias increased with thinning and fertilization treatments. In the Shawnigan Lake study, trees were destructively sampled 5 and 7 years after a thinning in which 2/3 of the basal area were removed. The remaining trees experienced much less competition than any of the sample trees from which the regression models were developed. Predicted foliage biomass of trees from thinned plots is in some cases based on an extrapolation of the model, which may account for some of the observed bias.

The contribution of competition indices to regression models which predict stemwood and stembark biomass was smaller than their contribution to crown biomass component models (Table 3.24). The signs of the regression coefficients associated with the CIs were reversed compared to those in crown biomass equations. The models predict that of two trees with the same dbh, the one that experiences less competition will have the smaller stemwood and stembark biomass. Wood specific density in Douglas-fir is primarily a function of cambium age and not of ring width (Jozsa *et al.* 1989). This suggests that the form factor

(Husch *et al.* 1982) decreases with decreasing competition, as can be observed in Douglas-fir (R.E. Carter, pers. comm.).

Bias in predicting stemwood biomass for the entire data set was -1.0% and -0.6% for models 3.36 and 3.37, respectively (Table 3.27). Bias increased when the data set was stratified by Installation. The greatest bias, -25.2% (Model 3.36) and -15.7% (Model 3.37) was observed in Installation 2. Specific gravity of the stemwood of the trees in this Installation (SG=0.403, S.D.=0.024, n=7) was significantly (p=0.005) lower than that of the trees in the other five Installations (SG=0.440, S.D.=0.032, n=32). Therefore stemwood biomass in Installation 2 is overestimated somewhat by the regression models.

This study showed that competition indices can contribute significantly to biomass regression models. Sample trees for this study originated from 6 sites that covered a range of site indices. Further testing of the regression models should be conducted with additional independent data sets. The 39 sample trees of this study cover a large range of the possible combinations of dbh and competition index, but open-grown trees (no competition) and large trees with little competition are not included in the data set. Future studies should attempt to include such sample trees.

3.6 CONCLUSIONS

The review of existing regression models for the prediction of biomass of Douglas-fir has shown that the range of predicted biomass for the same diameter differs widely between models. The lack of criteria by which to judge the suitability of existing models for the prediction of biomass components in specific stand conditions emphasizes the need to find a new approach to biomass regression models. This new approach should attempt to include an independent variable which might account for the between-stand differences in the biomass regression models.

Competition indices, which account for the competitive status of individual trees, contributed significantly to regression models for the prediction of all above-ground biomass components. Their contribution was highest in foliage and branchwood biomass regression models. Of the competition indices tested, GSI (Lin 1974) contributed most to regression models for the prediction of foliage, branch, and stemwood biomass.

The new models for the prediction of foliage biomass were tested against an independent data set from the Shawnigan Lake research project and performed very satisfactorily, in particular in unthinned and unfertilized plots. Thinning and fertilization increased the bias of the predicted values.

4. ABOVEGROUND AND COARSE ROOT BIOMASS AND PRODUCTION

4.1 INTRODUCTION

A quantitative understanding of the production of all major above- and belowground biomass components is a necessary foundation for many studies of forest ecosystems: carbon and nutrient budgets, the biology of tree response to silvicultural treatments, and the study of environmental influences on forest yield are some important examples. In this chapter, biomass and production of those tree components which can be predicted from allometric relationships will be reported. This includes the major aboveground components and coarse roots. Fine and small root biomass and production will be reported in the next chapter.

The first objective of the research presented in this chapter was to quantify the biomass of major tree components in twelve Douglas-fir stands growing over a range of site indices. The second objective was to quantify the net biomass production of these components over several measurement periods.

4.2 LITERATURE REVIEW

Net primary production (NPP) of a forest ecosystem is defined as the amount of organic matter produced by plants over a time period, usually a year (Waring and Schlesinger 1985, Satoo and Madgwick 1982). NPP includes all increments in the biomass of stemwood, stembark, branches, foliage, reproductive organs, and roots, plus the amounts of plant material that become detritus or are consumed by animals.

NPP can be estimated by determining, for each of the major biomass components, the net increment (Δ Biomass), the mortality of individual trees or their parts (detritus), and the amount of plant material consumed by animals (consumption) over the time period.

$$NPP = \Delta \text{ Biomass} + \text{Detritus} + \text{Consumption} \quad [4.1]$$

For general reviews of forest ecosystem biomass, production, and litterfall data see Cannell (1982), Reichle (1981), Bray and Gorham (1964), and Vogt *et al.* (1986).

4.2.1 Annual stemwood and stembark production

Stemwood and stembark are the most commonly measured components in studies of biomass production and growth and yield (cf. Cannell 1982), most of which consider only net increment and mortality of trees. The turnover component of stembark production, due to shedding of the outermost bark layers, is generally not considered in production studies.

4.2.2 Annual branchwood production

Annual branchwood production comprises the net increment of total branchwood biomass and the replacement of mortality. Few studies have attempted to include annual branchwood production in developing estimates of production at the stand level.

Satoo and Madgwick (1982) suggest two methods for deriving an estimate of branchwood production. The first method calculates the change in total branchwood biomass, based on regression equations, and adds a value for branchwood mortality derived from litterfall estimates. This method has several problems. Firstly, branch litterfall is likely to vary greatly between years depending on the occurrence of storms, snowfall, drought, and other factors. Secondly, large traps are required to obtain accurate estimates because of the spatial heterogeneity of branch litterfall. Thirdly, the origin of branchwood litterfall cannot be identified: some of it originates from dead trees, the rest from dead whorls of living trees. Only the latter component is of interest in the estimation of branchwood turnover, because branchwood mass of dead trees is not included when estimating stand branchwood biomass from regression equations. The second method suggested by Satoo and Madgwick (1982) is based on the assumption that the relative growth rate of branches is equal to the relative growth rate of stemwood. The authors warn, however, that this method may lead to underestimates of actual production.

The study of Douglas-fir biomass production by Dice (1970) omitted branchwood from the total aboveground production estimates. Mohren (1987) calculated annual branchwood mortality by assuming an average lifespan of 30 years for a Douglas-fir branch. However, stand density will affect live crown length (Carter *et al.* 1986, Ritchie and Hann 1987) and such an approach may not be appropriate in stands with differing density. Comeau (1986) calculated branchwood production of lodgepole pine stands by dividing tree branchwood biomass by the age of the oldest branches on the tree. This may result in the underestimation of branchwood production because the average lifespan, not the maximum lifespan, determines turnover rates.

4.2.3 Annual foliage production

There are several different approaches to the quantification of annual foliage production in evergreen coniferous stands (Satoo and Madgwick 1982, Newbould 1967). The amount of first year foliage, which is equal to foliage production, can be calculated from regression equations. Alternatively, annual foliage litterfall can be collected and, assuming that the foliage biomass of a stand has reached a steady state, annual foliage litterfall will be equal to annual foliage production (Fogel and Hunt 1979). Between-year variation in annual foliage litterfall and the litterfall component from dying trees can complicate calculations based on this approach.

4.3 MATERIALS AND METHODS

4.3.1 Site description

The study sites have been described in detail in Chapter 2.

4.3.2 Field measurements and data processing

Details of plot selection and establishment are described in Darling and Omule (1989). The main points relevant to this study will be summarized briefly. Each plot was 22.36 x 22.36 m (0.05 ha) and was surrounded by a 4.63 m buffer strip (0.05 ha). All trees within each plot were marked at breast height (1.3m), numbered, and their x-y coordinates determined. Diameter at breast-height (dbh) was measured to the nearest 0.1 cm for all trees greater than or equal to 5.0 cm dbh. Installations 71 and 72 were measured in the fall or winter of 1971, 1974,

1977, 1980, and 1983. The remaining four Installations were measured in 1972, 1975, 1978, 1981, and 1984. These dbh measurements were taken by the B.C. Forest Service Research Branch. Additional dbh measurements for this study were taken for all plots in the fall or winter of 1985 and 1987. The two data sets were merged and checked for inconsistencies. Obvious errors, such as trees classified as dead in one period and living in the next, were corrected. "Shrinking" of trees was occasionally observed if a suppressed tree was approaching death and then died in the next measurement period. "Shrinkage" was presumably caused by moisture loss in the stemwood and should not affect stemwood biomass on a dry weight basis. In the few situations where shrinkage was observed and followed by tree death in the subsequent measurement period, the dbh of such trees was held constant at its preceding maximum value. Such corrections amounted to increasing the dbh at the last measurement prior to mortality by one to two mm and avoided the calculation of decreasing biomass estimates. The merged and corrected data file was the basis for all subsequent computations.

At each measurement period, height measurements were taken on approximately 10 trees per plot. In 1985, the height of the five largest (by dbh) trees per plot was determined with a tripod-mounted relascope. Ages were determined by the B.C. Forest Service Research Branch from cores collected 30 cm above the germination point in at least 5 trees per plot.

Site indices (Bruce 1981, Mitchell and Polson 1988) for 1985 were calculated from total stand age (converted to age at breast height) and the mean height of the 5 largest trees per plot. Site indices for years prior to 1985 were calculated from total stand age (converted to age at breast height) and the mean height of the 5 largest trees for which height measurements were available. Site index calculations were based on height/age equations (Mitchell and Polson 1988) which

were iteratively solved for site index using the secant method (Gerald and Wheatley 1984).

Competition indices were calculated using the equations described in Chapter 2. Growing Space Index (GSI) (Lin 1974) and Competitive Stress Index (CSI) (Arney 1973) were computed for each tree in the plot at each measurement date using dbh data and x-y coordinates. These data were unavailable for trees in the buffer strip. Competition indices for trees near the edge of the plot were erroneous because of the lack of neighbours for these trees in the data set. The contour map of GSI values of Installation 2 Plot 6 (Figure 4.1A) shows the edge effect as increasing GSI values near the plot edge. This artefact was reduced by establishing a hypothetical stand around each plot. The plots were subdivided into 16 quadrats of equal size (5.59 x 5.59m), labelled A through P in Figure 4.2. The stand information of these quadrats was copied to similar quadrats surrounding the plot (labelled a through p in Figure 4.2) following the scheme outlined in Figure 4.2. Competition indices were calculated for trees inside the original plot, assuming the hypothetical stand structure in the area surrounding the plot. Figure 4.1B shows that this procedure effectively removed the edge effect observed in Figure 4.1A.

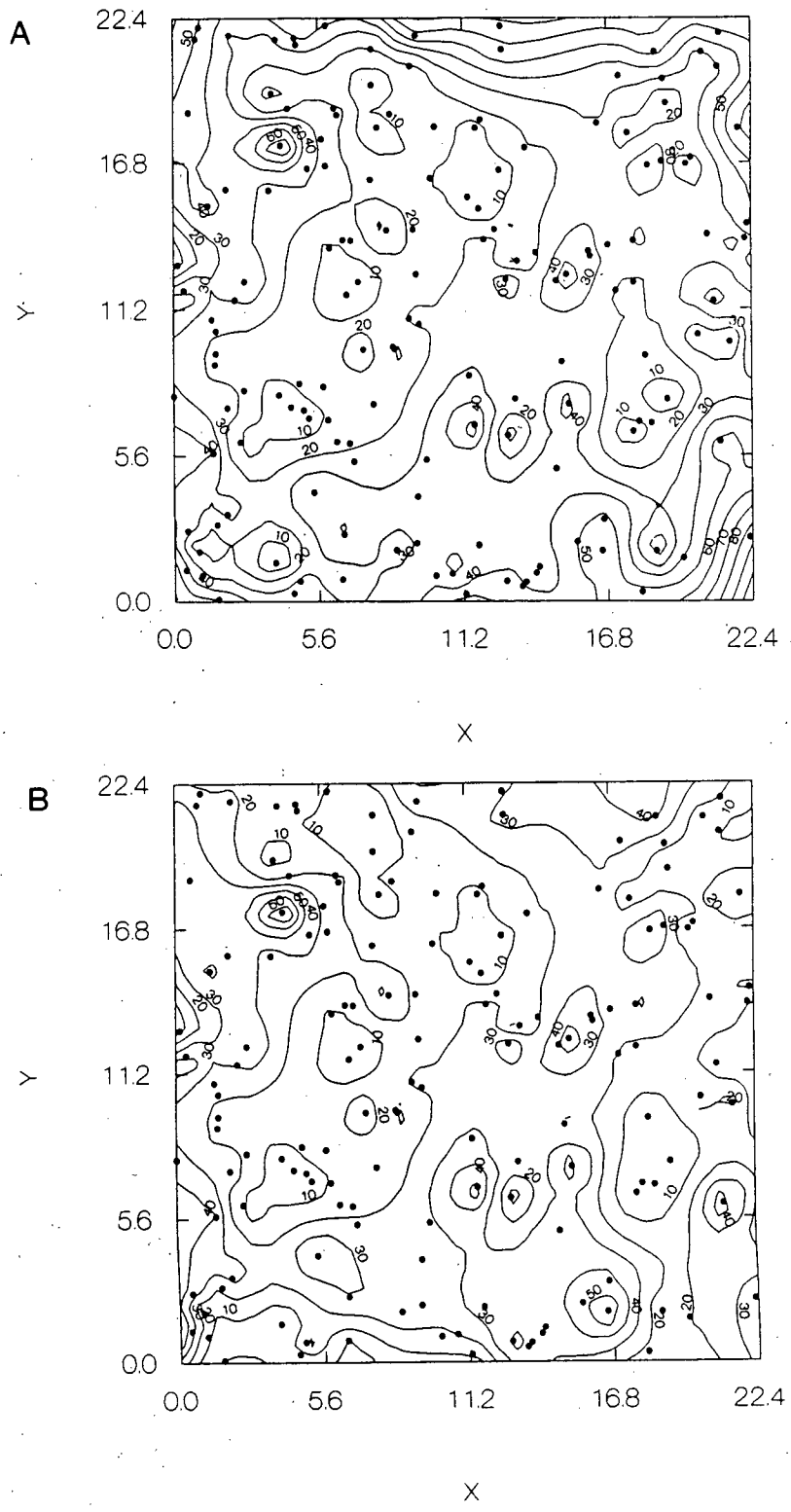

Figure 4.1. Contour maps of Growing Space Index (GSI) in Installation 2, Plot 6, without (A) and with (B) hypothetical buffer strip. Note the increase in GSI (less competition) towards the plot border in A. Tree locations are indicated by ●.

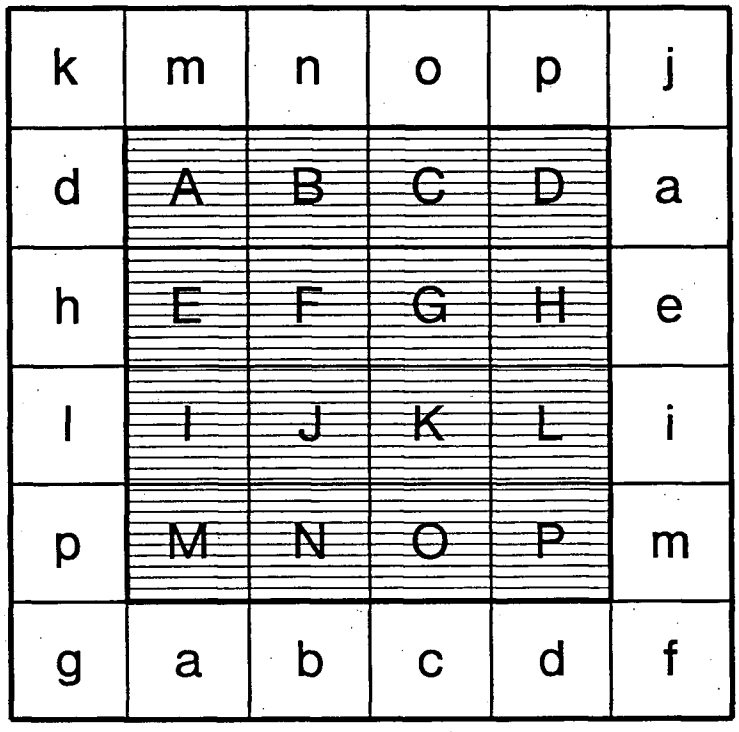

Figure 4.2. The scheme used to establish a hypothetical stand around each plot. Sixteen quadrats (A to P) of the actual plot (shaded area) were copied to locations surrounding the plot (a to p).

4.3.3 Calculation of biomass and net production

The tree components for which biomass and net primary production (NPP) were determined individually are stemwood, stembark, branches (including bark), foliage, and coarse roots. Biomass and production of reproductive organs were not quantified. The biomass of each major aboveground tree component and of coarse roots was calculated from regression equations applied to the data of every living tree with at least 5 cm dbh. All living trees were summed to obtain plot biomass which was converted to Mg ha^{-1}. The regressions for aboveground Douglas-fir biomass components were described in Chapter 3. Biomass components of western hemlock and western redcedar were calculated from published regressions (Gholz *et al.* 1979). Other species (western white pine, (*Pinus monticola* Dougl.), bigleaf maple (*Acer macrophyllum* Pursh.), and Hooker's willow (*Salix hookeriana* Barr. in Hook.)) were treated as Douglas-fir. White pine and bigleaf maple never occurred more than once per plot. In one plot, three willows were present, but they never accounted for more than 0.6% of total basal area.

Net primary production for any period was calculated as the sum of the net increment in biomass, plus mortality of trees, plus turnover:

$$\text{Production} = \Delta \text{ Biomass} + \text{Mortality} + \text{Turnover} \qquad [4.2]$$

Consumption of plant biomass by animals was not considered in this study as no data were available. For the period for which diameter measurements were taken, no outbreaks of defoliating insects had been recorded in the six installations.

Net annual increment for each of the biomass components was calculated as the difference between stand biomass at the beginning and end of each measurement period divided by the number of years in that period. The calculation of the mortality and turnover components of NPP differed between biomass components as described below. The exact year of tree mortality within each

measurement period was not determined. The biomass of all trees which died within a period was summed and evenly distributed among all years of the measurement period. Ingrowth, (i.e. trees which were recorded for the first time because they grew bigger than the diameter-recording limit of 5 cm), was treated as if the biomass of such trees had been produced entirely during the measurement period. Biomass production was evenly distributed among the years of that period.

4.3.3.1 Stemwood

The biomass regression equation with dbh and growing space index (GSI) as independent variables (Equation 3.37) was applied to compute stemwood biomass of each living Douglas-fir tree at each measurement date. Net increment was calculated from the difference in plot stemwood biomass at successive dates. Mortality was calculated as described above.

4.3.3.2 Stembark

Stembark production was computed in the same way as stemwood production. Douglas-fir biomass was predicted from dbh using regression equation 3.40. Mortality of individual trees was treated the same as that of stemwood production. Stembark turnover was not considered because no data were available.

4.3.3.3 Branchwood

Annual branchwood production (Mg ha^{-1} $year^{-1}$) in a stand can be partitioned into Δ biomass, mortality, and turnover. The change in total branchwood biomass (Δ biomass) is calculated as the difference in total live branchwood biomass at the beginning and end of a measurement period. Mortality refers to the branchwood biomass of trees which died during the measurement period. Turnover refers to death of branches at the bottom of the canopy and addition of new whorls on the top. At each measurement date, biomass is calculated from Equation 3.27 (Chapter 3). Mortality of branchwood, due to the death of individual trees, is treated in the same way as stemwood mortality (described above). Turnover of branchwood biomass is difficult to determine due to the large temporal and spatial variability in the occurrence of branchwood litterfall. Data on branchwood litterfall were not available for the 12 study plots. The following computational approach was developed to calculate the turnover component of branchwood production.

Under normal growing conditions, Douglas-fir produces one whorl of branches annually (lammas growth involving the terminal bud occurs only rarely in Douglas-fir, R.E. Carter, pers. comm.). Whorl number is therefore equivalent to the age of the whorl (i.e. growing seasons of production), if whorl number is counted from the top down during the dormant season. In a closed canopy stand in which the canopy has started to lift off the ground, one whorl will die approximately every year, thus maintaining, within a tree, a number of whorls which is relatively constant within a measurement period.

Annual branchwood production in Douglas-fir can be approximated from the following considerations. Suppose that annual branchwood production (BWP) within a whorl j is a function f of whorl number j.

$$BWP(j) = f(j) \qquad [4.3]$$

Suppose, further, that annual branchwood litterfall (BWL) within a whorl j is a function g of whorl number j.

$$BWL(j) = g(j) \qquad [4.4]$$

Branchwood biomass (BWB) of a whorl j can then be calculated as

$$BWB(j) = \sum_{i=1}^{j} (BWP(i) - BWL(i)) \qquad [4.5]$$

because whorl number and age of the whorl are approximately equivalent in Douglas-fir.

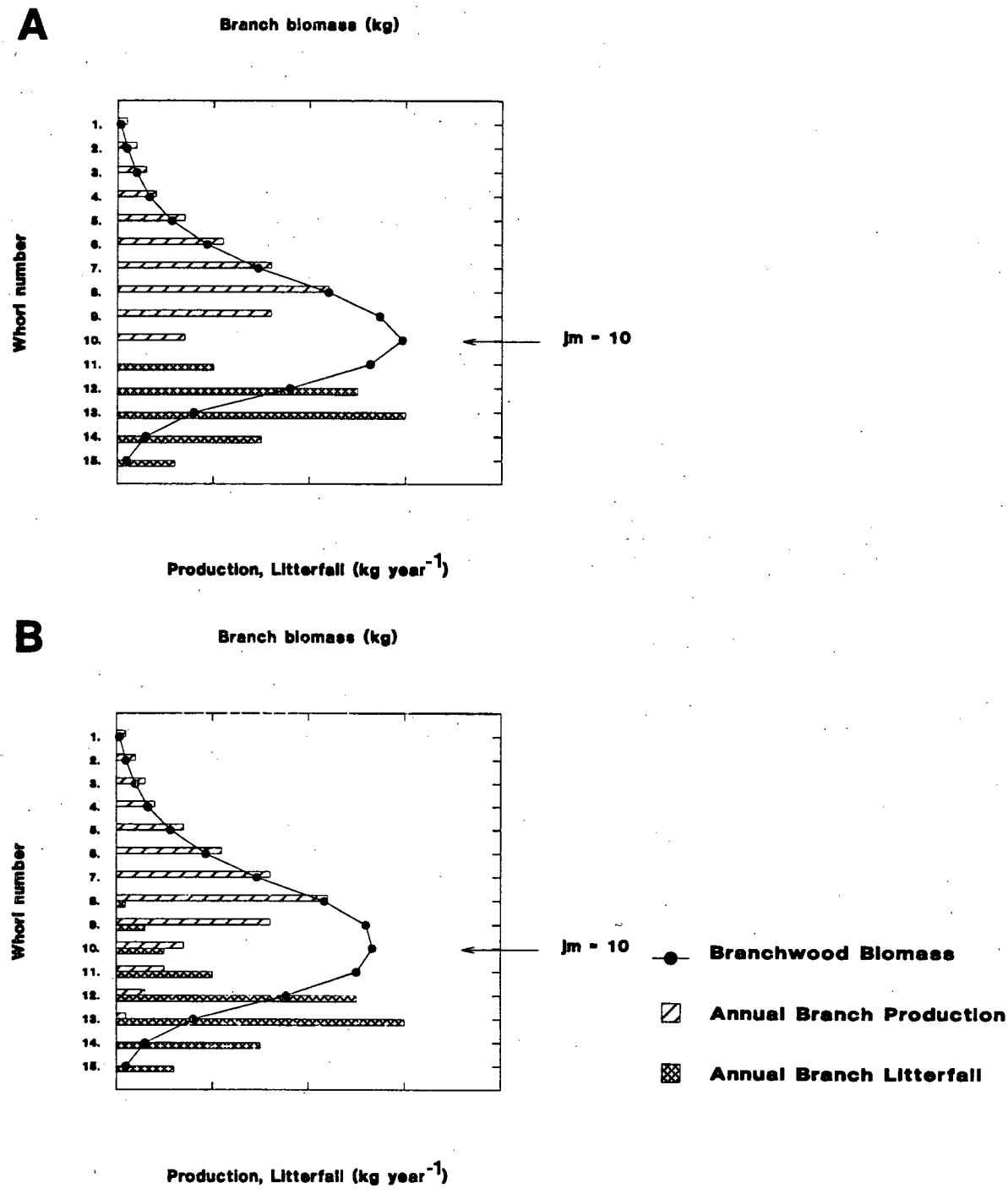

Figure 4.3. Theoretical distribution of branch biomass (——●——) by whorl number. At each whorl, annual branch production (hatched bars), and branch litterfall (cross-hatched bars) are shown, but at a different scale than biomass. A: Production occurrs in whorls 1 - 10 and litterfall in whorls 11- 15. B: Production occurrs in whorls 1 - 13 and litterfall in whorls 8 - 15. See text for further explanation.

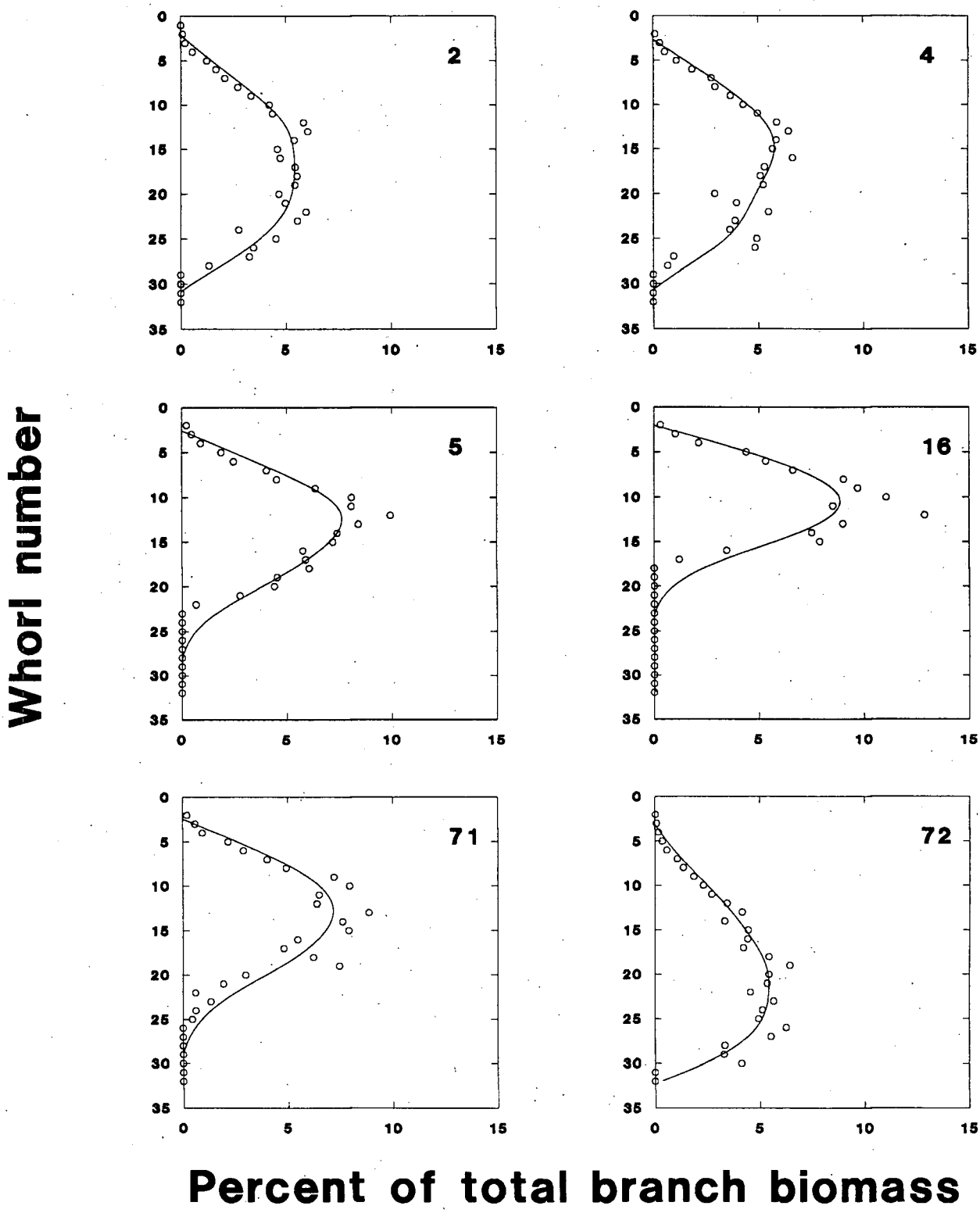

Figure 4.4. Branch biomass distribution of 39 destructively sampled trees from 6 plots. For each whorl, branch biomass (open circles) is expressed in percent of total plot branch biomass. The distribution is approximated by a distance weighted least square algorithm (solid line).

Tree branchwood production (TBWP) is defined as the sum of branchwood production of the n wood-producing whorls of the tree:

$$TBWP = \sum_{i=1}^{n} BWP(i) \qquad [4.6]$$

The distribution of branchwood biomass among whorls can be described by a bell-shaped curve (Figure 4.3a). One whorl in the lower section of the tree's crown will carry the maximum biomass, e.g. whorl 10 in Figure 4.3a. The biomass of this whorl (j_m) can be defined from equation 4.5 as:

$$BWB(j_m) = \sum_{i=1}^{j_m} BWP(i) - \sum_{i=1}^{j_m} BWL(i) \qquad [4.7]$$

If we assume (discussed below) that in a single whorl and measurement period either production or litterfall occur, but not both, and that production occurs in whorls 1 to whorl j_m and litterfall in all whorls from j_{m+1} to n (Figure 4.3b) then we can demonstrate that the branchwood biomass of whorl j_m is equal to the total branchwood biomass production of the tree. In equation 4.7, we can substitute the first summation with equation 4.6 and the second summation with zero and rewrite equation 4.7 as:

$$BWB(j_m) = TBWP \qquad [4.8]$$

This equation states that the maximum amount of branchwood in a single whorl can be used as an estimate of annual branchwood production. This relationship holds if the branchwood biomass of a single tree is at or near steady state, which is true if annual branchwood production and litterfall at each whorl number remain constant, i.e. Equations 4.3 and 4.4 do not change over time. This would be the case if competition from neighbouring trees prevents further increase of the individual tree's branchwood biomass. In Chapter 3 (Equation 3.27) it was shown that competition influences the branchwood biomass of a tree. Any increase

in total branchwood biomass of a tree during a measurement period is accounted for by the Δ biomass component of equation 4.2.

Violating the assumption that in a single whorl and measurement period either branchwood production or litterfall, but not both, occur will result in an underestimate of tree branchwood production (TBWP) in equation 4.8. Figure 4.3A gives an example of the assumption that production occurs only in whorls 1 through j_m and litterfall only in whorls j_{m+1} to the maximum number of live whorls. Figure 4.3B shows the simultaneous occurrence of branchwood production and litterfall in whorls 8 through 13. Data which could be used to assess how much overlap occurs between branchwood production and litterfall in particular whorls are not available.

The site specific biomass regressions described in section 3.4.1 were applied to calculate branchwood biomass for each live branch in each of the 39 sample trees. Total branchwood biomass per whorl and per tree was calculated from these data. Within each sample plot, the mean branchwood biomass at each whorl number was computed by summing the whorl biomass of the sample trees. The distribution of live branchwood biomass was expressed as the percentage of the total of the destructively sampled trees in each plot. Calculating plot averages rather than a mean derived from individual trees reduces the influence of intermediate and suppressed trees, which have smaller than average branchwood biomass and which may have unrepresentative crown shapes.

For the sample trees from each installation, the maximum percentage of total branchwood biomass present in a single whorl was determined. The turnover component of total annual branchwood biomass production was calculated by multiplying total branchwood biomass per tree at the beginning of the measurement interval by the maximum percentage value described above.

Within each plot all species were treated similarly. As no data are available, it was assumed that the turnover component of other species' annual branchwood production can be calculated in the same way as that of Douglas-fir. The mortality and Δ biomass component of western hemlock and western redcedar branch production were calculated from species specific regression equations (Gholz *et al.* 1979), as described for stemwood biomass.

4.3.3.4 Foliage

Annual foliage production was computed similar to branch production from the net change in total biomass plus the replacement of mortality due to tree death, plus the amount of foliage which is replaced annually. The biomass regression equation based on dbh and growing space index (GSI) (Equation 3.20) was applied to calculate total foliage biomass at each measurement date. The loss of foliage biomass due to tree mortality during a measurement period was evenly distributed among the years of that period. Annual turnover of foliage was assumed to be equal to the biomass of one-year-old foliage.

To derive an estimate of the proportion of total foliage in the first year age class, the percentage of foliage in the first year was calculated for each of the 267 sample branches which had been collected and analyzed (cf. Section 3.3.2). For each of the 6 Installations, a regression equation was developed which predicts the proportion of each whorl's foliage which is in the first age class.

Using these regression equations and the data for all live branches of the 39 sampling trees, the amount and proportion of foliage in the first year age class was computed for each branch and summed to obtain the totals for each tree. A

regression equation was developed from data from the 39 sample trees to predict the total amount of first year foliage as a function of dbh.

4.3.3.5 Coarse roots

Coarse root biomass for all species was calculated from a regression equation for Douglas-fir (Gholz *et al.* 1979, Dice 1970) which uses dbh as independent variable. The lower diameter limit for coarse roots used by Dice (1970) was 10 mm. No biomass regressions are available for roots 5 to 10 mm diameter. Mortality of individual trees was treated as described for stemwood. No attempt was made to quantify the turnover component of coarse root production. McMinn (1963) encountered no dead structural roots greater than 1 cm in diameter, except those of dead suppressed trees, when excavating root systems of Douglas-fir.

4.4 RESULTS

4.4.1 Branch biomass turnover

As described in Section 4.3.3.3, branch biomass production is derived from three estimates: the net change in branch biomass per hectare, the replacement of mortality due to death of trees, and the replacement of mortality due to death of whorls. The latter estimate, branch turnover, is assumed to be equal to the maximum percentage of total biomass encountered in a single whorl (see Section 4.3.3.3 for a derivation).

The percentage of total branch biomass plotted against whorl number is presented in Figure 4.4. To show the approximate distribution of branch biomass, lines based on a distance weighted least square smoothing algorithm (Wilkinson 1988a) have been added. The whorl number at which the largest proportion of total branch biomass was encountered ranged from whorl 12 in Installation 16 to whorl 19 in Installation 72 (Table 4.1). The maximum percentage of total branch biomass in a whorl ranged from 6.0 to 12.9%, which is equivalent to a mean lifespan of 16.7 to 7.8 years, respectively (Table 4.1). Total branch biomass at the beginning of each measurement period is multiplied by the maximum percentage values (Table 4.1) to estimate the branch turnover component of branch production.

Table 4.1. Maximum percentage of total branchwood biomass encountered in a single whorl (whorl number) for each of the six destructively sampled plots.

Installation	whorl number	percent of total	mean lifespan (years)
2	13	6.0	16.7
4	16	6.6	15.2
5	12	9.9	10.1
16	12	12.9	7.8
71	13	8.9	11.2
72	19	6.4	15.6

4.4.2 Foliage biomass turnover

The percentage of foliage on a branch which is in the first year age class declines with whorl number, if whorl number is counted from the top down. Figure 4.5 shows percent foliage biomass in the first year age class as a function of whorl number for 267 sample branches. The model which best described the data was

$$PERFOL = b_0 + b_1 * 1/WHORL + b_2 * 1/(WHORL)^2 \qquad [4.9]$$

where PERFOL is the percentage of a whorl's foliage which is in the first year age class, and whorl is the number of the whorl, counting from the top down. Regression lines (Table 4.2), fitted to the data from each Installation, are shown in Figure 4.5.

After applying the regression models described in section 3.4.1 to calculate foliage biomass per branch, and the regression equations listed in Table 4.2 to calculate the proportion of first year foliage, the results were summed for each tree. First year foliage biomass per tree (FOL1) was calculated from the model

$$\ln FOL1 = -1.598 + 3.125 * \ln dbh - 0.0514 * dbh \qquad [4.10]$$

where lnFOL1 is the natural logarithm of first year foliage biomass per tree (gram) and dbh is diameter at breast height (cm). Based on a sample size of 39 trees, the regression model is highly significant (R^2=0.868, $p < 0.001$, SEE=0.432 ln gram).

Table 4.2. Coefficients, sample size (n), R^2, and standard error of estimate (SEE) of six equations to calculate, for individual branches, the percentage of foliage in the first age class. The general model is described in equation 4.9. ($p < 0.001$ for all models and for all coefficients (except see footnote).

Inst	n	R^2	SEE (%)	b_0	b_1	b_2
2	54	.977	5.16	-9.91	213.23	-103.20
4	42	.982	4.79	-13.44	267.87	-154.37
5	52	.978	5.24	-11.52	245.95	-134.40
16	34	.987	4.49	-23.19	344.11	-220.84
71	39	.934	8.86	-5.77[a]	241.14	-135.41
72	46	.965	6.00	-3.42[b]	257.59	-154.34

[a] p=0.078
[b] p=0.068

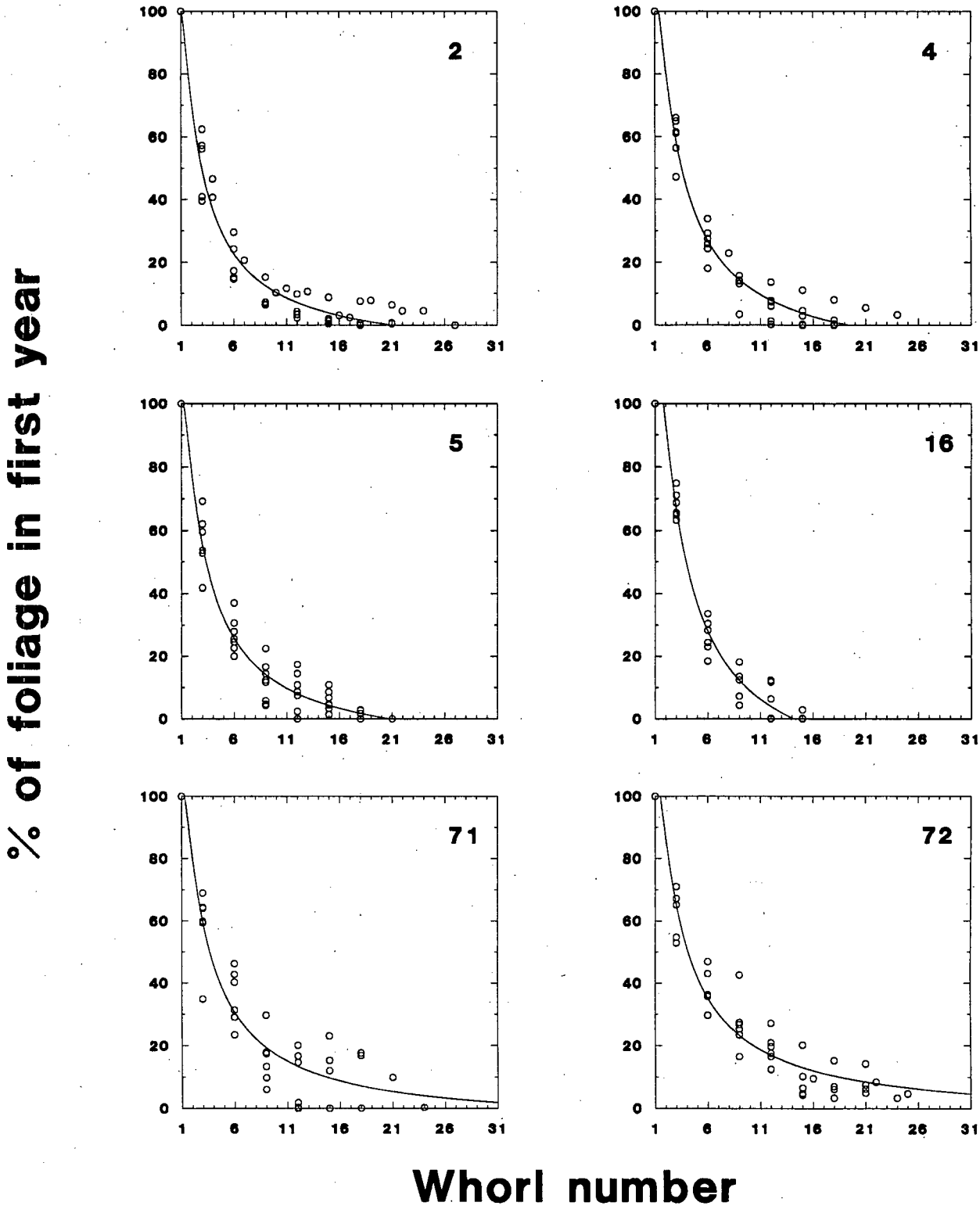

Figure 4.5. Percentage of foliage in the first year age class for 267 sample branches from 6 Installations (open circles). Regression equations (Table 4.2) are plotted as solid lines.

4.4.3 Aboveground and coarse root biomass and production

The results for the major ecosystem variables will be presented graphically for all 12 plots. In addition, results for either the year 1985 or the period 1985 to 1987 will be presented in tabular format.

Stand age, basal area, stand density, and site index for 1985 are summarized in Table 4.3. Stand age ranged from 32 to 70 years. Site index ranged from 19.5 to 41.3 meters at 50 years. Stand density in 1985 varied between 440 and 3400 stems per hectare (Table 4.3) and generally decreased over time (Figure 4.6). The only exception is Installation 2 Plot 11 where the number of both Douglas-fir (+8.6%) and western hemlock (+85.7%) stems with more than 5.0 cm dbh increased from 1972 to 1987.

In 1985, basal area of all species ranged from 33.6 to 75.3 m^2 ha^{-1} (Table 4.3) of which Douglas-fir represented 66.5 to 99.8%. Basal area increased with time in 11 of the 12 plots (Figure 4.7). Snowbreak in Installation 4 Plot 17 in the winter of 84/85 resulted in some tree mortality and a reduction in basal area in this plot.

Aboveground biomass changed in a pattern which closely followed the change in basal area (Figure 4.8). In 1985, aboveground biomass ranged from 135.0 to 573.6 Mg ha^{-1} (Table 4.4). Table 4.4 lists the biomass of each major aboveground component and of coarse roots. The distribution of biomass as a percentage of aboveground biomass is presented in Table 4.5. Coarse root biomass is expressed as a percentage of aboveground biomass, but is not included in its calculation.

In most plots, foliage biomass increased with time, but the rate of increase declined with time (Figure 4.9). In the two plots of Installation 72, however, foliage biomass was approximately constant (10 and 11 Mg ha^{-1}), despite the continuing

increases in basal area and total aboveground biomass. Installation 72 is both the oldest stand and the stand with the highest basal area.

Mean annual biomass production for the period 1985 to 1987 ranged from 5.6 to 16.0 Mg $ha^{-1}yr^{-1}$ (Figure 4.10, Table 4.6). The low production (4.7 Mg $ha^{-1}yr^{-1}$) in Installation 4 Plot 17 is due to tree mortality and reduced tree growth following snowbreak. Stemwood production was the single largest component of total aboveground biomass production, representing 42.4 to 68.5% of the total (Table 4.7). Foliage, which represented 1.8 to 6.4% of total aboveground biomass, accounted for 8.7 to 31.0% of aboveground production. Branches and stembark accounted for an additional 12.4 to 26.7% and 7.1 to 10.6% of total aboveground production, respectively. Coarse root production was estimated to be equal to 13.2 to 17.3% of total aboveground production.

Table 4.3. Stand age, site index (SI), basal area (BA), and stand density in 1985 for the 12 study plots. Douglas-fir (Df) BA and stand density are listed in absolute amounts and as a percentage of the total.

Inst	Plot	Age (yr)	SI (m @ 50)	Total BA (m^2ha^{-1})	Df BA (m^2ha^{-1})	%Df BA (% of tot)	Total Stems (st. ha^{-1})	Df Stems (st. ha^{-1})	%Df Stems (% of tot)
2	6	42	27.7	53.4	35.5	66.5	3000	1200	40.0
2	11	41	19.5	33.6	26.9	80.1	2840	2040	71.8
4	1	44	29.1	45.3	45.2	99.8	1840	1800	97.8
4	17	48	25.7	37.4	35.4	94.7	1640	1420	86.6
5	8	40	26.8	58.7	44.6	76.0	3400	1820	53.5
5	10	39	29.5	47.4	45.9	96.8	1420	1240	87.3
16	2	32	29.4	41.3	40.7	98.5	2000	1960	98.0
16	6	32	32.4	45.1	40.7	90.2	2520	2020	80.2
71	11	41	24.6	45.3	45.1	99.6	1880	1840	97.9
71	14	41	23.3	46.0	45.6	99.1	2460	2400	97.6
72	2	70	41.3	69.1	67.0	97.0	440	400	90.9
72	14	70	41.0	75.3	72.5	96.3	480	460	95.8

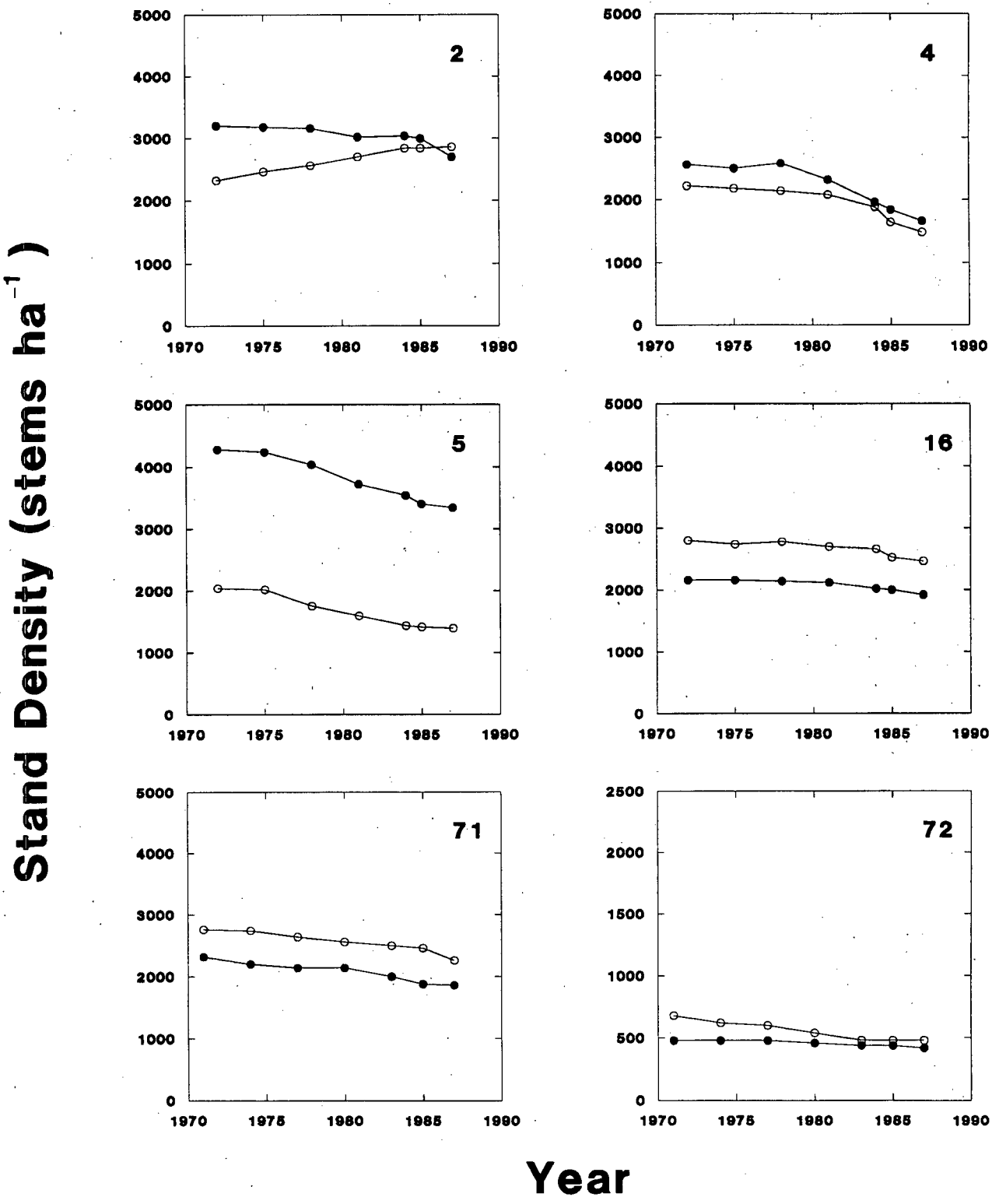

Figure 4.6. Total stand density plotted against time for the 12 sample plots. Installation numbers are in the upper right corner of each graph. Solid circles represent Installation (I) and Plot (P): I2-P6, I4-P1, I5-P8, I16-P2, I71-P11, and I72-P2. Open circles represent: I2-P11, I4-P17, I5-P10, I16-P6, I71-P14, and I72-P14.

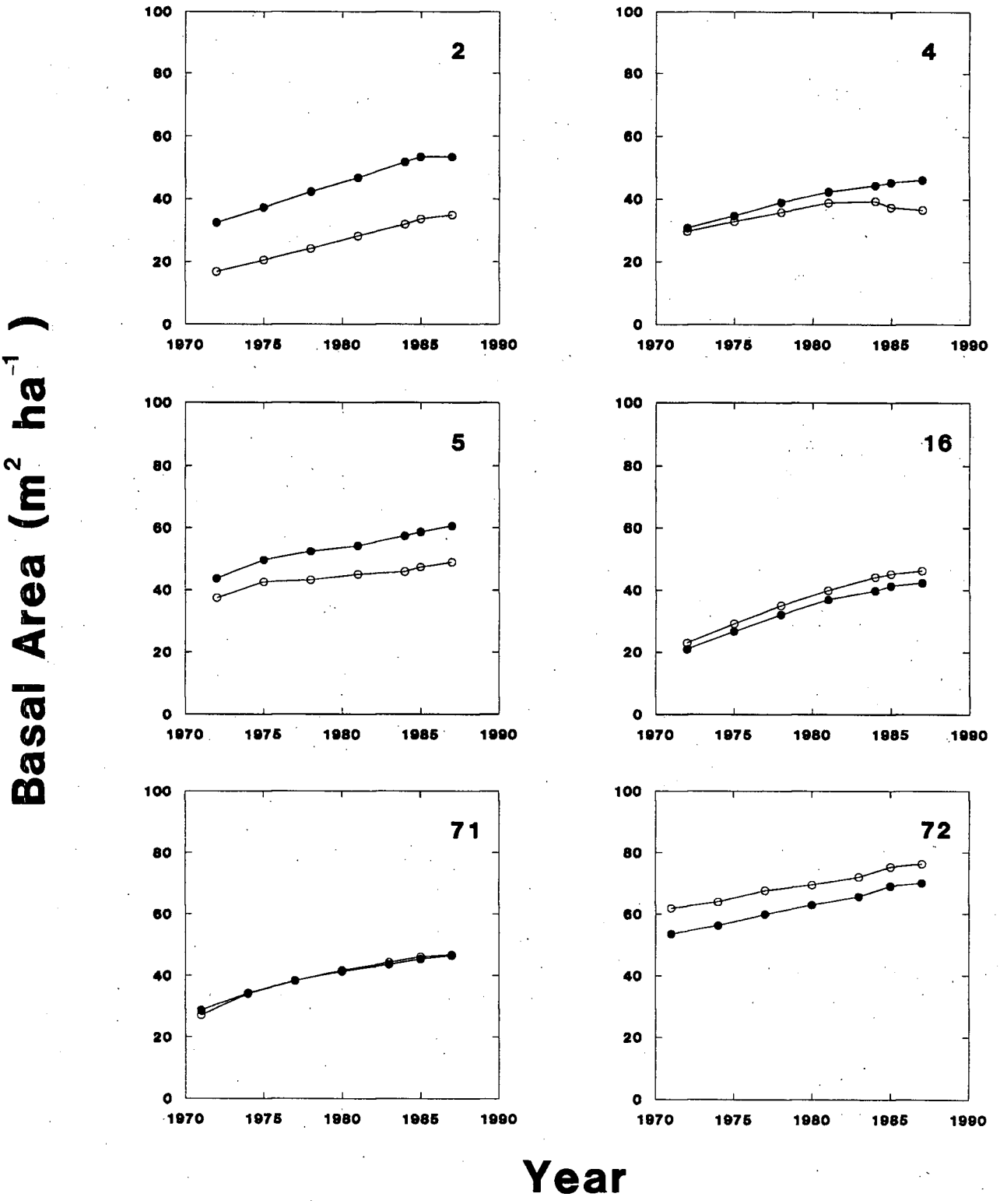

Figure 4.7. Basal area plotted against time. Legend as in Figure 4.6.

Table 4.4. Total stand biomass in 1985 of foliage, branches, stemwood, stembark, and coarse roots.

Inst	Plot	Age (yr)	SI (m @ 50)	Foliage	Branches	Stem wood	Stem bark	Σ Above ground	Coarse roots
				(Mg ha^{-1})					
2	6	42	27.7	13.08	20.83	176.8	27.77	238.4	49.66
2	11	41	19.5	8.60	11.64	98.1	16.68	135.0	26.31
4	1	44	29.1	10.48	14.39	158.9	28.15	211.9	47.18
4	17	48	25.7	9.05	11.75	122.5	21.60	164.9	35.48
5	8	40	26.8	13.54	19.72	186.9	29.49	249.7	49.74
5	10	39	29.5	10.13	13.68	169.4	28.35	221.6	48.18
16	2	32	29.4	9.77	12.04	127.9	22.47	172.2	35.13
16	6	32	32.4	11.49	14.34	142.3	24.11	192.2	39.52
71	11	41	24.6	10.35	12.93	145.1	25.35	193.7	40.34
71	14	41	23.3	10.00	12.55	146.4	25.17	194.1	38.96
72	2	70	41.3	9.87	26.47	441.5	71.96	549.8	123.00
72	14	70	41.0	10.50	25.32	463.1	74.61	573.6	129.70

Table 4.5. The distribution of the biomass components listed in Table 4.4, expressed as a percentage of aboveground biomass.

Inst	Plot	Age (yr)	SI (m @ 50)	Foliage	Branches	Stem wood	Stem bark	Σ Above ground	Coarse roots
				(% of Σ Aboveground)					
2	6	42	27.7	5.5	8.7	74.2	11.6	100.0	20.8
2	11	41	19.5	6.4	8.6	72.6	12.4	100.0	19.5
4	1	44	29.1	4.9	6.8	75.0	13.3	100.0	22.3
4	17	48	25.7	5.5	7.1	74.3	13.1	100.0	21.5
5	8	40	26.8	5.4	7.9	74.8	11.8	100.0	19.9
5	10	39	29.5	4.6	6.2	76.4	12.8	100.0	21.7
16	2	32	29.4	5.7	7.0	74.3	13.0	100.0	20.4
16	6	32	32.4	6.0	7.5	74.0	12.5	100.0	20.6
71	11	41	24.6	5.3	6.7	74.9	13.1	100.0	20.8
71	14	41	23.3	5.2	6.5	75.4	13.0	100.0	20.1
72	2	70	41.3	1.8	4.8	80.3	13.1	100.0	22.4
72	14	70	41.0	1.8	4.4	80.7	13.0	100.0	22.6

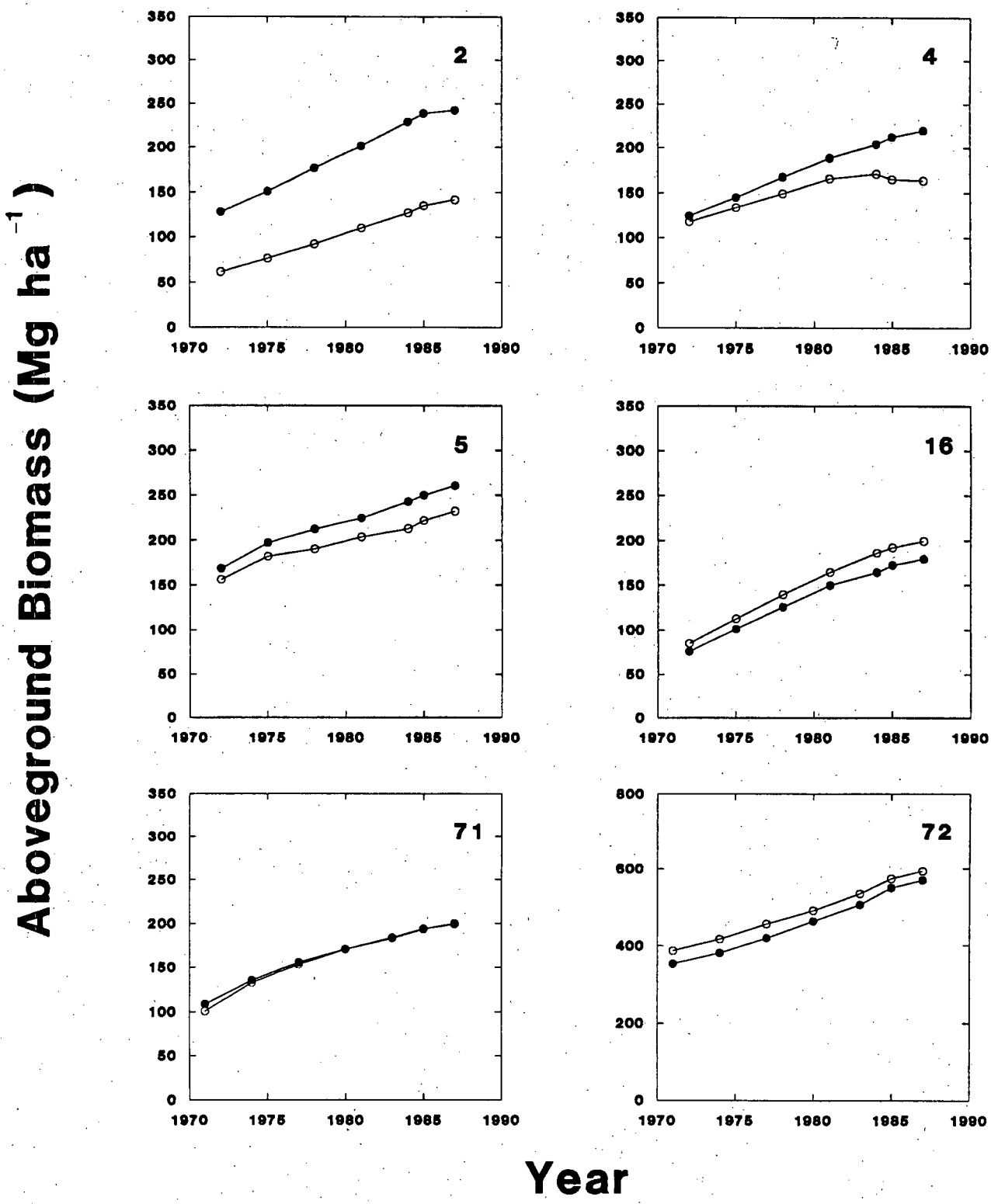

Figure 4.8. Aboveground biomass plotted against time. Legend as in Figure 4.6.

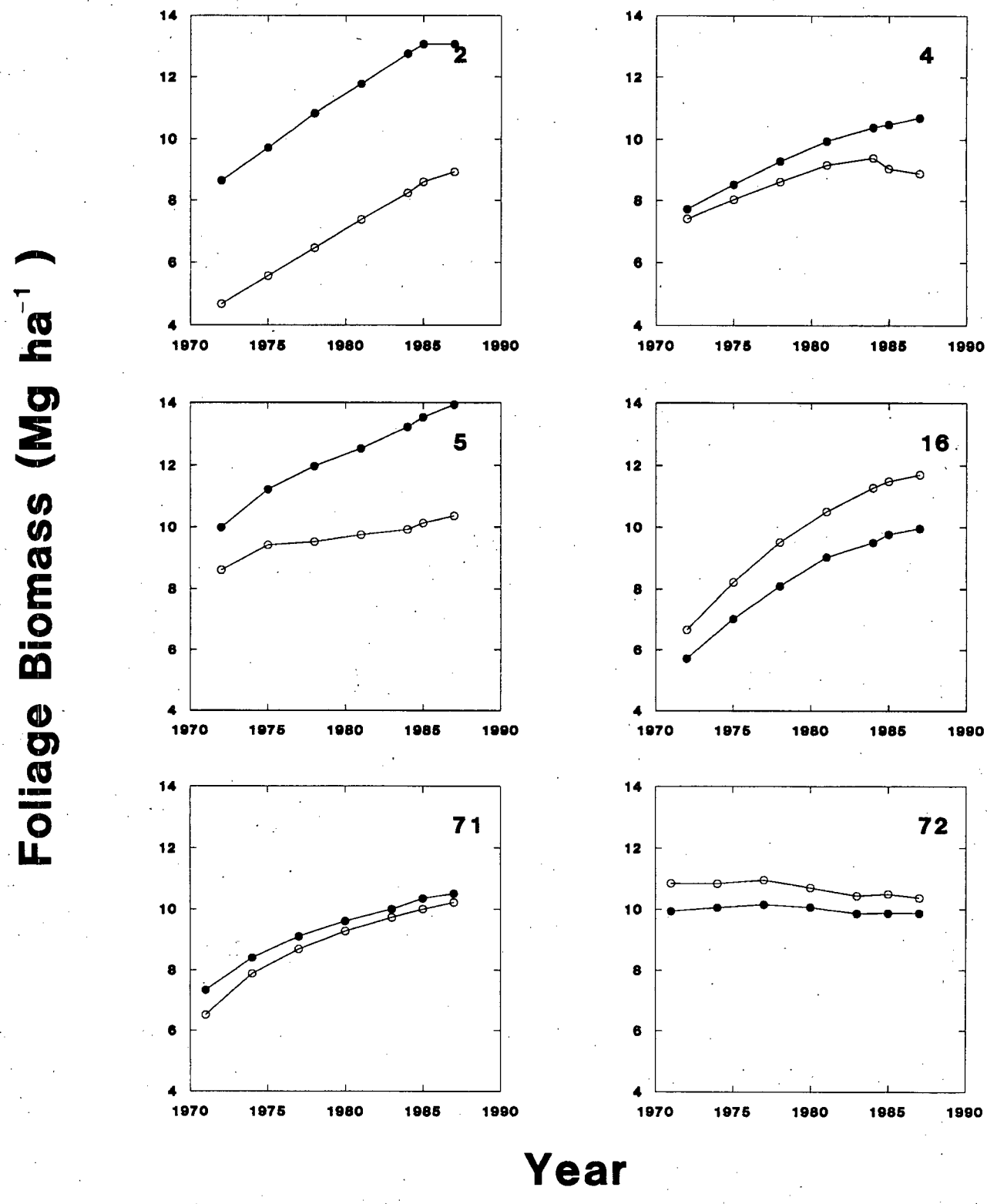

Figure 4.9. Foliage biomass plotted against time. Legend as in Figure 4.6.

Table 4.6. Annual production of foliage, branches, stemwood, stembark, and coarse root biomass. Data represent the sum of all species for the period 1985 to 1987.

Inst	Plot	Age (yr)	SI (m @ 50)	Foliage	Branches	Stem wood	Stem bark	Σ Above ground	Coarse roots
				(Mg ha^{-1}yr^{-1})					
2	6	42	27.65	2.58	1.61	3.53	0.60	8.32	1.13
2	11	41	19.50	1.38	1.01	2.77	0.40	5.56	0.78
4	1	44	29.05	1.39	1.25	4.06	0.69	7.39	1.28
4	17	48	25.66	1.21	0.95	2.18	0.36	4.71	0.69
5	8	40	26.75	2.62	2.41	4.67	0.69	10.39	1.37
5	10	39	29.45	1.55	1.61	4.46	0.67	8.29	1.28
16	2	32	29.38	1.33	1.80	4.06	0.64	7.83	1.18
16	6	32	32.39	1.42	2.12	3.78	0.61	7.94	1.17
71	11	41	24.62	1.39	1.29	2.67	0.41	5.76	0.76
71	14	41	23.27	1.47	1.36	3.36	0.54	6.74	1.00
72	2	70	41.34	1.39	2.16	9.55	1.55	14.66	2.30
72	14	70	41.03	1.40	1.99	10.97	1.65	16.01	2.55

Table 4.7. The distribution of the production listed in Table 4.6, expressed as a percentage of aboveground biomass production. Data represent the sum of all species for the period 1985 to 1987.

Inst	Plot	Age (yr)	SI (m @ 50)	Foliage	Branches	Stem wood	Stem bark	Σ Above ground	Coarse roots
				(% of Σ Aboveground)					
2	6	42	27.7	31.0	19.4	42.4	7.2	100.0	13.6
2	11	41	19.5	24.8	18.2	49.8	7.2	100.0	13.9
4	1	44	29.1	18.8	16.9	54.9	9.3	100.0	17.3
4	17	48	25.7	25.7	20.2	46.3	7.7	100.0	14.5
5	8	40	26.8	25.2	23.2	44.9	6.6	100.0	13.2
5	10	39	29.5	18.7	19.4	53.8	8.1	100.0	15.4
16	2	32	29.4	17.0	23.0	51.9	8.2	100.0	15.1
16	6	32	32.4	17.9	26.7	47.6	7.6	100.0	14.7
71	11	41	24.6	24.1	22.4	46.4	7.1	100.0	13.2
71	14	41	23.3	21.8	20.2	49.9	8.1	100.0	14.8
72	2	70	41.3	9.5	14.7	65.1	10.6	100.0	15.7
72	14	70	41.0	8.7	12.4	68.5	10.3	100.0	15.9

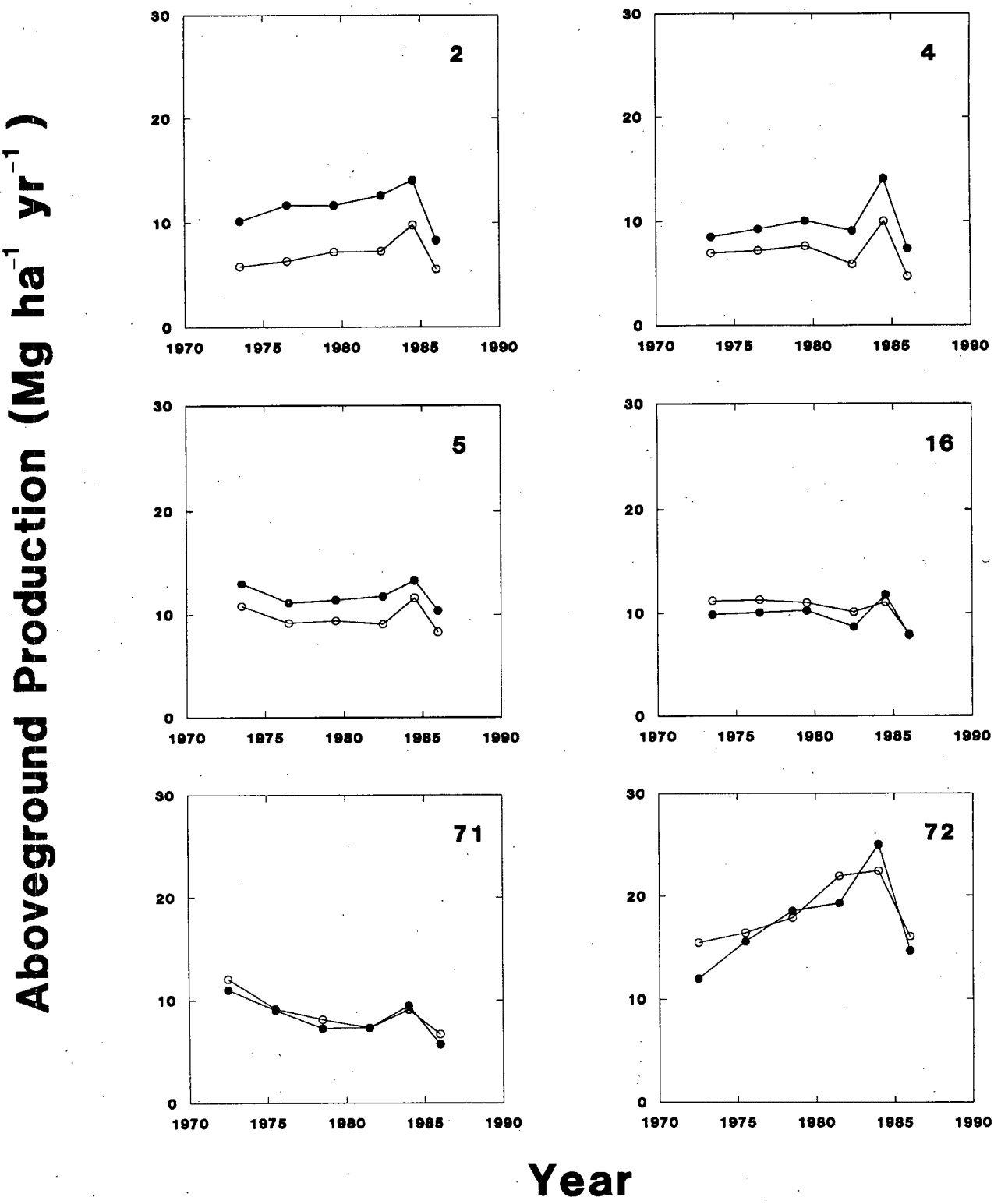

Figure 4.10. Aboveground production plotted against time. Legend as in Figure 4.6.

4.5 DISCUSSION

The use of a competition index as an independent variable in biomass regression models makes it necessary that the locations of trees in research plots are known. The X-Y coordinates and the dbh and mortality data for up to 16 years were available for trees inside the research plots, but not for the trees in the surrounding buffer strips. Competition indices for trees near the plot edge are biased because of the lack of neighbouring trees in the data set. This problem can be reduced by either establishing a buffer strip inside the existing plot or by creating, based on available plot information, a hypothetical stand surrounding the plot.

A buffer strip of adequate width inside the plot would have reduced the inner plot to one third to one quarter of its original size. An external buffer strip could have been created by "mirroring" the trees along the plot border. This method, however, amplifies existing irregular tree distribution patterns. A small gap or a large tree near the plot edge will be duplicated on the opposite side of the plot border. The method chosen in this study, whereby plot sections from one side of the plot were copied adjacent to the opposite side, overcomes this problem. Furthermore, it maximizes the use of available information because dbh data from all trees can be utilized. Although this method does not use "actual" X-Y coordinates or dbh data for the trees in the buffer strip, the error introduced by using these "hypothetical" stand data will probably be small because the plots have been established to include buffer strips of similar stand structure as in the plots themselves (Darling and Omule 1989).

In this study, a competition index was used, in addition to dbh, as an independent variable in regression models for the prediction of foliage biomass. In the two plots with the highest basal area (Installation 72), total foliage biomass

reached a maximum of about 10 and 11 Mg ha^{-1} and decreased slightly thereafter (Figure 4.9), despite the continuing increase in basal area (Figure 4.4). In comparison, the dbh-based regression model of Gholz *et al.* (1979), which has frequently been used in biomass studies, predicts an increase in foliage biomass from 13.1 to 16.1 and from 15.5 to 16.6 Mg ha^{-1} for the period 1971 to 1987 for plots 2 and 14 of Installation 72, respectively. The stabilization of foliage biomass predicted by the regression model developed in this study is consistent with the observation that, during stand development, foliage biomass levels off at a site specific maximum value (Tadaki 1966, Albrektson 1980). A similar prediction could be obtained from regression models that use sapwood basal area as independent variable. As is often the case, sapwood basal area data were not available in this study because coring of the trees in the long-term sample plots was not permissable. Using a competition index in combination with dbh data is a suitable alternative approach to predicting stand foliage biomass.

Biomass of western hemlock and western redcedar, where present, was estimated from published regression equations (Gholz *et al.* 1979). Some of the problems of using regional rather than site-specific regression models have been discussed in Chapter 3, but site-specific models for these species were not available. In 1985, Douglas-fir represented at least 90% of total basal area in 9 of the 12 plots, and never less than 66.5% (Table 4.3). The error introduced by using regional models for a small component of the trees in a stand is probably small.

For other tree species, which occurred only rarely in some of the plots, biomass components were predicted from Douglas-fir regression equations. The single bigleaf maple in Installation 72, Plot 14, accounted for 4.0% of total basal area in 1974, the year in which it reached the maximum proportion of total basal area. Similarly in 1987, a single white pine in Installation 4, Plot 17, accounted for

2.1% of total basal area. Installation 5, Plot 8, initially contained three small willows which, in 1972, accounted for 0.6% of total basal area. On a plot basis, the errors associated with using Douglas-fir equations for these few cases are probably minor.

A comparison of biomass and production values between different studies is always complicated by differences in the methodology employed to derive the estimates. Cannell (1982) summarized many biomass studies for Douglas-fir stands. The total aboveground biomass data for non-fertilized, non old-growth (<150 years) Douglas-fir stands from Cannell (1982) and data from Espinosa Bancalari and Perry (1987), and Binkley (1983) are summarized in Figure 4.11. The scatter plot shows that the relationship between total aboveground biomass and total stand basal area obtained in this study (solid circles) is consistent with the relationship observed in other published studies (open circles).

The turnover components of branch and foliage production estimates have been derived using approaches specifically developed in this study. Many production studies do not account for branch turnover at all (Dice 1970) and foliage turnover is often simply assumed to represent 20% of total foliage biomass (Keyes and Grier 1981).

The branchwood turnover estimates derived in this study represent an improvement over the alternative of omitting this production component. The method used in this study is only applicable to determinate tree species, such as Douglas-fir, which produce one whorl per year. A second assumption which must be met is that the number of live whorls remains approximately constant over a measurement period. The fact that only one production estimate was derived for both plots in each Installation could introduce some error, in particular in Installations where stand density differs between the two plots, e.g. Installation 5

has 3400 and 1420 stems ha^{-1} in Plots 8 and 10, respectively. Errors are probably also introduced from the calculation of branch turnover for species other than Douglas-fir, because the same mean lifespan of branches was used for all species. The contribution of this source of error will increase as the proportion of Douglas-fir in the stand decreases. All three components of branch production combined, (Δ biomass, mortality, and turnover, cf. equation 4.2) represent 12.4 to 26.7% of total aboveground production (Table 4.7). The combined effects of errors in the branch turnover estimate is not likely to greatly affect total production estimates.

A comparison of Douglas-fir production data from 38 stands reported in Cannell (1982), Espinosa Bancalari and Perry (1987), Binkley (1983), and in this study is complicated by the differences in methods used, in stand ages and in stand densities. Figure 4.12 shows the relationship between stand foliage biomass and total aboveground production for these Douglas-fir stands less than 150 years of age and not fertilized. Total aboveground production increases with increasing foliage biomass (r^2=0.143, p=0.019). The large variation in the data is due to the different regression equations used to calculate foliage biomass, and differences in stand densities, stand ages, and between-year variation in annual production. The 12 data points from this study (solid circles) fall well within the range of data reported in the literature (open circles).

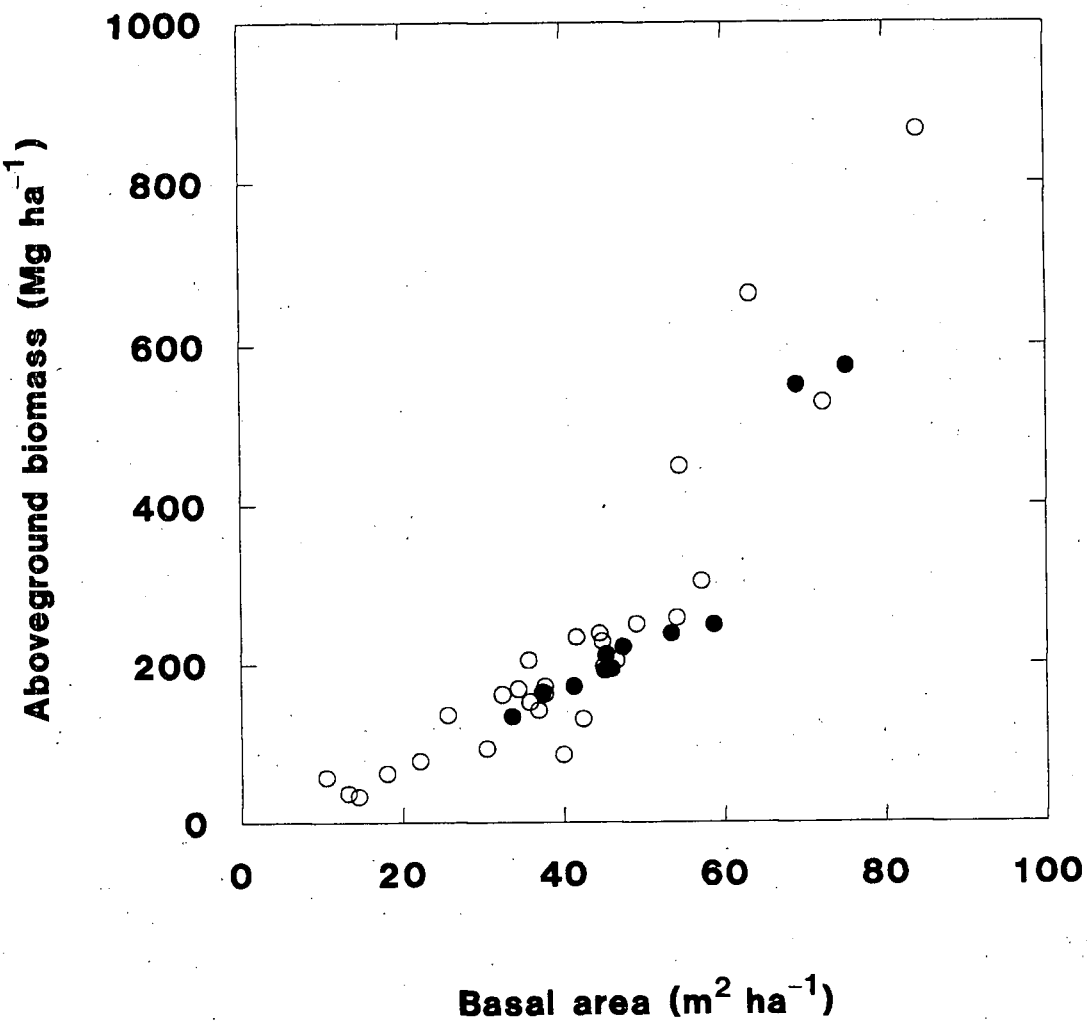

Figure 4.11. Total aboveground biomass versus basal area from 42 different Douglas-fir stands. Solid circles are stands from this study. Open circles represent unfertilized, non old-growth (<150 years) Douglas-fir stands from Cannell (1982), and data from Espinosa Bancalari and Perry (1987), and Binkley (1983).

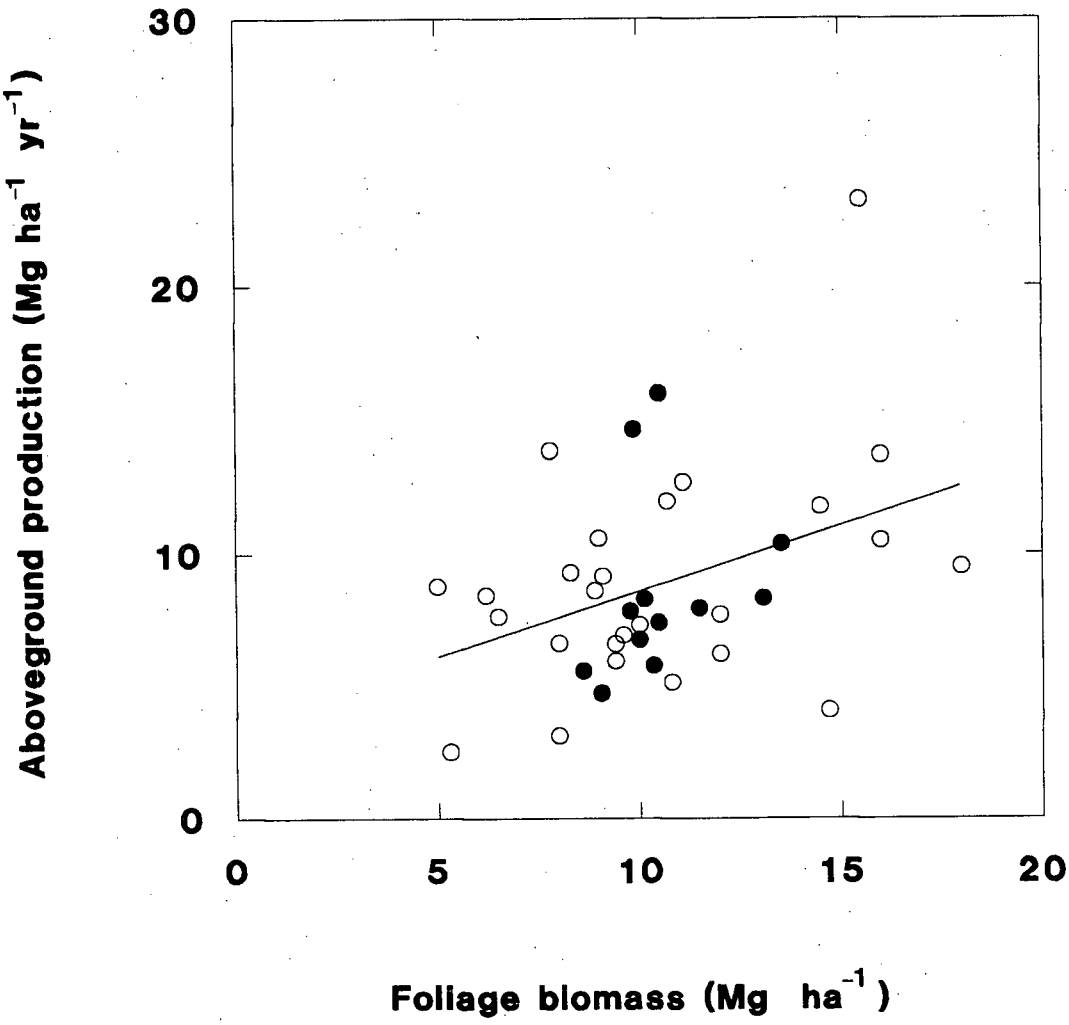

Figure 4.12. Total aboveground production versus foliage biomass from 38 different Douglas-fir stands. Solid circles are stands from this study. Open circles represent unfertilized, non old-growth (<150 years) Douglas-fir stands from Cannell (1982), and data from Espinosa Bancalari and Perry (1987), and Binkley (1983).

5. FINE AND SMALL ROOT BIOMASS AND PRODUCTION

5.1 INTRODUCTION

In the past, both forest management and forest research have focussed primarily on the aboveground portion of forest stands. The belowground component is not utilized, difficult to quantify, and was rarely studied. It is only in the last decade or so that researchers began to realize that while belowground biomass, especially fine roots, includes only a small portion of total biomass, its share of total annual stand production is disproportionately large (Agren *et al.* 1980, Keyes and Grier 1981). A large but variable proportion of net annual photosynthate production is allocated to belowground biomass components, especially fine roots (Agren *et al.* 1980, Harris *et al.* 1980, Vogt *et al.* 1983).

Estimates of the proportion of total photosynthate production allocated to fine roots vary among species and with site and stand conditions. Between-stand variation in harvestable forest production is attributable to differences in both total production and allocation of production to above- and belowground biomass components. Recent research results (Keyes and Grier 1981, Grier *et al.* 1986) suggest that between-stand differences in photosynthate allocation to above- and belowground biomass components account for much of the observed spatial variation in harvestable production of a tree species.

The difficulties in obtaining estimates of fine root biomass and turnover in forest ecosystems are reflected in the paucity of available information. Our understanding of production and mortality of belowground biomass components is very limited, particularly when compared to our understanding of the aboveground components of the same ecosystems. Improved understanding of belowground processes may provide explanations for the differences in stand responses to a

variety of forest management activities such as thinning and fertilization. It will also be useful in predicting forest ecosystem responses to changing environmental and climatic conditions.

The objectives of the work presented in this chapter were 1) to establish the seasonal pattern of live and dead fine and small root biomass in second growth Douglas-fir stands of five different site qualities, and 2) to quantify annual fine root production and mortality in these stands.

Although it would have been desirable to include in the study of belowground biomass and production all twelve stands for which aboveground data were available, this was technically impossible because of the logistical difficulties of processing the root samples. Five of the 12 plots were selected to include one low, one high, and three medium productivity stands.

5.2 LITERATURE REVIEW

5.2.1 Estimating fine root biomass

The estimation of fine root biomass in forest stands is an extremely time consuming and labour intensive task. The difficulty in obtaining the necessary field data is reflected in the paucity of information about belowground processes in forest ecosystems.

Quantitative estimates of fine root biomass are normally obtained from soil samples taken either as cores (cf. Moir and Bachelard 1969, Vogt *et al.* 1981, Santantonio *et al.* 1977) or in the form of excavated soil blocks (cf. Harris *et al.* 1977, Kimmins and Hawkes 1978). Soil cores generally contain a smaller soil

volume, and therefore require less processing time to separate fine roots from the mineral and organic matter. This permits the collection and processing of a larger number of replicate samples.

5.2.2 Horizontal and vertical distribution of fine roots

Within a site, fine root density (expressed as weight per unit soil volume or as root length per unit soil volume) generally is related to nutrient availability and decreases with increasing soil depth (Persson 1980, 1983). The majority of fine roots is in the upper 50 cm of forest soil and most of the absorbing roots can be found in the top 20 cm (Hermann 1977, Kimmins and Hawkes 1978, Gislason 1984).

Horizontal variability in the distribution of fine roots within forest stands depends on stand and site conditions. Moir and Bachelard (1969) found no correlation between the total amount of fine roots extracted from the soil cores and the distance of the sampling point to the nearest live stem in a 19-year-old *Pinus radiata* D. Don plantation. Similarly, Santantonio *et al.* (1977) applied a polygon sampling method in an old-growth Douglas-fir forest and found little or no correlation between small root (<10 mm) biomass and distance of the sample point to the centre of sample trees. In contrast, Persson (1980) found that fine root biomass (<2 mm) decreases with increasing distance from the nearest tree in a 15- to 20-year-old *Pinus sylvestris* L. plantation in central Sweden. An effect of sampling position on fine root weight per sample was also observed in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantation which had been ploughed prior to planting in order to reduce water-logging (Ford and Deans 1977).

Horizontal variability of fine root density in closed forest stands is probably determined primarily by heterogeneous soil conditions and not by distance to the nearest tree. It is impossible, however, to determine soil conditions of the sampling location prior to extracting the soil core. Therefore, no *a priori* stratification of the sampling position should be attempted and sampling points should be selected at random.

5.2.3 Nutrient availability and fine root biomass

A number of seemingly contradictory observations concerning the relationship between fine root biomass and nutrient availability have been reported in the literature. Many of the hypotheses derived from these observations are not mutually exclusive, but relate to differences in the spatial scale, ranging from microsite to whole-site scales, of the research on which the hypotheses are based.

Plants appear to allocate root growth preferentially to microsites with greater nutrient availability (Drew *et al.* 1973). In a laboratory split-root experiment with Sitka spruce seedlings, in which one part of the root system was supplied with water and nutrients while the other received water only, root diameters and mass increased in the pot with the greater nutrient availability (Coutts and Philipson 1976, Philipson and Coutts 1977). Although transfer of nutrients to the roots in the water-only pot occurred, it did not stimulate root growth in that pot.

Several studies have demonstrated the same phenomenon in the field; within a site, fine roots preferentially exploit regions with higher nutrient availability (Meyer 1967). In experiments with ingrowth bags containing nutrient

poor and nutrient rich substrates, St.John (1983) found that while there was an equal probability that fine roots would enter both types of ingrowth bags, a significantly greater fine root biomass developed in the nutrient rich material. Similarly, Coopersmith (1986) observed 5 to 10 times as much live coniferous fine root biomass in nutrient-enriched ingrowth bags compared with sand or soil filled bags in a coastal Douglas-fir stand on Vancouver Island, British Columbia. Such results have also been reported by Cuevas and Medina (1983) for an Amazon moist forest.

Friend (1988) found that localized increases in nitrogen availability led to greater fine root proliferation in the nitrogen richer environment. In both Douglas-fir seedlings and stands, the root response to greater local N availability was more pronounced when the seedlings or stands were N-stressed.

The above examples are concerned with the relationship between root growth and nutrient availability at the microsite level. This relationship can be different when considered at the whole stand level. In a series of laboratory experiments with a number of tree species (Ingestad 1979, 1981, Ingestad and Lund 1979, Ingestad and Kähr 1985) it was observed that increasing nutrient availability to seedlings resulted in greater overall seedling growth, but that the proportion of this increased growth which was allocated to roots decreased. Furthermore, the morphology of fine roots differed: roots in nutrient-poor solutions were longer and possessed fewer side branches (Ingestad and Lund 1979).

Several field fertilization experiments have supported the finding that increased nutrient availability decreases the proportion of total photosynthate production allocated to fine roots. This does not necessarily imply that fine root biomass is reduced in fertilized plots. In fact, if overall production increases as

nutrient availability increases, fine root production and biomass may also increase even if the allocation to fine roots generally becomes proportionately less.

Linder and Axelsson (1982) found both an overall decline in fine root production and a decline in the proportion of photosynthates allocated to fine roots in irrigated and fertilized plots of *Pinus sylvestris* compared with control plots. Grier *et al.* (1986) reported higher fine root biomass (<2mm) in control than in urea-nitrogen fertilized Douglas-fir stands. Nitrogen fertilization in a 35-year-old *Picea sitchensis* plantation resulted in decreased production of mycorrhizae, finest roots (<1mm) and fine roots (1-5mm). Mortality of these root classes was also reduced by fertilization, however, and the combined effects led to an increase in mean biomass in each category (Alexander and Fairley 1983). Urea fertilization of coastal western hemlock significantly reduced the number of mycorrhizae and accelerated the rate of mycorrhizal mortality (Gill and Lavender 1983).

To satisfy the tree's nutrient demand it would appear to be necessary for the tree to increase fine root surface area as nutrient availability decreases. Comparisons within one species have shown a greater fine root biomass on poor and dry sites than on rich and moist sites (Keyes and Grier 1981, Santantonio and Hermann 1985, Vogt *et al.* 1983). In contrast, Nadelhoffer *et al.* (1985) report that fine root production increases with greater nitrogen availability. This relationship was confounded, however, with a change in overstory species composition. Furthermore, the estimates of fine root production were based on a nitrogen budget approach which will be discussed in the next section.

5.2.4 Estimating fine root production and turnover

There is no direct way to measure fine root production, mortality and decomposition. Consequently, all indirect methods have to invoke a number of assumptions about the observed system. There is no consensus among scientists about the best method of estimating fine root production, but the advantages and disadvantages of some of the methods have been discussed in the literature.

Estimates of fine root production have been derived from a variety of measurements of different ecosystem components and processes, and have used a variety of different computational methods. Methods most commonly used are based on sequential estimates of fine root biomass obtained from soil cores (Moir and Bachelard 1969, Santantonio and Hermann 1985, Vogt *et al.* 1980). Other approaches are based on root ingrowth bags (Ericsson and Persson 1980, Coopersmith 1986), observation windows (Keyes and Grier 1981, Bohm 1979), and on the balancing of nitrogen budgets (Nadelhoffer *et al.* 1985). These methods will be discussed below.

Estimates of fine root biomass of an ecosystem are based on destructive samples taken in several locations. Any particular location cannot be sampled more than once. It must therefore be assumed that differences in observed fine root biomass between two sampling dates are due to production and/or mortality and not to spatial heterogeneity of the system being sampled. Spatial variation of fine root biomass in forest ecosystems is typically high, however, and few (if any) studies use sample sizes sufficiently large to permit an accurate differentiation between sampling error and true seasonal changes in fine root biomass (Vogt *et al.* 1986, Singh *et al.* 1984). The total number of samples that can be taken and processed in a study is generally restricted by the long processing time required for each sample.

Estimates of fine root production and turnover which are based on seasonal dynamics of fine root biomass incorporate several important assumptions (Kurz and Kimmins 1987). Production, mortality, and disappearance are rate variables (i.e. processes) which are to be derived from the measurements of state variables (i.e. quantities). Each state variable (live and dead fine root biomass) is determined by two rate variables and changes in the state variable cannot unequivocally be attributed to only one rate variable. For example, live fine root biomass at time t_2 is equal to live fine root biomass at time t_1 plus production minus mortality. Whenever these two processes occur simultaneously, an estimate of one of the rate variables obtained from the observed change in the state variable will be an underestimate (Kurz and Kimmins 1987).

Seasonal dynamics of fine root biomass and production traditionally have been determined by sequential sampling of fine root biomass. The implicit assumption is that the peaks and troughs in the seasonal pattern coincide with the sampling dates. Failure to capture peaks and troughs will lead to an underestimation of fine root biomass production (Kurz and Kimmins 1987). Increasing the sampling frequency will increase the probability that all peaks and troughs are included. If the total number of samples which can be processed in a project is restricted, however, an increase in the sampling frequency will reduce the number of samples which can be taken at any one sampling date. This, in turn, will reduce the researcher's ability to distinguish "true" changes in fine root biomass from those attributable to random error. Furthermore, if two processes occur simultaneously (e.g. production and mortality), increasing the sampling frequency does not reduce the degree of underestimation in the production estimate. Vogt *et al.* (1986) recommended that information on root phenology should be used when root sampling protocols are designed.

Different computational methods have been used to calculate fine root production and mortality from data on the seasonal dynamics of fine root biomass (Persson 1978, McClaugherty *et al.* 1982, Santantonio and Hermann 1985, Fairley and Alexander 1985). It is generally recognized that separating fine root biomass into the live and dead components enhances the detection of seasonal dynamics and therefore improves the accuracy of production and mortality estimates.

A second approach to estimating fine root biomass production is based on ingrowth bags (Ericsson and Persson 1980, Coopersmith 1986). By introducing a root-free medium into the forest floor and mineral soil, the problem of simultaneous occurrence of production and mortality can be overcome. All live and dead fine roots encountered in the bag after it has been in the forest for a certain time period have been produced during that period. Although ingrowth bags solve some of the problems of the sequential coring method, the estimates of fine root biomass obtained from ingrowth bags may be biased by artefacts inherent in this method. Within a stand, fine root density in microsites increases with greater soil fertility, as discussed above. Introducing a disturbed, root-free medium into the soil may create a fertility gradient from the surrounding soil to the ingrowth bag. If the fertility in the bag is greater than in the surrounding soil, fine root density will be higher in the bag and *vice versa* (cf. St. John 1983, Coopersmith 1986, Cuevas and Medina 1983 as discussed in Section 5.2.3). Furthermore, the consequences of fine root tip severing (Rost and Jones 1988) in the process of inserting the root ingrowth bag have not been examined for forest trees.

A third approach to measuring fine root dynamics involves observation windows or observation tubes. These are transparent plates or tubes which are placed in the forest floor and mineral soil. They permit regular monitoring of the same population of fine roots over a period of time. A number of artefacts are

introduced by such observation devices (Bohm 1979). Observation windows are generally not suitable for quantitative estimates of fine root production but are a valuable tool in the determination of fine root growth rhythms.

Nadelhoffer *et al.* (1985) used a nitrogen budget approach to determine fine root production and turnover. They established complete nitrogen budgets for several forest ecosystems and estimated fine root production by assuming that mineralized N not accounted for by plant uptake and allocation to aboveground litterfall and perennial tissues had been taken up by vegetation and allocated to fine roots. Fine root production and turnover were then estimated from this N quantity and N concentrations in fine roots. The estimate of unaccounted N, however, also contains the cumulative error of all other estimates of the N-budget.

The development of an annual nutrient budget at an ecosystem level is a complex task which involves many assumptions concerning the unaccounted-for portion of the nitrogen budget. One assumption made by Nadelhoffer *et al.* (1985) was that "nitrogen use efficiency" (i.e. the amount of N required to produce one unit of N in fine root biomass) was the same for all species and levels of nitrogen availability. It is difficult to accept this assumption in the absence of any consideration of internal redistribution of N in above- and belowground biomass components. Many other processes have to be understood and measured in more detail before an ecosystem level N-budget can become a reliable method of estimating fine root production and turnover.

From this review it is concluded that estimating fine root production from direct measurements of the seasonal dynamics of fine root biomass is, in spite of its shortcomings, the most reliable of the currently available approaches in ecosystems where a strong seasonal amplitude in live and dead fine root biomass can be expected.

5.3 METHODS

5.3.1 Location and description of the study sites

Detailed site descriptions are presented in Chapter 2. Only five of the 12 plots were selected for belowground sampling. These stands represent a range of site indices from 23.3 to 41.0 m@50 years (Table 5.1). Three medium productivity stands with site indices ranging from 27.7 to 29.5 m@50 years were selected to give an indication of the variability of fine root biomass and production over a narrow range of site indices. Additional details about stand composition and aboveground biomass are presented in Chapter 3.

5.3.2 Sample Collection

Sample dates were selected to coincide with anticipated peaks and troughs in the seasonal pattern of fine root biomass, as recommended by Vogt *et al.* (1986). The first and last sampling dates were just prior to bud break, at which time the largest amount of live fine roots can be expected (cf. Kramer and Kozlowski 1979). Samples were collected at six additional dates throughout the remainder of the year. Laboratory processing required over 24 hours per core, and only the samples from five collections were processed for all sites. Samples from a sixth sampling date were processed for one plot. Table 5.2 lists sampling dates, the intervals in weeks between those dates, and the number of cores which were processed.

Sample locations within each plot were randomly selected within an x-y grid. Rocks, which occurred frequently in some of the plots, occasionally clogged up the soil corer or prevented its penetration of the soil. If it was impossible to obtain a sample at the selected position, an adjacent location was chosen at random.

Table 5.1 Stand age, site index (SI), basal area (BA), and stand density in 1985 for the five study plots. Douglas-fir (Df) BA and stand density are listed in absolute amounts and as a percentage of the total. See Table 2.5 for a complete listing of species distribution.

	Inst	Plot	Age (yr)	SI (m @ 50)	Total BA (m^2ha^{-1})	Df BA (m^2ha^{-1})	%Df BA (% of tot)	Total Stems (st. ha^{-1})	Df Stems (st. ha^{-1})	%Df Stems (% of tot)
A	71	14	41	23.3	46.0	45.6	99.1	2460	2400	97.6
B	2	6	42	27.7	53.4	35.5	66.5	3000	1200	40.0
C	16	2	32	29.4	41.3	40.7	98.5	2000	1960	98.0
D	5	10	39	29.5	47.4	45.9	96.8	1420	1240	87.3
E	72	14	70	41.0	75.3	72.5	96.3	480	460	95.8

Table 5.2 Sampling dates, sampling interval, and number of cores processed per stand.

Dates	Interval (weeks)	Processed	Cores per plot
May 13 - 18, 1985	-	5 Plots	17
June 24 - 29, 1985	6	5 Plots	10
Aug. 10 - 14, 1985	7	5 Plots	10
Oct. 3 - 6, 1985	8	5 Plots	10
Feb. 3 - 6, 1986	18	1 Plot	10
May 12 - 16, 1986	14 [1]	5 Plots	10

[1] For four plots the sampling interval of processed cores was 32 weeks.

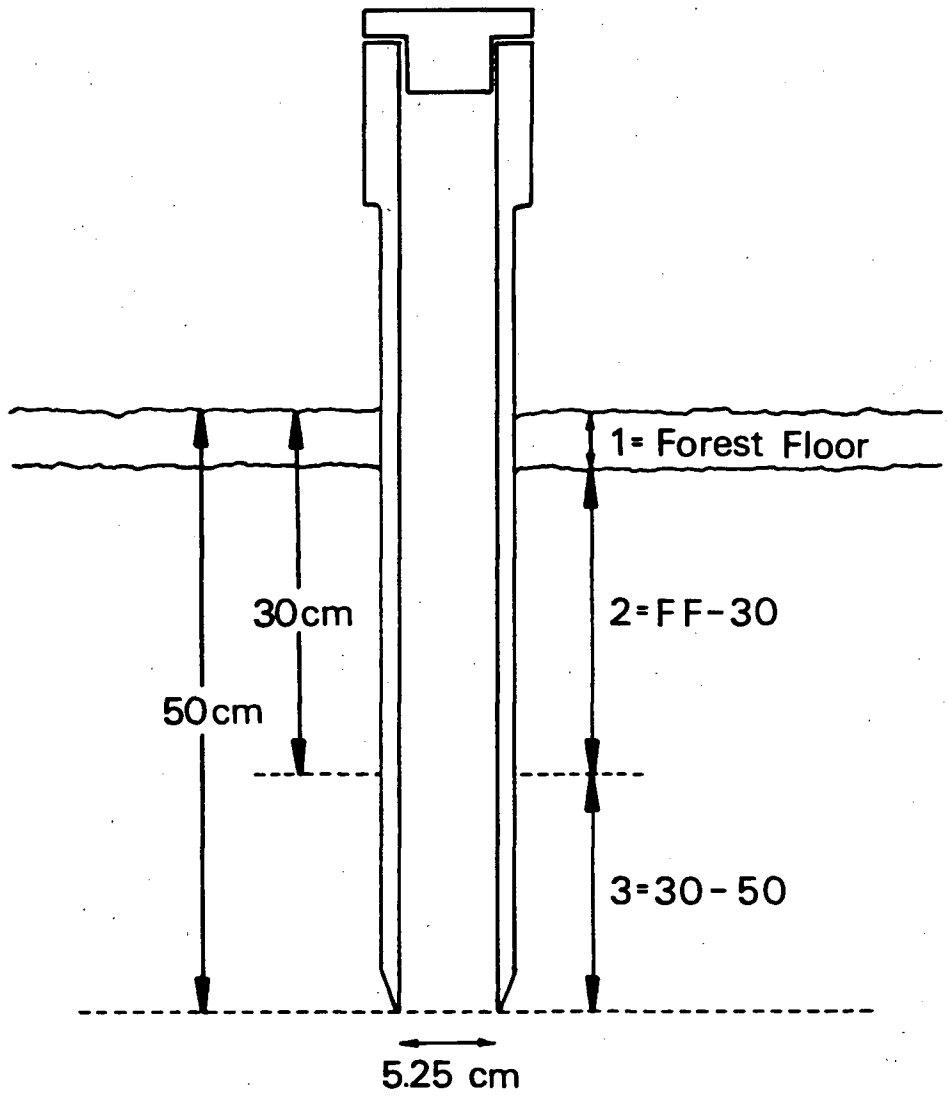

Figure 5.1 Schematic diagram of the soil corer and the sampling depths collected with it.

Soil cores were obtained with a 90 cm long steel pipe, (Schedule 40, 5.25 cm inside diameter, 4 mm wall thickness), which had a reinforcement welded to the top (Figure 5.1). A four pound sledge hammer was used to drive the pipe into the soil. After reaching a depth of 30 cm, the corer was removed from the soil and the sample was carefully emptied into a plastic bin. Mineral soil and forest floor sections of the sample were separated and packaged in labelled plastic bags. The pipe was then re-inserted into the hole to remove a sample from the 30 to 50 cm soil depth.

After returning to Vancouver samples were placed in cold storage at 2°C until processed. Samples were not frozen because this would have increased the difficulties in distinguishing live from dead fine roots during processing (K. Vogt, pers. comm.).

5.3.3 Sample Preparation

In the laboratory, samples were carefully rinsed with tap water over two nested sieves, the upper one with a 2 mm and the lower one with a 0.5 mm mesh size. After most fine sand and clay particles had been washed through the sieves, the contents of each sieve were emptied into shallow plastic trays. Organic materials were separated from the remaining coarse mineral material by carefully pouring off the water with the organic material. The organic material from the 2 mm sieve was then processed according to the criteria described below. The fine organic material from the 0.5 mm sieve consisted of plant components in various stages of decomposition, charcoal particles, and some fine root tips. Further processing of this material required the use of a dissecting microscope. The origin

of most organic fragments could not be identified clearly and processing was prohibitively time consuming. After initial trials it was decided not to sort this material, and the organic material in the 0.5 mm sieve was thereafter simply dried and weighed.

5.3.4 Decision criteria for the sorting of roots

At the outset of the study, roots were collected from a variety of species present on the study sites. A set of reference samples was established to assist in the subsequent identification of species. Fine and coarse roots and other organic material in the 2 mm mesh size sieve were hand sorted into 12 classes. Non-root organic material was discarded. During processing the root material was continuously immersed in water. Classified root segments were transferred into labelled plastic petri dishes containing deionized water.

Both live (CL) and dead (CD) coniferous roots were classified into four diameter classes (0-1 mm=CL0 or CD0; 1-2 mm=CL1 or CD1; 2-5 mm=CL2 or CD2; and > 5mm= CL3 or CD3). The 0-1 mm diameter class of both live and dead roots was further subdivided into fine roots with "clay" particles (probably a mixture of clay- and silt-sized particles) adhering to the surface (CL0-C and CD0-C, respectively) and those without. Soil particles embedded in the mycorrhizal mantle and in mycorrhizal clusters could not be removed but were accounted for by applying ash content correction factors (see below). Mycorrhizal hyphae and other fungal materials were classified in a separate category (M).

Non-coniferous roots (NC) were not separated into subclasses. The very small diameter of the roots of many herbaceous and shrub species did not permit

classification into live and dead roots. In retrospect, between-sample variation in this category could have been reduced by separating the larger diameter rhizomes of ferns (*Polystichum munitum, Pteridium aquilinum)*, which were found in some samples, from other non-coniferous roots.

The most difficult and time consuming task was the differentiation between live and dead coniferous fine roots. We employed criteria from the literature (Santantonio and Hermann 1985, Persson 1983), from personal communications with other researchers, and from our own observations. These criteria included colour, texture and tensile strength of the roots. When in doubt, iodine stain was used to test for the presence of starch granules. If starch was present roots were classified as living at the time of sampling. Details of the criteria are as follows.

COLOUR: The periderm of live coniferous roots is almost black, sometimes with some red. The secondary xylem is off-white. In contrast, the surface colour of dead roots is grayish. The secondary xylem is brownish to yellowish.

TEXTURE: Dead roots are brittle with a low tensile strength. Tensile strength was assessed subjectively and varied with root diameter. Pulling a live fine root apart using stainless steel tweezers causes a "snapping" sound which is much less audible in dead roots. The secondary phloem of dead roots separates readily from the secondary xylem and the root often shows a "distinct girdled pattern" of separated bark segments along the central cylinder. Dead roots often feel soggy or mushy and are not pliable.

FLOTATION: A root segment which floats on the surface is most likely dead. Only some of the dead roots float, however.

We placed great emphasis on a consistent application of the sorting criteria. Samples were often cross-checked by an experienced technician. New staff were

carefully trained and their work was closely monitored and re-examined. After some training, very consistent results were obtained by all technicians.

Processing times varied greatly depending on the characteristics of the samples. Forest floor samples, although of much smaller volume, tended to require more time than mineral soil samples. An average of approximately 8 hours per sample or about 24 hours per core was required for sorting. Additional time was required for drying, weighing, and, for a subset of samples, ash content determination.

When the processing of a sample was completed, roots were dried in a forced air oven at 70°C for 48 hours. Root samples were weighed to the nearest .001 gram. In total, 986 samples were processed: this involved the drying and weighing of about 8000 petri dishes with classified root material.

5.3.5 Ash content

Soil particles adhering to the surface of roots after careful rinsing and washing cannot be removed without loss of organic substance from the fine roots. If soil particles are included in the dry weights of roots, an overestimate of fine root biomass can occur. This error, which can be serious in fine textured soils, can be corrected by obtaining ash-free dry weights. Ovendry samples (redried at 70°C for 24 hours) were weighed into porcelain crucibles and heated to 470°C for 4 hours. Ash content was expressed as a percentage of ovendry weight.

5.3.6 Data processing and analyses

A computer program, developed for the conversion of root dry weights to ash-free dry weights, verified, for each of the approximately 8000 samples, whether or not the ash content had been determined. If this was the case, the sample's actual ash content was used for the conversion to an ash-free dry weight. Otherwise, the mean ash content for that sample's installation, horizon, and root class was used for the conversion. If this mean was based on less than 3 observations, the mean of the sample's root class and horizon based on all five installations was used.

The ash-free weights of the CL0 plus CL0-C and the CD0 plus CD0-C root classes were then added to obtain the ash-free dry weights of the live and dead roots in the 0-1 mm diameter classes, respectively. Two additional classes represent live and dead fine roots in the 0-2 mm diameter class. Root samples originated from three different soil layers: forest floor (1), 0-30 cm mineral soil (2), and 30-50 cm mineral soil (3). Three additional horizons were introduced which represent forest floor plus the upper mineral soil layer (4=1+2), the sum of the two mineral soil layers (5=2+3), and the sum of all three horizons (6=1+2+3).

The computer program calculated, for each of the 2700 sampling strata (5 Installations x 6 sampling dates x 6 horizons x 15 root classes), the mean, standard deviation, and standard error of the ash-free root dry weights. These results were printed to a tabulated output file and to a second output file which subsequently served as the input data file for the computation of fine root production and mortality.

5.3.7 Calculation of production and mortality estimates

An interactive computer program was developed to calculate fine root production and mortality estimates by applying three different computational methods to the data describing the seasonal dynamics of live and dead fine root biomass. The three methods are based on (1) the decision matrix (Fairley and Alexander 1985, McClaugherty *et al.* 1982), (2) all changes in live fine root biomass, and (3) significant changes in live fine root biomass.

DECISION MATRIX: The decision matrix (DM) presents a series of equations which calculate fine root production, mortality, and disappearance based on the observed changes in both live and dead fine root biomass. The decision as to which set of equations to apply for a given sampling interval is based on a matrix which describes all possible combinations of increases and decreases in live and dead fine root biomass (Figure 5.2).

The computer program calculates changes in live and dead fine root biomass between sampling dates and applies the appropriate set of equations for the computation of production and mortality estimates. The annual totals are based on the sum of the estimates obtained for each sampling interval.

ALL CHANGES: The second method, (AC), is based only on the observed changes in the live fine root biomass. All increases in live fine root biomass from one sampling date to the next represent production, and all decreases represent mortality. The sums of the estimates for all sampling periods constitute the annual totals.

SIGNIFICANT CHANGES: The third method (SC) is again based only on the observed changes in live fine root biomass, but in this method only significant changes in fine root biomass are attributed to production or mortality. The student

t-test (Zar 1984) is applied at $p \leq .05$ to successive means of live fine root biomass to test for statistical differences. If the means at t_i and t_{i+1} are not significantly different, the direction of change between the two means is determined. If this trend is continued from the mean at t_{i+1} to the mean at t_{i+2} then the means at t_i and t_{i+2} are tested for significant differences. If the direction of change reverses, the means at t_{i+1} and t_{i+2} are tested for significant difference. When two sample means are compared, the program first tests whether or not the two variances associated with the means are equal. If yes, the student t-test is applied, otherwise Welch's approximate t-test is applied (Zar 1984:131). The sum of all significant increases represents annual production and the sum of all significant decreases represents annual mortality.

The computer program was used to calculate fine root production and mortality for each of five root classes (0-2 mm, 0-1 mm, 1-2 mm, 2-5 mm, >5 mm) and for each of six horizons (see above) using the three computational methods. The program also calculates a number of additional statistics which facilitate the comparison of the different computational methods.

Fine roots in the three sampled soil horizons are experiencing different environmental conditions. Soil temperature and soil moisture amplitudes, for example, are greater in the forest floor than at 30-50 cm depth. It is therefore possible that fine roots in the three soil layers display different seasonal dynamics. Fine roots in the forest floor might stop growing or die due to soil moisture stress while others continue to grow at greater soil depth (Teskey and Hinkley 1981). Similarly, roots in the 0-1 mm diameter class may show seasonal dynamics that differ from those of the 1-2 mm diameter class.

For the computation of production and mortality rates, fine roots were divided into four different groups of populations (Table 5.3). Group I includes all

fine roots in the 0-2 mm diameter class in the FF-50 cm depth range. Group II separates the diameter classes 0-1 mm and 1-2 mm into two populations and treats the FF-50 cm soil profile as one layer. Group III separates the roots according to their soil layer of origin but does not separate the different diameter classes. Group IV treats the two root diameter classes separately in each of the three soil layers and therefore recognizes 6 individual populations. In each case, the annual estimates for production and mortality are the sum of the estimates for each population.

The ability to identify differences of the seasonal patterns in both the diameter classes and the soil layers increases from Group I to Group IV. This can be advantageous if, for example, a decrease in the biomass of the 0-1 mm diameter class in the forest floor occurs during the same interval as an increase in the 1-2 mm root biomass in the 30-50 cm layer. These opposing trends would not be detected if only one population is recognized (Group I). On the other hand, as the number of independent estimates increases from Group I to Group IV, so does the number of error terms associated with the estimates of the annual totals.

LIVE ROOT BIOMASS

DEAD ROOT BIOMASS	increase	decrease	
		$\Delta B_{dead} > \Delta B_{live}$	$\Delta B_{live} \geq \Delta B_{dead}$
increase	$P = \Delta B_{live} + \Delta B_{dead}$ $M = \Delta B_{dead}$	$P = \Delta B_{live} + \Delta B_{dead}$ $M = \Delta B_{dead}$	$P = 0$ $M = -\Delta B_{live}$
decrease	$P = \Delta B_{live}$ $M = 0$	$P = 0$ $M = -\Delta B_{live}$	

Figure 5.2 The decision matrix (Fairley and Alexander 1985), modified. The equations for estimating fine root production (P) and mortality (M) are selected on the basis of changes in live and dead fine root biomass (ΔB) during the interval between two sampling dates.

Table 5.3 The populations of fine roots are subdivided into one (0-2 mm) or 2 diameter classes (0-1 mm, 1-2 mm) and/or one (FF-50 cm) or 3 soil horizons (FF, 0-30 cm, 30-50 cm). Production and mortality estimates of fine roots for Groups I through IV are based on the sums of 1 to 6 individual estimates.

Group	Diameter classes	Soil horizons	Number of classes
I	1	1	1
II	2	1	2
III	1	3	3
IV	2	3	6

5.4 RESULTS AND DISCUSSION

5.4.1 Ash content of root samples

Ash contents of 2225 root samples in 195 strata (5 study sites x 3 horizons x 13 root classes) were determined. Table 5.4 presents means for the combined data from the five study sites for each of ten root classes and 3 horizons. Ash contents increased with depth in the soil and, with one exception, were higher for dead than for live roots in the same diameter class (Figure 5.3). Similar trends were reported by Vogt and Persson (in press) for *Abies amabilis* in Washington.

The roots in the 0-1 mm diameter class were divided into two categories: with and without "clay" particles adhering to the mycorrhizal clusters (see Section 5.3.4). Although only a small portion of the fine roots of most samples was classified as "with clay" (CL0-C, CD0-C), the data in Table 5.4 confirm the need for this extra category. The "with clay" classes had two to four times greater ash contents than the "without clay" classes. Failing to separate these two additional classes would have introduced considerable bias and increased the variability in the estimates of ash-free fine root dry weights.

5.4.2 Fine root biomass in May 1985

Seasonal patterns of live and dead fine root biomass will be described in the next section. The static comparison of live fine root biomass at the five study sites presented in this section is based on the values obtained in May 1985. In some cases these values differ considerably from the values in May 1986; this will be discussed later.

Total mean live root biomass and biomass in each of the three soil layers in May 1985 are shown in Table 5.5. Forest floor thickness (FFT) based on 20 measurements per plot is shown in the same table. Fine root biomass in the forest floor ranged from 23.6 g m^{-2} in Stand E to 212.3 g m^{-2} in Stand B, a nine-fold difference. The mineral soil layer to a depth of 30 cm (measured from the upper surface of the forest floor, Figure 5.1) contained the highest amount of fine roots, ranging from 109.9 to 436.6 g m^{-2}. The 30 to 50 cm mineral soil layer contained from 48.5 to 142.5 g m^{-2} fine roots. Total fine root biomass ranged from 182 g m^{-2} in Stand E to 791 g m^{-2} in Stand B, more than a four-fold difference.

The distribution of live fine roots among the 3 soil layers was approximately 1:2:1 for the forest floor : 0-30 cm : 30-50 cm layers (Table 5.6). Thirteen to 28% of all live fine roots to a depth of 50 cm were found in the forest floor. About 51% to 60% were present in the 0-30 cm mineral soil layer, and 20% to 27% were in the 30-50 cm soil layer. Mean forest floor thickness was less than 2 cm in all five study sites and fine roots were predominantly found at the interface of forest floor and mineral soil.

The importance of the upper soil layer and the forest floor becomes even clearer when fine root biomass is expressed on a per volume (g m^{-3}) rather than on a per area (g m^{-2}) basis (Table 5.6). Live fine root biomass (g m^{-3}) decreased from 11057 g m^{-3} in the forest floor to 713 g m^{-3} in the 30-50 cm layer in Stand B. In Stand E, the live fine root biomass ranged from 1934 g m^{-3} in the forest floor to 243 g m^{-3} in the 30-50 cm mineral soil layer.

Table 5.4 Mean and standard error of the mean (...) of ash content expressed as percent of sample dry weight for three horizons and ten root classes. Data represent mean values for the five study sites. n = sample size.

Root Class	Horizon					
	Forest floor		FF-30 cm		30-50 cm	
CL0 [1] 0-1 mm [2]	10.30	(0.58) n= 104	14.49	(0.50) n= 113	17.11	(0.79) n= 94
CL0-C 0-1 mm	44.39	(2.55) n= 35	44.74	(1.20) n= 96	43.56	(1.65) n= 63
CL1 1-2 mm	6.45	(0.72) n= 47	9.83	(0.55) n= 91	12.66	(0.75) n= 61
CL2 2-5 mm	4.28	(0.51) n= 15	10.51	(0.81) n= 59	12.68	(0.92) n= 41
CD0 0-1 mm	15.92	(0.86) n= 82	21.16	(0.78) n= 101	22.07	(0.88) n= 92
CD0-C 0-1 mm	49.31	(3.07) n= 20	53.54	(1.44) n= 73	53.29	(1.70) n= 47
CD1 1-2 mm	5.61	(1.21) n= 6	14.22	(1.23) n= 39	17.17	(1.37) n= 33
CD2 2-5 mm	9.61	(1.79) n= 5	14.65	(1.23) n= 39	21.99	(2.44) n= 17
NC	14.97	(1.47) n= 55	20.92	(1.35) n= 87	17.33	(1.25) n= 46
M	57.15	(2.41) n= 58	64.51	(1.92) n= 48	64.19	(4.69) n= 9

[1] C = coniferous, L = live, D = dead, NC = non-coniferous, M = fungal hyphae.
[2] diameter range.

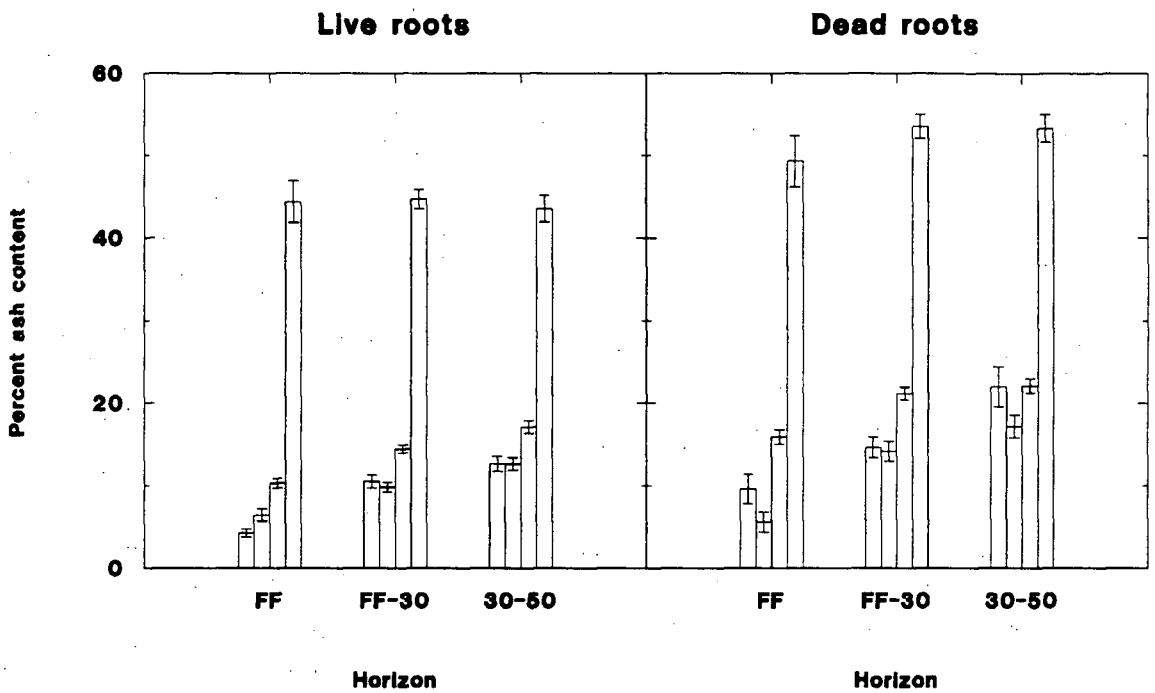

Figure 5.3 Mean and standard error of the mean of ash content expressed as percent of dry-weight for live and dead roots from three soil horizons and four diameter classes. In each horizon, bars from left to right represent diameter classes: 2-5 mm, 1-2 mm, 0-1 mm, and 0-1 mm with clay.

Table 5.5 Mean and standard error of the mean (...) of live fine (0-2 mm) root biomass in May 1985 at the five study sites. Mean and standard error of forest floor thickness (FFT) are based on 20 measurements taken in each stand. SI refers to the Site Index in meters at breast-height age 50, n = sample size.

Stand	SI (m@50)	FFT (mm)	Live fine root biomass ($g\ m^{-2}$)				
			n	FF	0-30 cm	30-50 cm	FF-50 cm
A	23.3	18.1 (1.0)	15	63.4 (16.7)	243.5 (49.1)	98.0 (23.9)	404.9 (80.7)
B	27.7	19.2 (2.5)	17	212.3 (24.8)	436.6 (44.1)	142.5 (23.2)	791.5 (56.2)
C	29.4	13.3 (1.2)	17	97.6 (17.5)	228.1 (31.2)	106.7 (20.0)	432.5 (42.5)
D	29.5	13.9 (1.3)	16	87.6 (24.8)	160.3 (24.5)	63.2 (12.8)	311.2 (43.3)
E	41.0	12.2 (1.1)	17	23.6 (11.7)	109.9 (12.8)	48.5 (14.9)	182.0 (17.6)

Table 5.6 Live fine root biomass in May 1985 in three horizons, expressed as a percentage of the total fine root biomass, and on a volume basis (g m^{-3}) for each of three horizons and the total profile to a depth of 50 cm.

	% of total			gram m^{-3}			
Stand	FF	0-30cm	30-50cm	FF	0-30cm	30-50cm	FF-50 cm
A	15.7	60.1	24.2	3503	864	490	810
B	26.8	55.2	18.0	11057	1555	713	1583
C	22.6	52.7	24.7	7338	796	534	865
D	28.1	51.5	20.3	6302	560	316	622
E	13.0	60.4	26.6	1934	382	243	364

5.4.3 Seasonal dynamics of fine roots

Seasonal dynamics of live and dead fine (0-2 mm) root biomass are reported here. The dynamics of small (2-5 mm) roots and of non-coniferous roots will be presented below. Roots greater than 5 mm in diameter were only occasionally present in the soil cores, and data on this root class will not be presented.

Seasonal dynamics of live and dead fine root biomass of all five study sites are shown in Figure 5.4. Figure 5.5 displays live and dead fine root biomass with standard errors for each stand individually. Live fine root biomass shows a very similar trend in all 5 study sites. It peaked in both the spring of 1985 and 1986 and was lowest at the early October or mid August sampling dates. From May to June (1985), live fine root biomass declined slightly in four study sites and increased slightly in Stand B. This was followed by a sharp decline at the August sampling date in all five stands. From August to early October, live fine biomass continued to decline in four stands and showed a small increase in Stand E. From the low in the fall, biomass increased again to the May 1986 sampling date.

We were able to process the samples for one additional sampling date (early February) for Stand E. The resulting data point suggests that most of the increase in live fine root biomass occurred from February to May, i.e. during the spring rather than during the winter months.

Dead fine root biomass also showed similar trends in all five stands (Figures 5.4 and 5.5). Values increased in Stands A, D, and E but decreased in Stands B and C from mid May to the end of June. In all stands, this was followed by a sharp increase to the August sampling date. For Stands A, D, and E, dead root biomass showed little change from August to October, but continued to increase during this period in Stands B and C. From October to May 1986 dead root biomass decreased in all five stands. The additional data point (February 1986) for Stand E suggests

that disappearance was greater from February to May than during the winter months.

Live and dead fine root biomass dynamics displayed a very symmetrical pattern (Figure 5.5). Most of the decreases in live fine root biomass were accompanied by increases in dead fine root biomass. When live fine root biomass increased, the dead biomass component decreased, presumably through decomposition.

Fine root mortality can be induced by moisture stress (Deans 1979). All five study sites experience a soil moisture deficit in a typical year. Figure 5.6 shows the 30 year average of mean monthly precipitation at Nanaimo Airport (Environment Canada 1982) and the actual monthly precipitation for 1985 and the first six months of 1986 (Environment Canada pers. comm.). The summer of 1985 was unusually dry, with below-average rainfall from May through August and no precipitation at all in July. Precipitation in October 1985 was well above the 30 year average at Nanaimo Airport, but this rainfall occurred after the sampling date in the first week of October.

Daily precipitation data were obtained from the Cowichan Lake Research Station, about 1 km from the location of Stand E. Figure 5.7 shows daily precipitation at the Research Station and live fine root biomass in Stand E. Only 16.8 mm of precipitation fell from June 24 to August 22, most of it on two consecutive days in early August. About 54 mm of precipitation occurred in early September, followed by another rain-free period of 21 days prior to the October sampling date.

These periods of extreme drought may explain why so few live fine roots were found at Stand E at both the August and the October sampling dates. This

rich lower slope stand receives seepage for most of the year (pers. observation), but the soil was very dry to a depth of 50 cm at the August and October 1985 sampling dates.

The seasonal dynamics of live and dead fine roots showed similar trends in the three soil layers which were sampled. The amplitude of the changes, however, differed between horizons. Figures 5.8 and 5.9 show fine root biomass for live and dead roots respectively, separated by horizon. The greatest change in fine root biomass occurred in the forest floor layer. The amplitude of the seasonal changes decreased with increasing depth in the soil for both live and dead fine root biomass.

The sum of live plus dead fine root biomass yields total biomass as shown in Figure 5.10. There is little seasonal change in the total fine root biomass of the five study sites, but considerable variation in the ratios of dead to live fine roots. This result confirms the importance of determining live and dead fine root biomass separately if production or mortality rates are to be derived from the data.

Ratios of live to dead fine root biomass varied greatly between stands and also between the May 1985 and May 1986 sampling dates. The ratios ranged from 2.0 to 3.6 in May 1985, decreased sharply (0.03 to 0.6) in the summer and increased again (0.8 to 2.0) in May 1986.

The differences in live and dead fine root biomass in May 1985 and May 1986 show that there is considerable between-year variation. Figure 5.11 shows live and dead fine root biomass expressed as a percentage of May 1985 values (=100%). In Stand A, the stand with the lowest site index, total fine root biomass was 12% lower in May 1986 than in May 1985. Live fine root biomass represented only 56% of the May 1985 value, while dead roots represented 163%. The drought of the summer 1985 was associated with a high mortality of fine roots. In May 1986, live fine root

biomass had not yet recovered and dead roots had not yet decreased to the May 1985 levels. Stand E, the site with the highest site index, showed a very different pattern. In May 1986, live, dead and total biomass were almost the same quantities as in May 1985 (95%, 97%, and 96%, respectively). The recovery of live fine root biomass occurred within seven months, mostly during the spring (Figure 5.5). In Stand B, live fine root biomass in May 1986 represented 103% of the May 1985 value, while the comparable value for dead fine root biomass was 171%. Live root biomass in stands C and D recovered to 84% and 67% of the 1985 values, respectively. Dead root biomass in the two stands represented 150% and 216% of the quantities in May 1985.

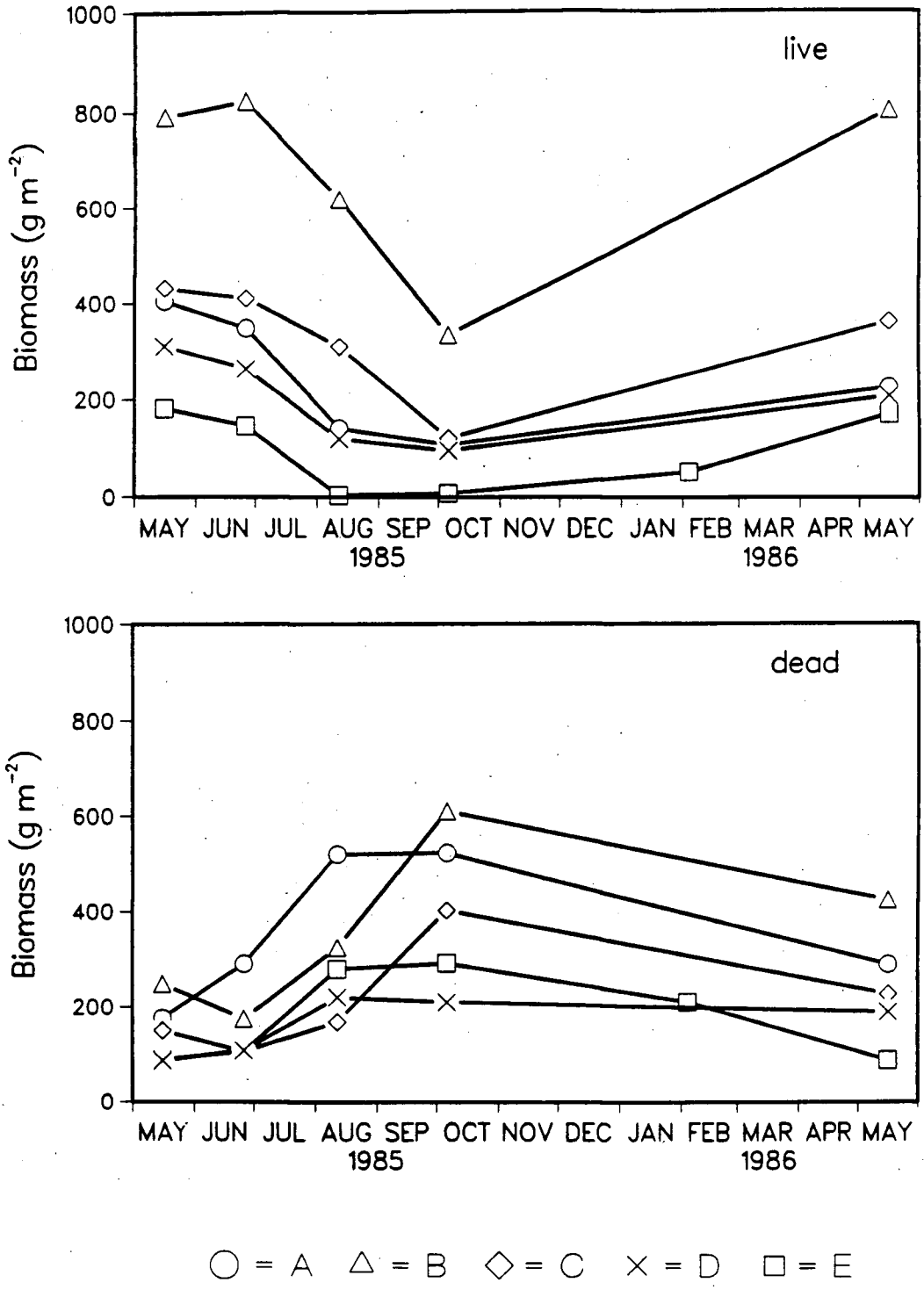

Figure 5.4 Seasonal dynamics of live (top) and dead (bottom) fine root biomass in the five stands. Data represent the mean of 10 samples per sampling date (15-17 for May 1985).

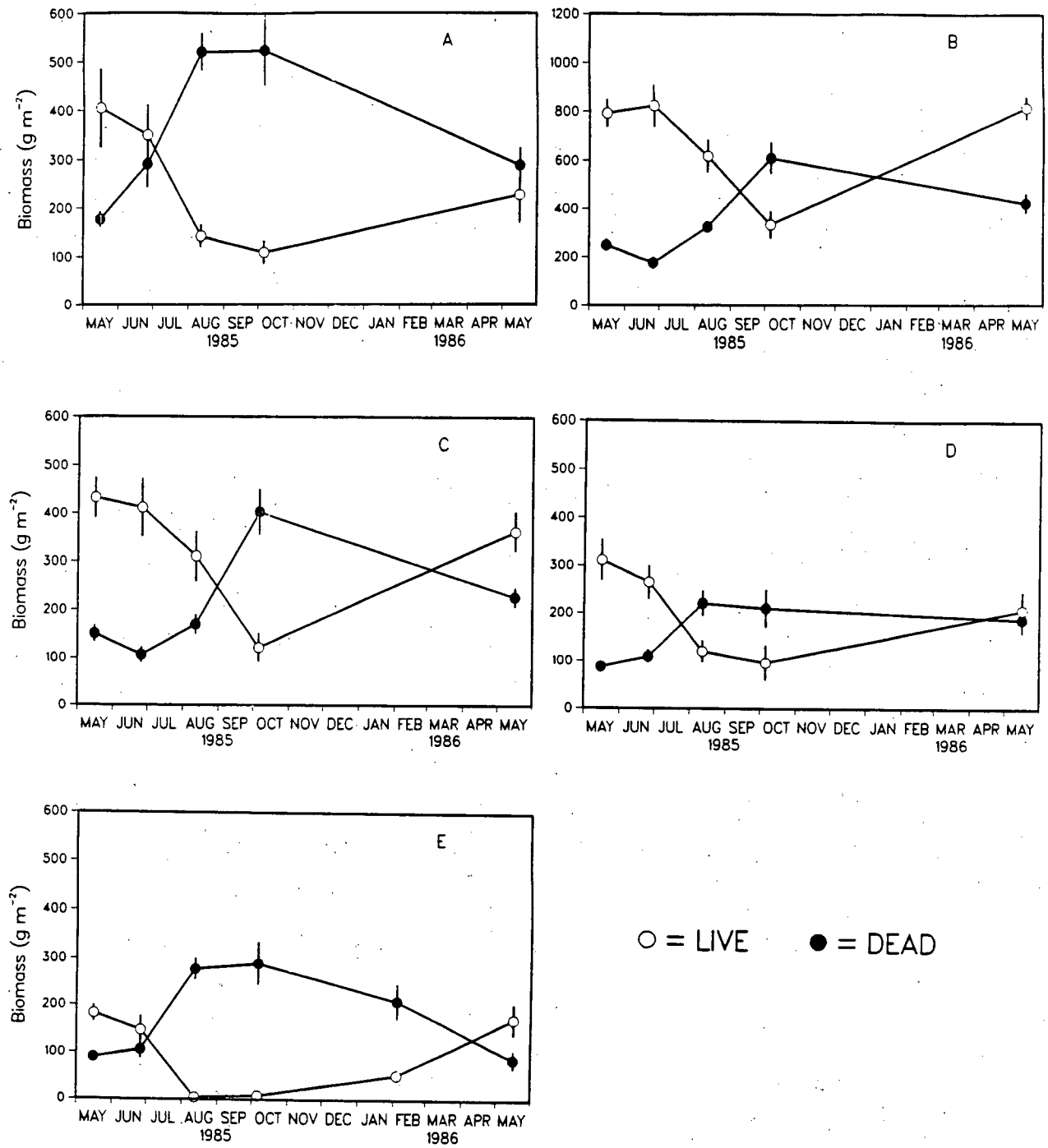

Figure 5.5 Seasonal dynamics of live and dead fine root biomass at each of the 5 Stands. Vertical bars represent ± 1 standard error.

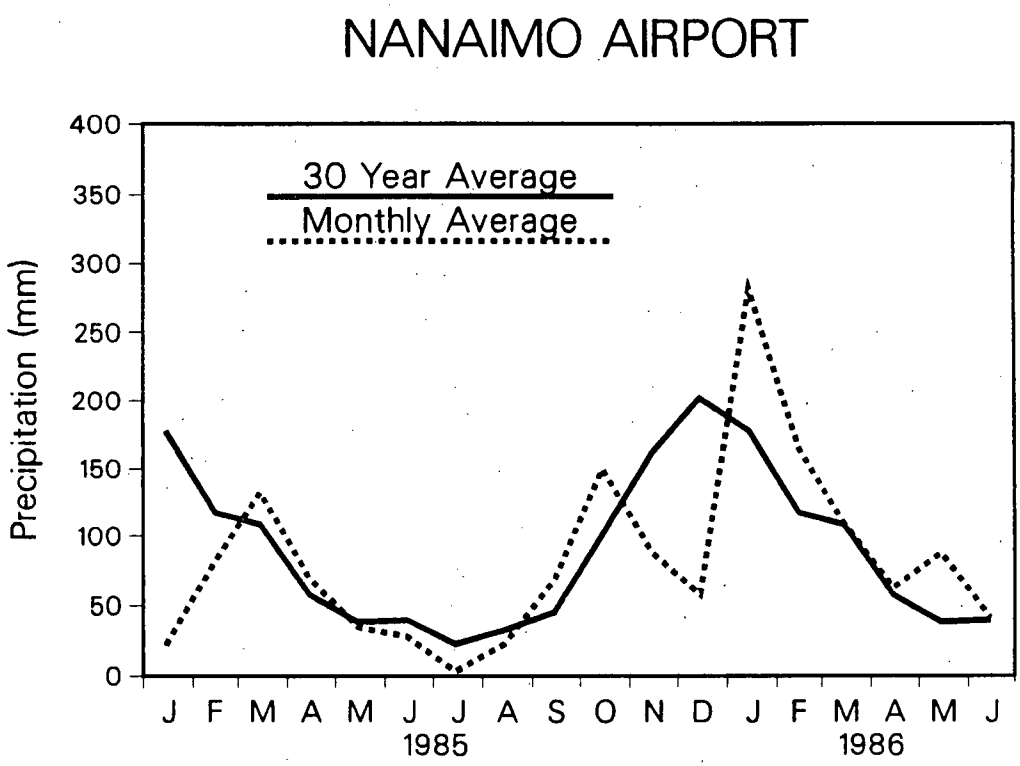

Figure 5.6 Mean monthly precipitation (30 year average) at Nanaimo Airport, and actual precipitation for 1985 and the first six months of 1986. (Environment Canada 1982 and pers. comm.)

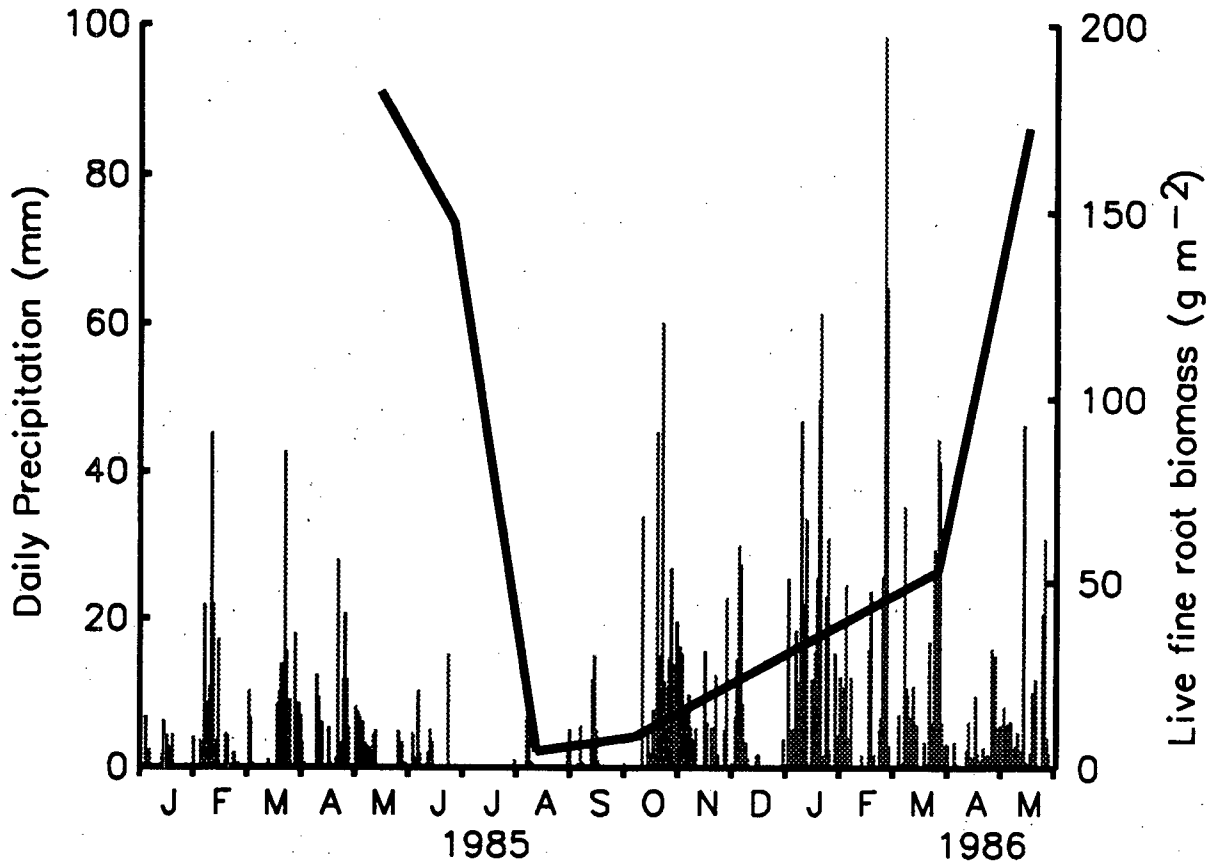

Figure 5.7 Daily precipitation at the Cowichan Lake Research Station for 1985 and the first six months of 1986, and the live fine root biomass at Stand E approximately 1 km from the climate station. (Precipitation data from B.C. Forest Service Cowichan Lake Research Station).

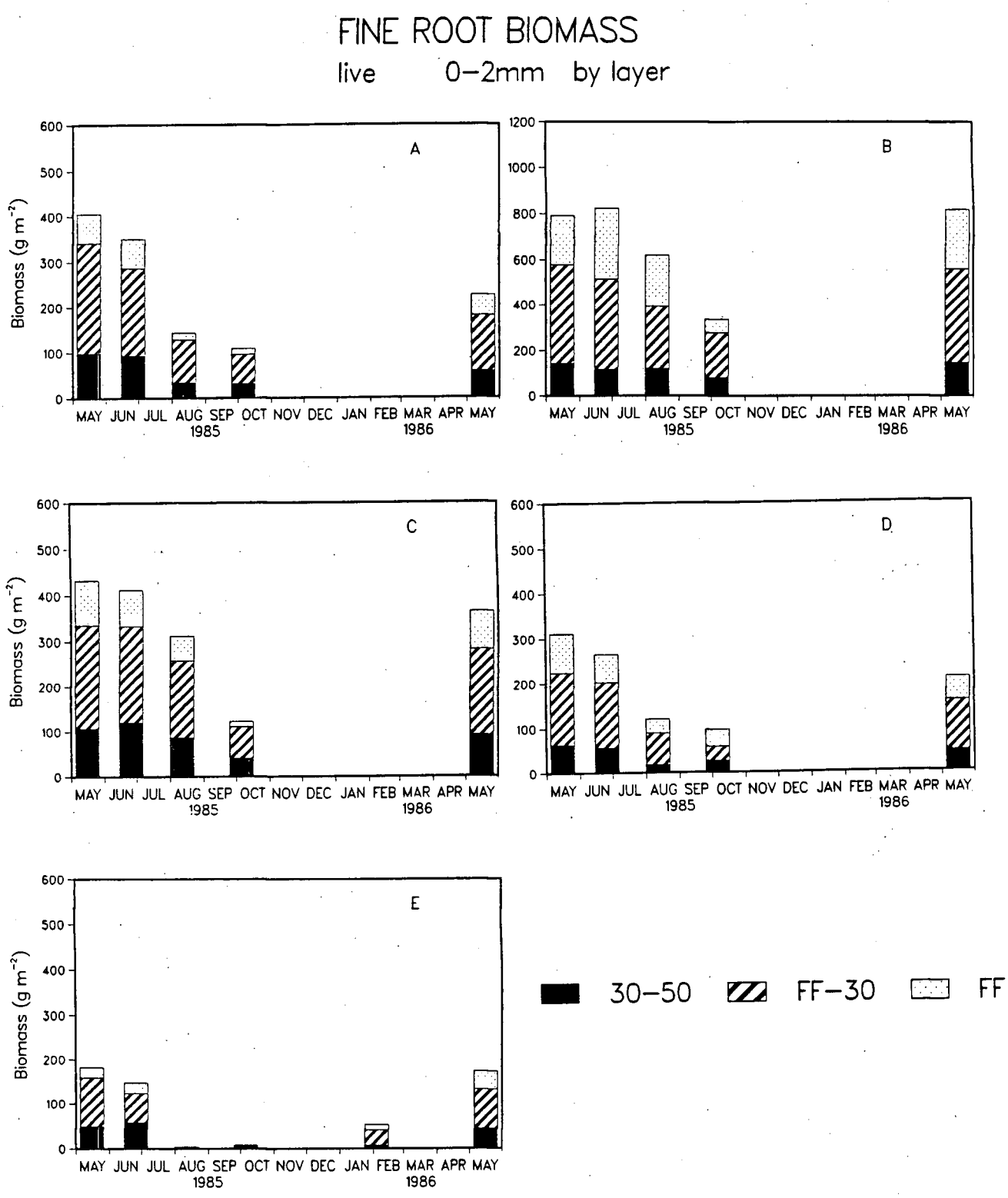

Figure 5.8 Live fine root biomass in three soil layers at each of the five study sites.

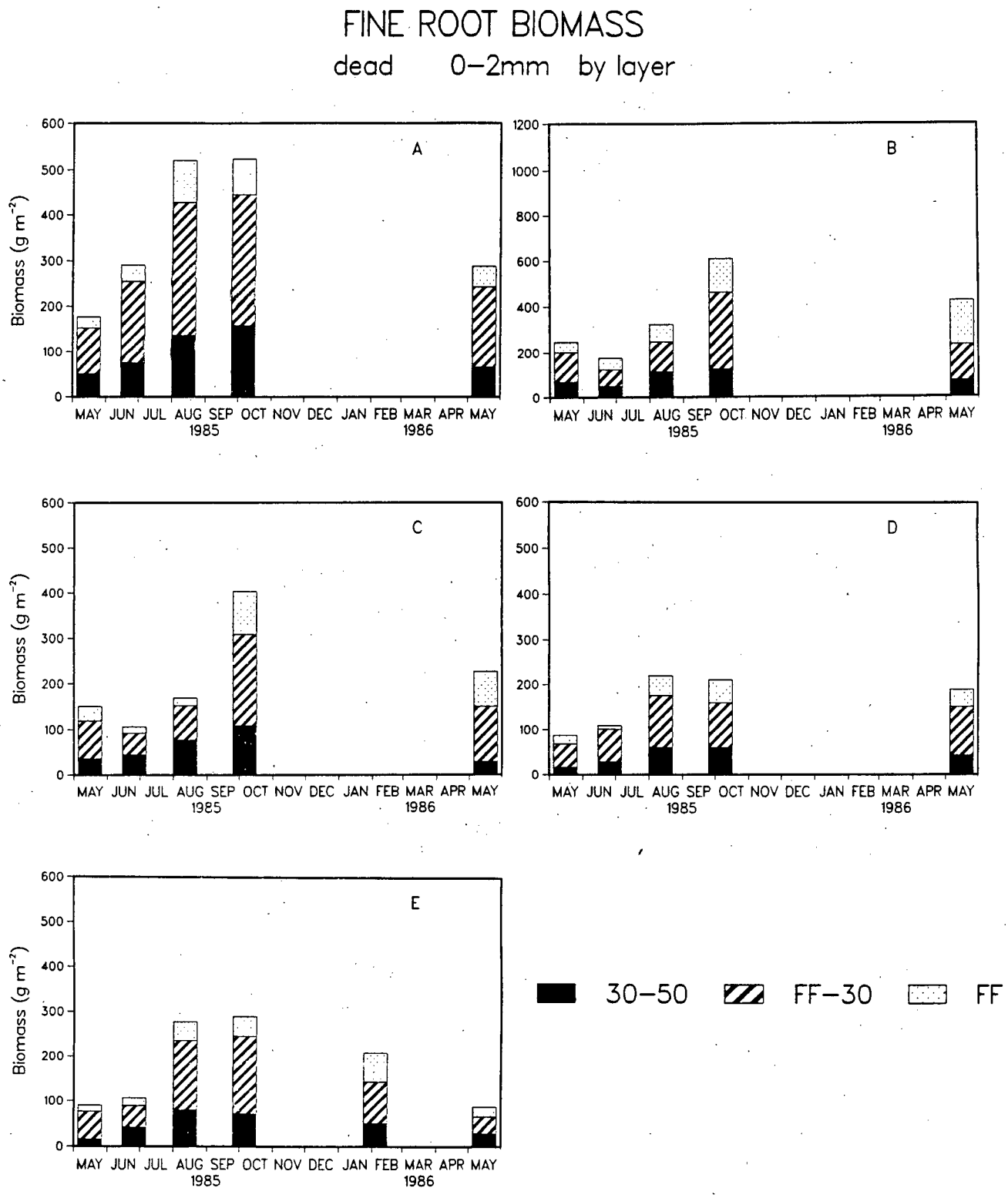

Figure 5.9 Dead fine root biomass in three soil layers at each of the five study sites.

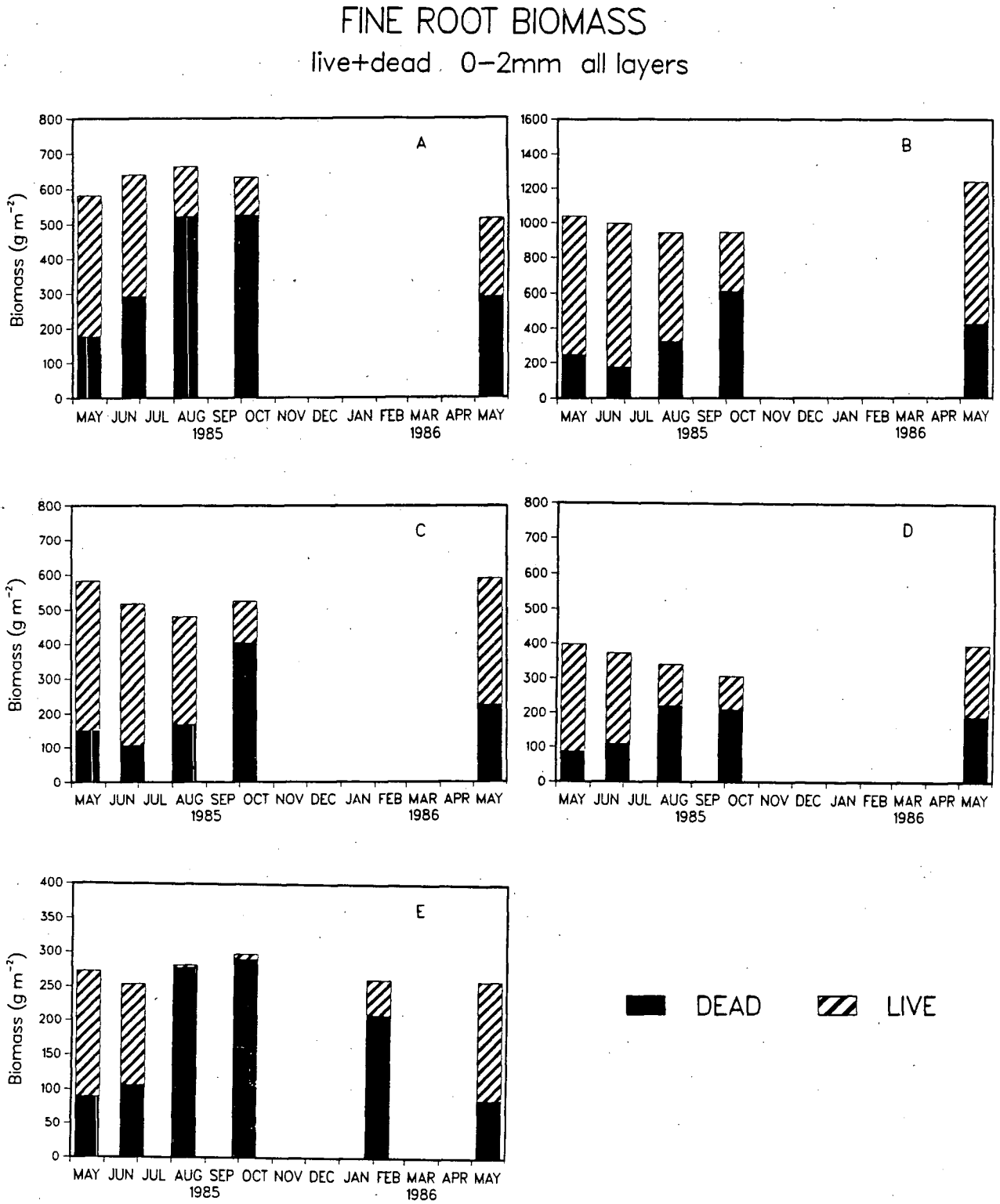

Figure 5.10 Total (live plus dead) fine root biomass at each of the five study sites.

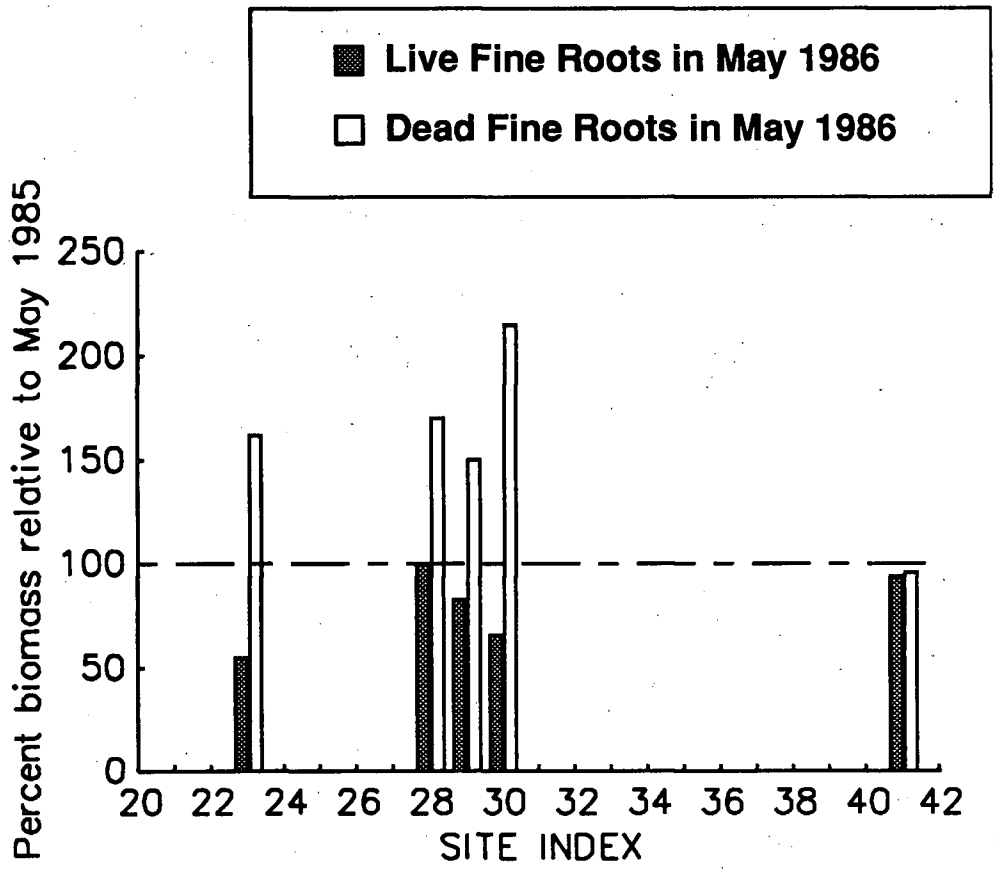

Figure 5.11 Live and dead fine root biomass in May 1986 expressed as a percentage of the May 1985 values.

5.4.4 Seasonal dynamics of small root biomass

Seasonal dynamics of live and dead small (2-5 mm) root biomass are shown in Figure 5.12 for all five stands. Live small roots showed a pattern similar to that of fine roots, with the annual maximum in May and the annual minimum in either August or October. Live small root biomass in May 1985 ranged from 410 g m^{-2} in Stand B to 60 g m^{-2} in Stand E. Intermediate values were observed in Stands A, C, and D with 108, 239, and 226 g m^{-2}, respectively (Table 5.7).

Results from the February sampling date, which was processed for Stand E only, suggest that most of the increase in live small roots occurred in the spring months, as was observed for the fine root component. Unlike the dead fine roots, however, most of the decrease in dead small roots in Stand E occurred from October to February.

The symmetry which was observed in the pattern of live and dead fine root biomass (i.e. decrease in live roots accompanied by an increase in dead roots) is not evident in the small root component. Stands A through E show a decrease in both live and dead small root biomass from May to June 1985. The observed high value for dead small root biomass in October in Stand E is somewhat surprising, because none of the 3 preceding sampling dates indicated that such a quantity of live small roots was present. Live small root biomass in May 1985 was lower than in May 1985 in 4 of the 5 stands. Only Stand E was able to re-establish its small root biomass to the previous year's level.

Table 5.7 Mean and standard error of the mean (...) of live small (2-5 mm) root biomass in May 1985 at the five study sites. Mean and standard error of forest floor thickness (FFT) are based on 20 measurements taken in each stand. SI refers to the Site Index in meters at breast-height age 50, n = sample size.

Stand	SI (m@50)	FFT (mm)	Live small root biomass ($g\ m^{-2}$)				
			n	FF	0-30 cm	30-50 cm	FF-50 cm
A	23.3	18.1 (1.0)	15	19.48 (19.48)	139.84 (38.93)	79.88 (25.56)	239.21 (52.26)
B	27.7	19.2 (2.5)	17	35.56 (15.07)	216.85 (45.48)	157.53 (78.96)	409.94 (89.23)
C	29.4	13.3 (1.2)	17	12.74 (8.60)	143.72 (65.56)	69.66 (36.75)	226.12 (67.97)
D	29.5	13.9 (1.3)	16	9.53 (7.46)	85.98 (31.47)	12.84 (10.27)	108.35 (30.97)
E	41.0	12.2 (1.1)	17	8.59 (8.59)	22.69 (11.03)	28.40 (15.57)	59.67 (24.50)

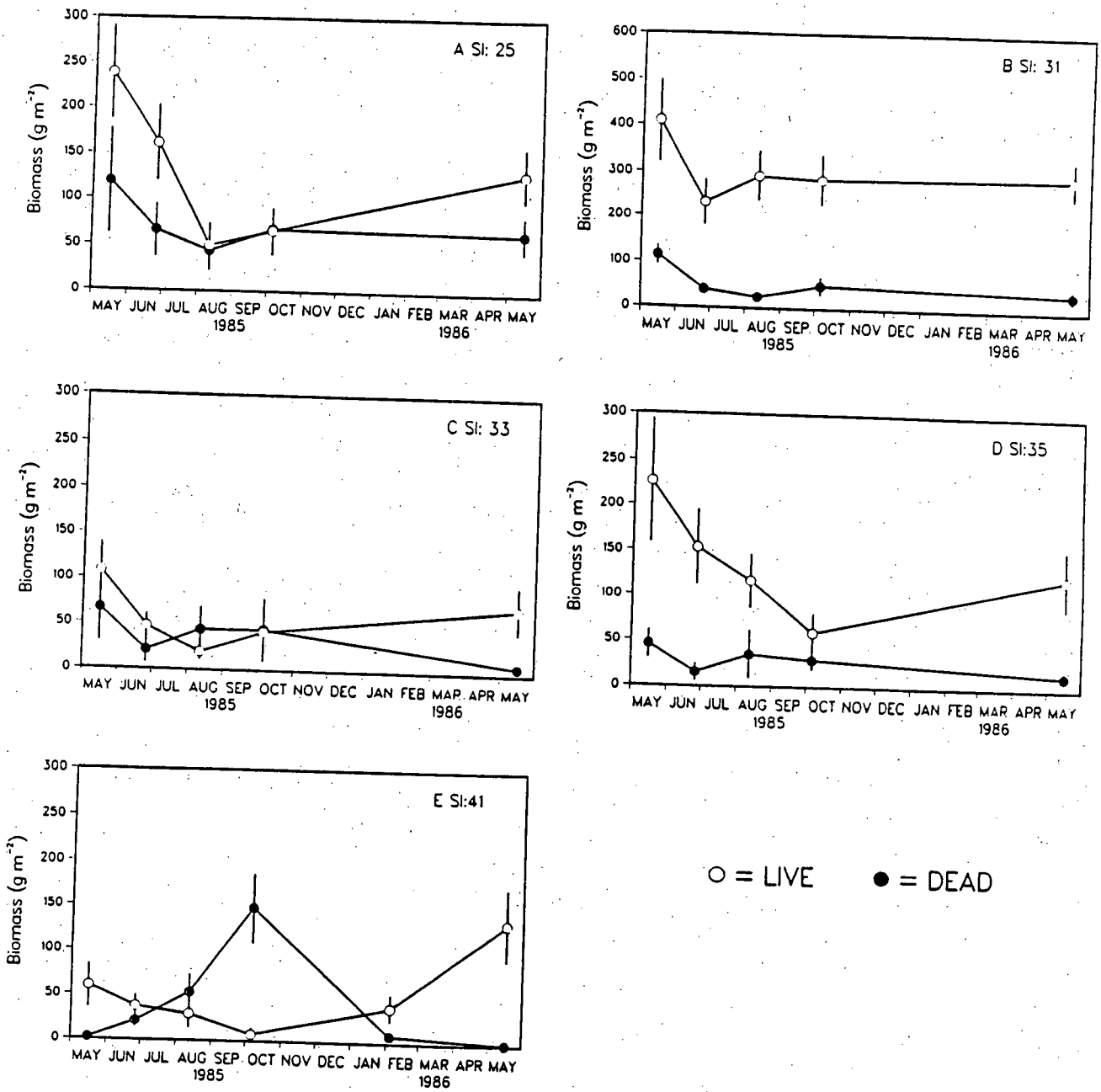

Figure 5.12 Seasonal dynamics of live and dead small root biomass for each of the five stands. Vertical bars represent ±1 one standard error.

5.4.5 Non-coniferous root biomass

This category includes both live and dead roots of all diameter classes. Non-coniferous roots belonged to understory species, with a single exception: Stand E contained one bigleaf maple (*Acer macrophyllum* Pursh). Most of the non-coniferous roots were in the 0-2 mm diameter range. Larger diameters were encountered when salal and fern rhizomes were found in a sample.

The seasonal dynamics of non-coniferous roots are more pronounced than the dynamics of the live plus dead coniferous fine root component (Figure 5.13). As with coniferous roots, there were large differences in biomass between stands. The maximum non-coniferous biomass was encountered during different sampling months in the five study sites. Root biomass of the understory vegetation of Stand B, which consisted of dense salal and mahonia, peaked during August 1985. Stand C, which has fairly sparse understory vegetation, had the lowest amount of non-coniferous root biomass throughout most of the year.

5.4.6 Fine and Small Root Production

5.4.6.1 Calculating production and mortality estimates

Estimates of fine root production and mortality are commonly derived from observed seasonal changes in live and dead fine root biomass (Moir and Bachelard 1969, Santantonio and Hermann 1985, Vogt *et al.* 1980). Such estimates require two assumptions. First, it must be assumed that each observed change in live root biomass during a sampling interval was solely due to either production or mortality and that the two processes did not occur simultaneously (cf. Kurz and Kimmins 1987). This assumption is probably not fully satisfied in this study, particularly

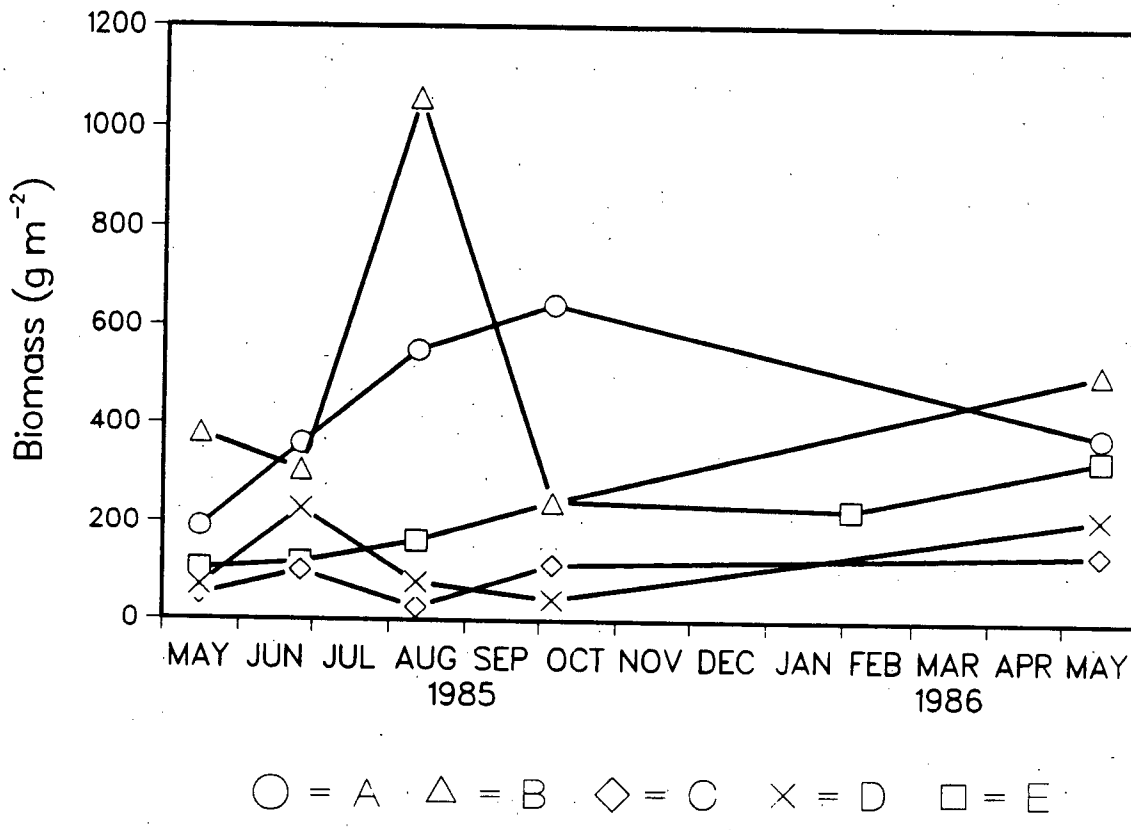

Figure 5.13 Seasonal dynamics of non-coniferous root biomass in the five study sites.

during the period from October 1985 to May 1986. The second assumption is that no additional peak or trough in either live or dead root biomass occurred between the sampling dates. This assumption is particularly critical for the fall and winter months from October to May. The October samples were taken only a few days before the fall rains started (Figure 5.7). If fine root mortality is correlated with soil moisture stress, we probably sampled at or close to the point at which live fine root biomass was at its annual low. Although samples had been collected in November, February, and March for all five study sites, we were unable to process those samples due to time and financial constraints. We managed to process the February samples for Stand E, and, as discussed above, the results support the assumption that no additional peaks in either live or dead fine root biomass occurred. Violating either of these two assumptions yields underestimates of the actual production and mortality rates (Kurz and Kimmins 1987). Thus, the estimates reported below are probably conservative.

Separating fine roots into several populations according to their diameter class and soil horizon had different effects on production and mortality estimates depending on the computational method which was applied. For a comparison of the results, estimates obtained for Group I were used as reference (100%) and estimates of the remaining three Groups were expressed as a percentage of the Group I estimate. Table 5.8 shows a comparison of the mean production and mortality estimates and their standard deviations based on the results of the 5 stands.

Production and mortality estimates averaged for the five stands and calculated with the decision matrix increased as a result of the separation of fine roots into different populations. Mean production estimates for Groups II, III, and IV were 31.8%, 23.0% and 54.8% above the Group I estimate, respectively (Table

5.8). Production and mortality estimates calculated from all observed changes in live fine root biomass were less affected by the separation of roots into different populations. Mean production estimates for Group II, III, and IV were 6.0%, 6.4% and 20.2% above those of Group I. For some stands, no change was observed and a 1% decrease was obtained once. The separation of fine roots into different populations caused a reduction in production estimates if these were based on only significant changes in live fine root biomass. The mean production estimates were 12.6%, 4.2% and 21.4% below the Group I estimate for Groups II, III, and IV, respectively. These, however, are average responses for the five stands.

For individual stands, production estimates ranged from 20% above to 72% below the Group I estimate. Mortality estimates based on significant changes in live fine root biomass were much less affected by the separation of fine roots into groups. Estimates obtained from the SC computational method are smaller because some of the observed seasonal changes in individual populations were not statistically significant. The increase in fine root biomass from the low in the summer of 1985 to the high in the spring of 1986 in stand A, for example, was not significant if the roots were separated into 2 diameter and/or 3 soil layer classes.

The largest differences for each of the three computational methods were between Groups I and IV. Group I yielded the most conservative estimates for the DM and AC computational methods, but it resulted in the highest estimates for the SC computational method. Estimates based on six individual populations (Group IV) require larger sample sizes to statistically assess the observed seasonal trends in each population. Treating fine roots in both diameter classes and all three soil layers as one population (Group I) can mask opposing trends in seasonal biomass changes of individual populations. This approach has been widely used in fine root production studies, however, and will also be used in this study.

Table 5.8 The effects of separating fine roots into populations according to diameter and/or soil layer (Groups I-VI) on estimates of production and mortality. Results obtained from three different computational methods are expressed as a percentage of Group I estimates and reported as means and standard deviations (...) of five plots.

Group[1]	Decision Matrix		All Changes		Significant Changes (p>0.05)	
PRODUCTION						
I	100.0		100.0		100.0	
II	131.8	(20.8)	106.0	(6.8)	87.4	(34.8)
III	123.0	(23.7)	106.4	(7.5)	95.8	(5.8)
IV	154.8	(23.3)	120.2	(17.9)	78.6	(32.9)
MORTALITY						
I	100.0		100.0		100.0	
II	113.8	(11.0)	103.2	(3.1)	103.2	(3.1)
III	127.2	(23.0)	104.8	(6.1)	100.0.6	(5.6)
IV	140.0	(15.4)	111.8	(8.1)	101.4	(8.9)

[1] Refer to Table 5.3 for an explanation of groups.

5.4.6.2 Fine root production and mortality estimates

Fine root production and mortality estimates based on three different computational methods for each of the five stands are reported in Table 5.9. All estimates are based on ash-free dry weights and are reported in g m^{-2}, which can be converted to Mg ha^{-1} (i.e. t ha^{-1}) by dividing the g m^{-2} values by 100.

For a comparison of the effects of the three computational methods, the same estimates have also been expressed as a percentage of the estimate obtained from the SC computational method (Table 5.10).

Production estimates, obtained from the AC and the SC methods, were identical with one exception: in Stand B the AC method calculated 6.4% more production than the SC method. Estimates based on the decision matrix were on average 23.6% higher than the estimates obtained from the SC method. Mortality estimates based on both the AC or the SC method were identical, while these based on the decision matrix were on average 13.1% higher.

As discussed in the preceding section, separation of fine roots into different populations according to diameter class and soil layer (Table 5.3) has different effects on production and mortality estimates depending on the computational method used. Consequently, the statement that the AC and SC computational methods yielded similar estimates cannot be generalized. Differences between the AC and SC methods were small in this study because the sampling frequency was low. The sampling intervals were large enough to show a clear seasonal trend with significant differences between the peaks and troughs in live and dead fine root biomass.

The estimates of annual production and mortality of fine roots differed between stands (Table 5.9, Figure 5.14). Production in Stand B was 481 g m^{-2} and

514 g m^{-2} based on the SC and DM method, respectively. This was over four times higher than in Stand D, which had a production of 112 g m^{-2} for all computational methods.

Based on the DM computational method, the stands with the lowest (Stand A) and highest (Stand E) site index had 199 g m^{-2} and 208 g m^{-2} of fine root production. The SC computational method yielded lower estimates and showed larger differences between the two stands: 118 g m^{-2} and 168 g m^{-2} for Stands A and E, respectively. Production estimates for Stand C were the second highest and ranged from 287 g m^{-2} for the DM method to 242 g m^{-2} for the SC method.

Estimates of annual fine root mortality also differed between the five stands, but they covered a narrower range than the production estimates. Based on the DM method, mortality estimates are lowest for stands D and E: 215 g m^{-2} and 218 g m^{-2}, respectively. The SC method calculated the lowest mortality estimates for Stand E (178 g m^{-2}) and yielded the second lowest estimate for Stand D (215 g m^{-2}). The highest mortality estimates, obtained for Stand B, range from 490 g m^{-2} to 487 g m^{-2} for the DM and SC method, respectively.

Figure 5.14 presents a comparison of fine root production and mortality estimates for each stand. Only in Stands B and E were the two estimates approximately equal. Mortality estimates in Stands A and D were approximately double the production estimates. In Stand C, production represented about 80% of mortality. These differences between production and mortality estimates are explained by the lower fine root biomass in May 1986 compared to that in May 1985 (Figure 5.11). This may nave been due to the heavy mortality which occurred during the unusually dry summer of 1985 and the inability of some stands to re-establish the fine root biomass by the following spring.

Table 5.9 Annual fine root production and mortality (g m^{-2} yr^{-1}) for the five stands calculated with three computational methods: decision matrix (DM), all changes (AC) and significant changes (SC). All fine roots (0-2mm diameter, FF-50 cm depth) are treated as one population.

Stand	SI (m@50)	Production			Mortality		
		DM	AC	SC	DM	AC	SC
		(g m^{-2} yr^{-1})			(g m^{-2} yr^{-1})		
A	23.3	199.5	118.2	118.2	377.7	296.4	296.4
B	27.7	514.3	511.9	481.1	489.5	487.1	487.1
C	29.4	286.6	241.8	241.8	355.6	310.7	310.7
D	29.5	112.1	112.1	112.1	214.8	214.8	214.8
E	41.0	207.9	168.2	168.2	217.7	178.0	178.0

Table 5.10 Annual fine root production and mortality for the five stands expressed as a percentage of the estimates obtained from the SC computational method.

Stand	SI (m@50)	Production			Mortality		
		DM	AC (% of SC)	SC	DM	AC (% of SC)	SC
A	23.3	168.6	100.0	100.0	127.7	100.0	100.0
B	27.7	106.9	106.4	100.0	100.6	100.0	100.0
C	29.4	118.6	100.0	100.0	114.5	100.0	100.0
D	29.5	100.0	100.0	100.0	100.0	100.0	100.0
E	41.0	123.8	100.0	100.0	122.5	100.0	100.0
Mean		123.6	101.3	100.0	113.1	100.0	100.0
S.D.		(26.9)	(2.9)		(12.6)		

5.4.6.3 Small root production and mortality estimates

As was observed with fine roots, estimates of small root production and mortality differ between stands and are affected by the computational method used. Small root production calculated by the DM method ranged from 50.7 to 222.3 g m^{-2} (Table 5.11). The high production estimate for stand E is largely due to the increase in dead root biomass from August to October 1985 (Figure 5.12). The other two computational methods consider only changes in live small root biomass and yield identical production estimates of 125.9 g m^{-2}. In Stands B and C, the SC method yields zero production estimates because the observed increases in small root biomass were not statistically significant (p=0.05).

Mortality estimates ranged from 88.5 to 212.0 g m^{-2} for the DM computational method. The two other methods both resulted in a range of mortality estimates from 52.2 to 189.6 g m^{-2}. With the exception of Stand E, mortality estimates were always higher than production estimates (Figure 5.15). The differences between the three computational methods were generally small with the exception of the two zero production estimates (Stands B and C) obtained from the SC method, and the high production estimate obtained from the DM method in Stand E (Figure 5.15).

Table 5.11 Annual small root production and mortality (g m^{-2} yr^{-1}) for the five stands calculated using three computational methods. DM = decision matrix, AC = all changes, and SC = significant changes.

Stand	SI (m@50)	Production			Mortality		
		DM	AC (g m^{-2} yr^{-1})	SC	DM	AC (g m^{-2} yr^{-1})	SC
A	23.3	105.0	81.7	81.7	212.9	189.6	189.6
B	27.7	84.7	66.1	0.0	203.7	185.0	177.3
C	29.4	61.9	61.9	0.0	166.7	166.7	166.7
D	29.5	50.7	50.5	50.5	88.5	88.4	88.4
E	41.0	222.3	125.9	125.9	148.6	52.2	52.2

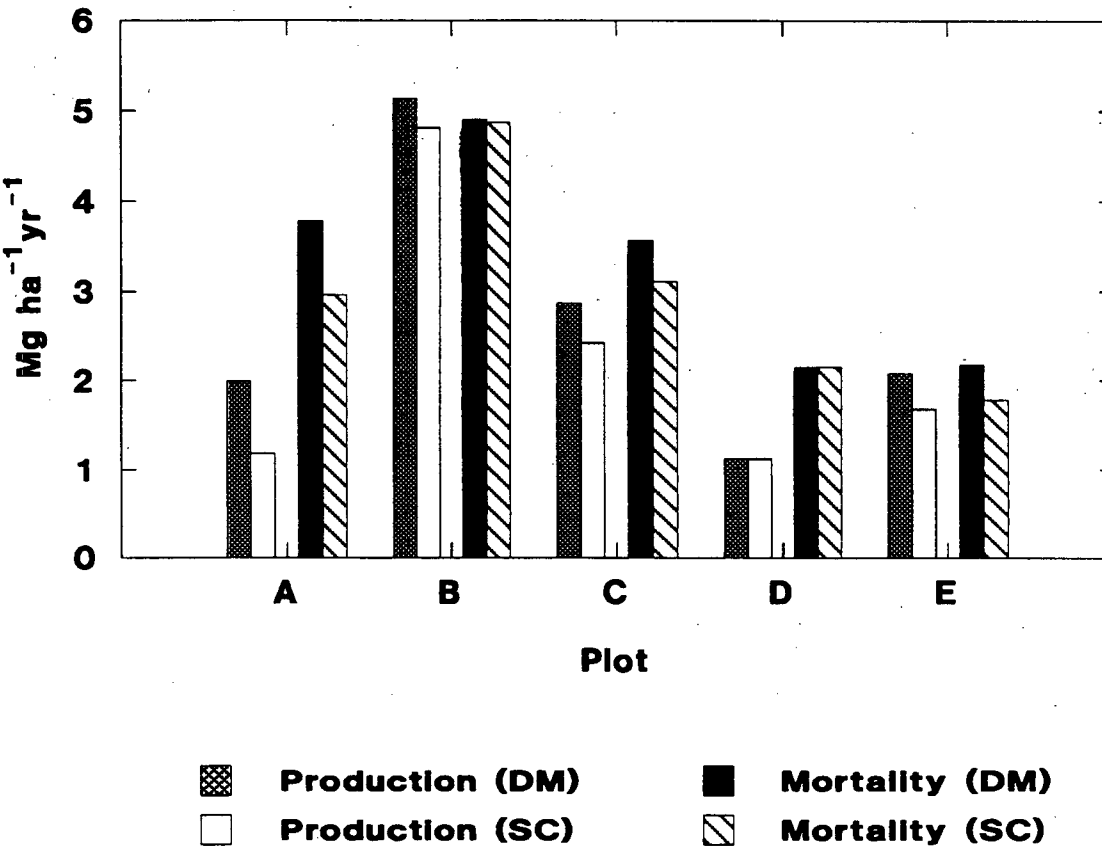

Figure 5.14 Estimates of fine root production and mortality for five plots based on the Decision Matrix and Significant Changes methods. Bars within each plot, from left to right, represent production (DM), production (SC), mortality (DM), and mortality (SC).

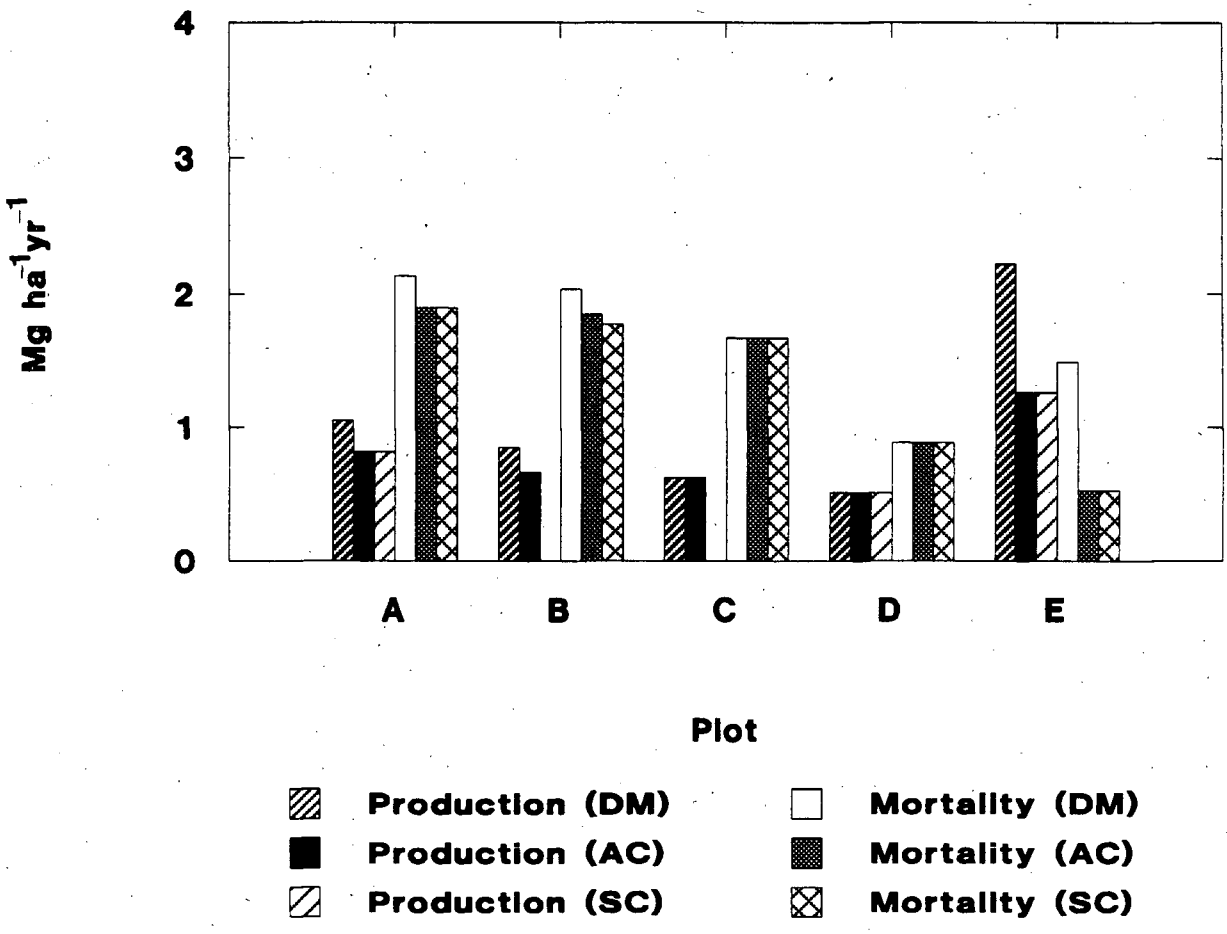

Figure 5.15 Estimates of small root production and mortality for five plots based on the Decision Matrix and Significant Changes methods. Bars for each stand represent, from left to right, production DM-, AC-, and SC-methods and mortality DM-, AC-, and SC-methods.

5.4.6.4 Turnover rates of fine and small roots

Both production and mortality rates of roots are a measure of turnover, and, therefore, two sets of turnover rates are calculated based on the ratios of production to root biomass and of mortality to root biomass in May 1985. As discussed above, the estimates of annual root production and annual mortality differ in some stands. These differences are also apparent in the calculated turnover rates of fine (Table 5.12) and small (Table 5.13) roots.

Turnover rates of fine roots based on production range from 0.36 to 1.14 $year^{-1}$ for production estimates calculated using the DM method and from 0.29 to 0.92 $year^{-1}$ for production estimates based on the AC or SC method. Between-stand differences for turnover rates based on mortality estimates are smaller and range from 0.62 to 1.20 $year^{-1}$ for DM-derived estimates and from 0.62 to 0.98 $year^{-1}$ for AC- or SC-derived estimates.

Mean life span is calculated as the inverse of turnover rates. Figure 5.16 shows mean life span of fine roots in the 5 stands based on both production and mortality estimates. Mean life span ranges from 0.83 to 3.43 years.

Table 5.12 and Figure 5.16 show that stand E, the site with the highest site index, has the highest turnover rate and consequently the shortest fine root lifespan. While there is some debate in the literature as to whether a more nutrient (specifically nitrogen) rich site has higher or lower turnover rates than a poorer site, it is not clear that the results obtained in this study can support either argument. The unusually long summer drought of 1985 led to about 100% mortality of fine roots in Stand E, whereas in the other stands, a smaller proportion of the live fine roots died. The differences in turnover rates are therefore primarily drought induced and are probably less related to nutrient availability.

Table 5.12 Turnover rates ($year^{-1}$) of fine roots calculated as the ratios of annual fine root production / fine root biomass in May 1985 and annual fine root mortality / fine root biomass in May 1985. Production and mortality estimates are based on three computational methods which are described in the text.

Plot	Biomass May 85 ($g\ m^{-2}$)	Production/biomass			Mortality/biomass		
		DM	AC ($year^{-1}$)	SC	DM	AC ($year^{-1}$)	SC
A	404.9	0.49	0.29	0.29	0.93	0.73	0.73
B	791.5	0.65	0.65	0.61	0.62	0.62	0.62
C	432.5	0.66	0.56	0.56	0.82	0.72	0.72
D	311.2	0.36	0.36	0.36	0.69	0.69	0.69
E	182.0	1.14	0.92	0.92	1.20	0.98	0.98

Table 5.13 Turnover rates ($year^{-1}$) of small roots calculated as the ratios of annual small root production / small root biomass in May 1985 and annual small root mortality / small root biomass in May 1985. Production and mortality estimates are based on three computational methods which are described in the text.

Plot	Biomass May 85 ($g\ m^{-2}$)	Production/biomass			Mortality/biomass		
		DM	AC ($year^{-1}$)	SC	DM	AC ($year^{-1}$)	SC
A	239.2	0.44	0.34	0.34	0.89	0.79	0.79
B	409.9	0.21	0.16	0.00	0.50	0.45	0.43
C	226.1	0.27	0.27	0.00	0.74	0.74	0.74
D	108.3	0.47	0.47	0.47	0.82	0.82	0.82
E	59.7	3.72	2.11	2.11	2.49	0.87	0.87

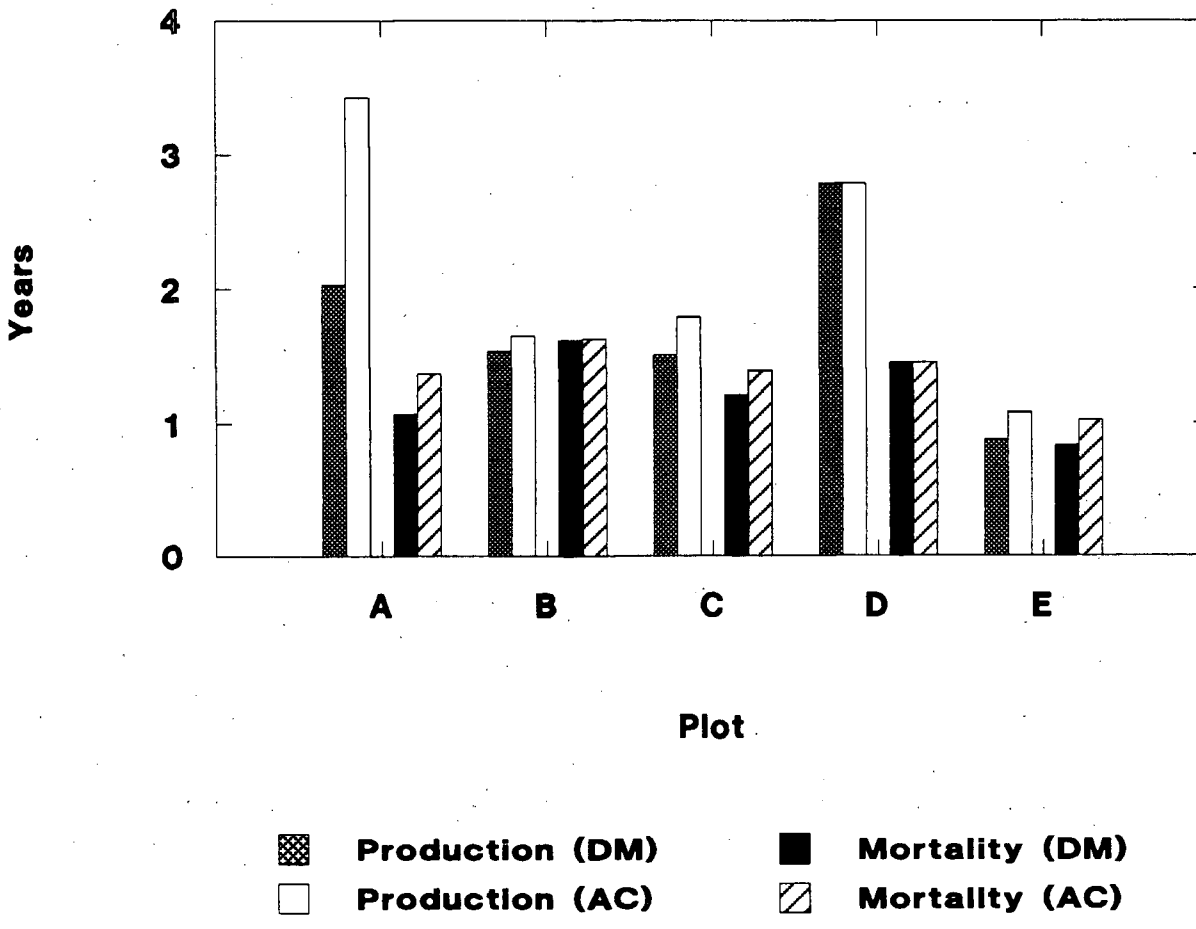

Figure 5.16 Fine root mean life span for 5 plots based on produciton and mortality estimates obtained with two computaional methods. Bars within each plot, from left to right, represent mean life span calculated from estimates of production (DM), production (SC), mortality (DM), and mortality (SC).

Small root turnover rates, derived from production estimates, cover a much wider range than those of fine roots (Table 5.13). Extreme values are 0 $year^{-1}$, for the two stands in which the SC method calculated zero production, and 2.1 to 3.7 $year^{-1}$ for Stand E, for which the highest turnover rates are calculated by all three methods. Turnover rates for other stands or methods fall in the range 0.16 to 0.47 $year^{-1}$. Mortality-based turnover rates range from 0.43 to 0.89 $year^{-1}$, with one additional very high value of 2.5 $year^{-1}$ (Stand E, DM-method). The much higher estimates of turnover rates of small roots in Stand E are probably a consequence of sample variation rather than real turnover rates, because they are two to three times higher than the turnover estimates obtained for fine roots in the same stand. Furthermore, such high turnover rates would imply a mean life span of only 4 to 6 months for roots that are 2 to 5 mm in diameter. Roots of such diameters had to undergo secondary thickening and often have growth rings indicating that the roots have lived through more than one growing season.

5.4.6.5 Site quality and fine and small root production

Many factors determine the "quality" of a site and there has been much discussion in the literature about an appropriate measure of site quality (Hägglund 1981). In this study, site quality is expressed as site index (meters at breast-height age 50) (Bruce 1981, Mitchell and Polsson 1988). Several approaches can be taken to obtain estimates of fine root production and to date there appears to be no agreed-upon method of determining fine root production, mortality and turnover, as discussed above.

Table 5.14 lists coefficients of determination (r^2), significance levels (p), slopes, and intercepts of the relationships between site index and several measures of fine root production, mortality, and turnover for the five sites of this study. The correlations between fine root production or mortality and site index were always negative, but never significant (Table 5.14). Fine root turnover was significantly (p=.042 to .068) negatively correlated with site index when turnover was calculated from production estimates. When turnover was calculated from mortality estimates, however, it was positively correlated with site index and was either less significant or non-significant (p=.078 to .233).

Small root production was positively but not significantly correlated with site index, whereas small root mortality was negatively correlated with site index (significance levels rang from .062 to .172, Table 5.14). Turnover rates of small roots were significantly and positively correlated with site index (p=.028 to .051) when based on production estimates. Similarly, turnover rates based on mortality estimates of small roots were positively correlated with site index, but these estimates were only significant for estimates calculated with the decision matrix (p=.048). The four significant correlations between small root turnover and site index can be attributed to the single, very high turnover estimate obtained for Stand E. Concern about the reliability of this result has already been expressed above.

Table 5.14 The relationships between site index and several measures of fine and small root production and mortality. Three different computational methods (DM, AC, and SC) are used. All relationships are based on the data from all five stands (n=5), r^2 = coefficient of determination, p = significance.

Variable	p	r^2	Intercept	Slope
Fine Root Prod. (DM)	0.781	.030	3.859	-0.040
Fine Root Prod. (AC)	0.845	.015	3.234	-0.031
Fine Root Prod. (SC)	0.857	.013	3.037	-0.026
Fine Root Mort. (DM)	0.269	.379	6.622	-0.110
Fine Root Mort. (AC)	0.342	.297	5.976	-0.099
Fine Root Mort. (SC)	0.342	.297	5.976	-0.099
Turnover Fine Root Prod. (DM)	0.068	.724	-0.501	0.039
Turnover Fine Root Prod. (AC)	0.057	.752	-0.446	0.033
Turnover Fine Root Prod. (SC)	0.042	.797	-0.471	0.034
Turnover Fine Root Mort. (DM)	0.233	.425	0.169	0.023
Turnover Fine Root Mort. (AC)	0.078	.698	0.220	0.017
Turnover Fine Root Mort. (SC)	0.078	.698	0.220	0.017
Small Root Prod. (DM)	0.128	.593	-1.394	0.081
Small Root Prod. (AC)	0.172	.516	-0.201	0.032
Small Root Prod. (SC)	0.348	.291	-0.830	0.045
Small Root Mort. (DM)	0.477	.179	2.612	-0.032
Small Root Mort. (AC)	0.067	.724	3.805	-0.081
Small Root Mort. (SC)	0.062	.738	3.756	-0.080
Turnover Small Root Prod. (DM)	0.030	.834	-5.346	0.211
Turnover Small Root Prod. (AC)	0.028	.844	-2.764	0.114
Turnover Small Root Prod. (SC)	0.051	.768	-2.959	0.117
Turnover Small Root Mort. (DM)	0.048	.778	-2.157	0.107
Turnover Small Root Mort. (AC)	0.498	.165	0.427	0.010
Turnover Small Root Mort. (SC)	0.508	.158	0.413	0.011

5.4.7 General Discussion

Comparison of the results from different root studies has always been complicated by the lack of common methodology and definitions. Diameter classes recognized by different studies are not uniform. Sampling depth varies among studies, as do the root sorting methods used. Some studies report root dry weights on an ash-free basis (e.g. Vogt *et al.* 1987, Keyes and Grier 1981) while others do not correct their data (Espinosa Bancalari and Perry 1987). Many studies separate live from dead fine root biomass; others report total root biomass data.

Estimates of root biomass and production obtained in this study are well within the range of values reported in the literature for coastal Douglas-fir stands in Oregon and Washington (Keyes and Grier 1981, Santantonio and Hermann 1985, Vogt *et al.* 1987). The combined data sets of Keyes and Grier (1981), Santantonio and Hermann (1985), and Vogt *et al.* (1987) have been used to investigate the relationships between fine and small root biomass and production and site index. Site indices for Santantonio and Hermann (1985) and for Vogt *et al.* (1987) were estimated from the published productivity classes by assuming that all plots within a productivity class were at the midpoint of the range this class. Productivity Classes II, III, and IV have mean site indices of 38.1, 32.0, and 25.9 m at 50 years, respectively (King 1966).

The methods used by Keyes and Grier (1981) were very similar to those used in this study, the only obvious difference being that they used a sample depth of 45 cm instead of 50 cm. Vogt *et al.* (1987) sampled only to a depth of 15 cm. Santantonio and Hermann (1985) classified roots with 0-1 mm diameter as fine and those with 1-5 mm diameter as small roots. They did not correct to ash-free values and sampled to a depth of 100 cm. The other three studies used definitions of 0-

2mm and 2-5mm diameter for fine and small roots, respectively, and corrected for ash-free dry weights.

The regression between site index and fine root biomass is highly significant ($p=0.001$, $r^2=0.45$, $n=20$) (Figure 5.17), but that between small root biomass and site index is not significant ($p=0.384$, $n=10$) (Figure 5.17). The estimates of small root biomass obtained by Santantonio and Hermann (1985) are somewhat higher than those obtained by Keyes and Grier (1981) and in this study, probably because the former study only included roots in the 1-5 mm diameter class, compared to 2-5 mm in the latter two studies. Neither of the regressions between fine and small root production and site index was significant (Figure 5.17). The high estimate of small root production in Stand E in this study is probably not realistic, as discussed above.

These results show that, within one species, fine root biomass decreases with increasing site quality, as expressed by site index. This suggests that as nutrient and moisture availability increase, fewer fine roots are required to meet the forest stands' demands for soil-provided resources. No significant relationship between site index and fine root production exists. Many factors can account for the between-stand variation in fine root production. Methodological differences between studies, differences in stand age and stand density, and between-year variation could all contribute to the variation in fine root production estimates.

Fine and small root production are only two components of stand productivity. In this chapter, only the belowground components of biomass and production were addressed. The final chapter will summarize the results of the aboveground (Chapter 4) and belowground (Chapter 5) biomass and production studies, and will investigate allocation to aboveground and belowground stand components.

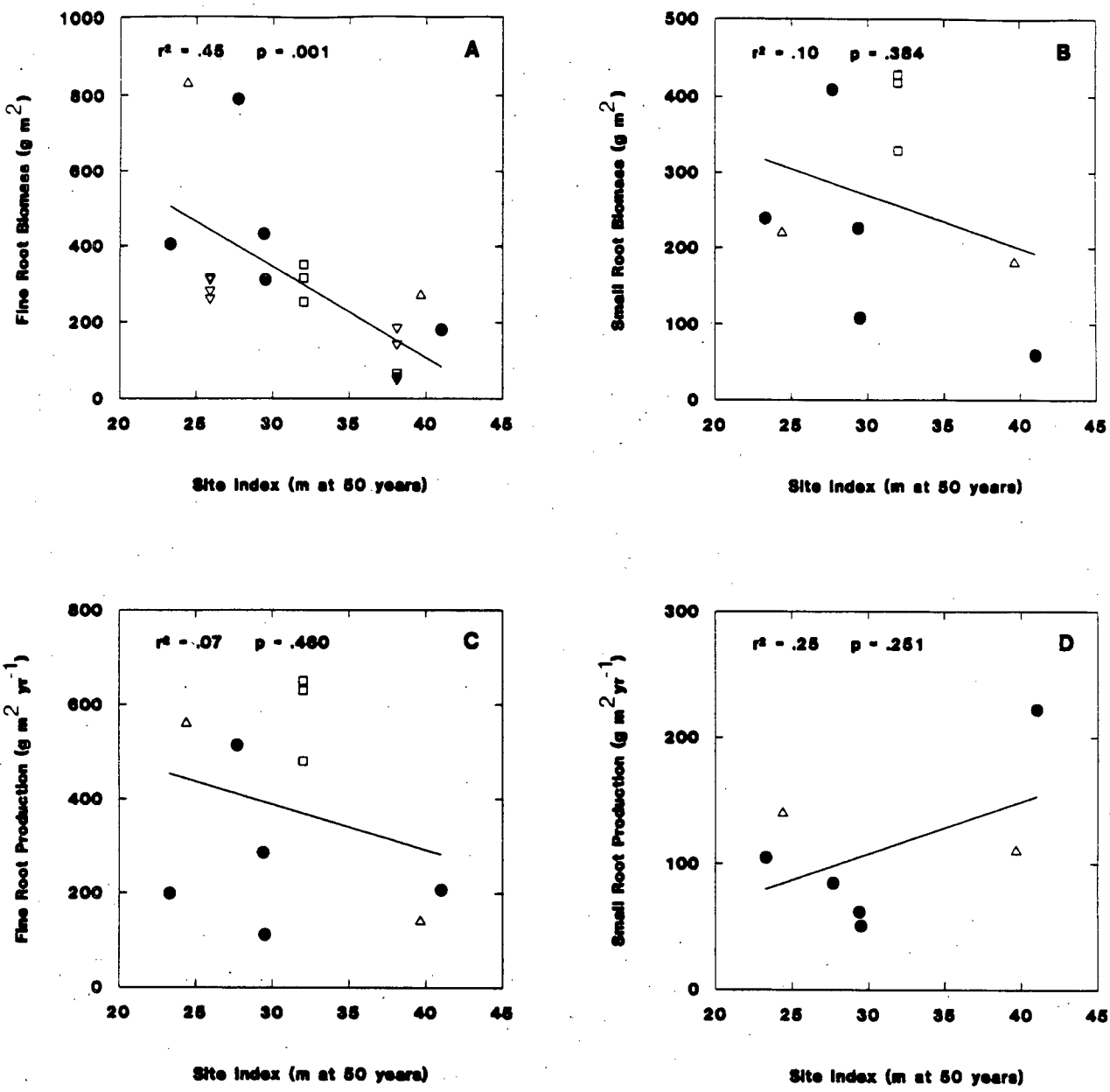

Figure 5.17 The relationships between fine and small root biomass and production and site index based on data from this and several published studies. ∇=Keyes and Grier 1981, Δ=Vogt *et al.* 1987, ❑=Santantonio and Hermann 1985, ◐=this study.

6. THE RELATIONSHIPS BETWEEN SITE INDEX AND FOLIAGE BIOMASS, FOLIAGE EFFICIENCY, PRODUCTION, AND PRODUCTION ALLOCATION

6.1 INTRODUCTION

The prediction of biomass production and future yields is central to many aspects of forest science and management. Some of the different approaches to yield forecasting involve computer simulation models of forest stands or ecosystems (Mitchell 1975, Wykoff *et al.* 1982). The conceptual framework that is common to many simulation models of forest growth is centered around the relationships between foliage biomass (or area) and stand production (Mitchell 1975, Barclay and Hall 1986, Kimmins *et al.* 1986, Ford and Bassow 1988).

A common conceptual approach for many models is to simulate site and stand factors, such as moisture and/or nutrient availability, which control the amount of foliage biomass carried by a stand. Foliage biomass, or a derivative thereof, is multiplied by some measure of "foliage production efficiency" to obtain an estimate of total production. Total production is then partitioned between different above- and belowground components of the forest stand using fixed or variable allocation strategies or allocation hierarchies (Mäkelä and Hari 1986, Bossel 1986, Barclay and Hall 1986). Some models invoke feedback between fine root biomass, which supplies nutrients and moisture at considerable carbon cost, and foliage biomass which provides the required carbon through photosynthesis (Mäkelä 1986, 1988, Thornley 1972). While such approaches to simulating forest ecosystem production do not require the large amount of data commonly needed for physiologically-based simulation models, they do require an understanding of some of the fundamental determinants of forest ecosystem production. Some of the

important questions which should be considered when developing simulation models of forest ecosystems are:

1) What is the relationship between site quality and stand foliage biomass?

2) Does foliage efficiency change with site quality?

3) What are the relative contributions of changes in total production and changes in production allocation to the observed between-stand differences in aboveground production?

A strong correlation between total overstory leaf area and site water balance has been demonstrated for forest ecosystems along west to east transects through central Oregon (Grier and Running 1977, Gholz 1982). These studies cover a very wide range of site moisture conditions and atmospheric moisture demand, but the observed changes in total ecosystem leaf area are confounded with changes in species composition from coastal to interior sites. Forest ecosystems respond to short term fluctuations in soil moisture status by controlling transpiration through stomata (Helms 1965, Helms 1976, Running 1976). Prolonged dry conditions lead to increased leaf litterfall and increased mortality of suppressed trees, thus effectively reducing total stand leaf area. It would therefore seem reasonable that leaf area of stands of a particular species would be correlated with moisture availability along a local, topographically- or edaphically-induced site moisture gradient. However, the existing studies have not quantified how foliage biomass is affected by such local variations in soil moisture availability within a given climatic regime.

The influence of site nutrient conditions on total foliage biomass has frequently been demonstrated in fertilization studies. Increased availability of nutrients, in particular nitrogen, resulted in increased foliage biomass in the

fertilized stands (Brix 1983). These increases are most pronounced in stands that have been thinned prior to fertilization, and they may be less or not at all obvious in fully stocked stands because tree mortality may accelerate following fertilization (Lassoie *et al.* 1985). There appear to be no published studies, however, that have investigated the relationships between stand foliage biomass and the local variation in site quality in Douglas-fir ecosystems.

Foliage efficiency, defined as the amount of biomass (total, aboveground, or stemwood, etc.) produced per unit of foliage (biomass or area), has been used to calculate biomass production from foliage estimates (Barclay and Hall 1986), and as an indicator of tree vigor (Waring *et al.* 1980). An estimate of foliage efficiency integrates many physiological processes over time and is particularly useful in experiments in which total production can be measured easily, as with seedlings or agricultural crops. In forest ecosystems, however, foliage efficiency has often been expressed on an aboveground or stemwood production basis (Waring *et al.* 1980, Satoo 1967, Lavigne 1988), because of the difficulty in quantifying belowground production. The interpretation of between-stand differences in foliage efficiency, or the comparison of foliage efficiency estimates from different stands, is complicated by the fact that the observed differences in aboveground or stemwood production may be due to either changes in net production, changes in production allocation, or both. Few studies, however, have the data required to be able differentiate the relative contribution of these two major determinants of aboveground production. One such study, in 40-year-old Douglas-fir stands in western Washington, reported that aboveground production represented 53.3% and 86.5% of total production on a low and a high productivity site, respectively (Keyes and Grier 1981).

The objectives of the research reported in this chapter were to investigate whether total foliage biomass, foliage efficiency, and production allocation change

with site index in second-growth Douglas-fir stands. Site index (meters at 50 years) integrates the past growth performance of a stand, and, although competing vegetation and other factors affect it, site index is generally considered to be a good index of site growth potential (Hägglund 1981). Site index was therefore chosen in this study as the integrating measure of site quality. The data and results of the previous chapters are combined and extended to address the three questions identified above. The chapter concludes with a general discussion of the results and implications of the research reported in this thesis.

6.2 MATERIALS AND METHODS

This part of the study is based on the 12 Douglas-fir stands described in Chapter 2. Biomass regression equations for the calculation of component biomass have been described in detail in Chapter 3. The application of the biomass regression equations to stand information to compute component biomass, production, and mortality has been described in Chapter 4. Biomass, production, and mortality estimates of fine and small roots for five of the 12 plots have been described in Chapter 5.

Production and mortality estimates for all aboveground components and for coarse roots are reported as mean annual rates for the last available measurement period (1985 - 1987). Biomass estimates for these components are reported for 1985. Fine and small root production and mortality estimates are based on a single year, May 1985 to May 1986. Fine and small root biomass estimates refer to May 1985. All relationships which are presented are based on data from these years or measurement periods only, unless specifically stated otherwise.

6.3 RESULTS

6.3.1 Foliage biomass versus site index

Foliage biomass calculated for the 12 plots using the regression model based on dbh and Growing Space Index (the "GSI model") as independent variables (Chapter 3, Equation 3.20), ranged from 8.6 to 13.5 Mg ha^{-1} (Figure 6.1A and Table 4.4). However, there was no significant relationship between total foliage biomass in 1985 and site index (r^2=0.011, p=0.746). It is interesting to note that a different conclusion would have been reached if the regional Douglas-fir foliage biomass regression model (Gholz *et al.* 1979; the "regional-model") which has been used in previous studies (Gholz 1982) had been used instead of the regression model developed for this study. The relationship for the 12 plots between foliage biomass predicted by the regional model and site index (Figure 6.1B) is significant (r^2=0.374, p=0.035). The mean and standard deviation of predicted foliage biomass in 1985 for the GSI model are 10.57±1.47 Mg ha^{-1} compared to 14.39±2.17 Mg ha^{-1} for the regional model. These means are significantly different (t-test, p<0.001).

6.3.2 Foliage efficiency (ANPP) versus site index and foliage biomass

Foliage efficiency (aboveground production per unit foliage biomass, FE_{ANPP}) during the period between 1985 and 1987, increased as site index increased over the 12 plots in this study (r^2=0.39, p<0.001) (Figure 6.2B), but was not correlated with foliage biomass (r^2=0.003, p=0.871) (Figure 6.2A). Foliage efficiency (ANPP) ranged from 0.52 to 0.82 (Mg yr^{-1} Mg^{-1}) for 10 of the plots, but was much higher for the two plots of Installation 72 (1.48 and 1.53 Mg yr^{-1} Mg^{-1}). The relationship

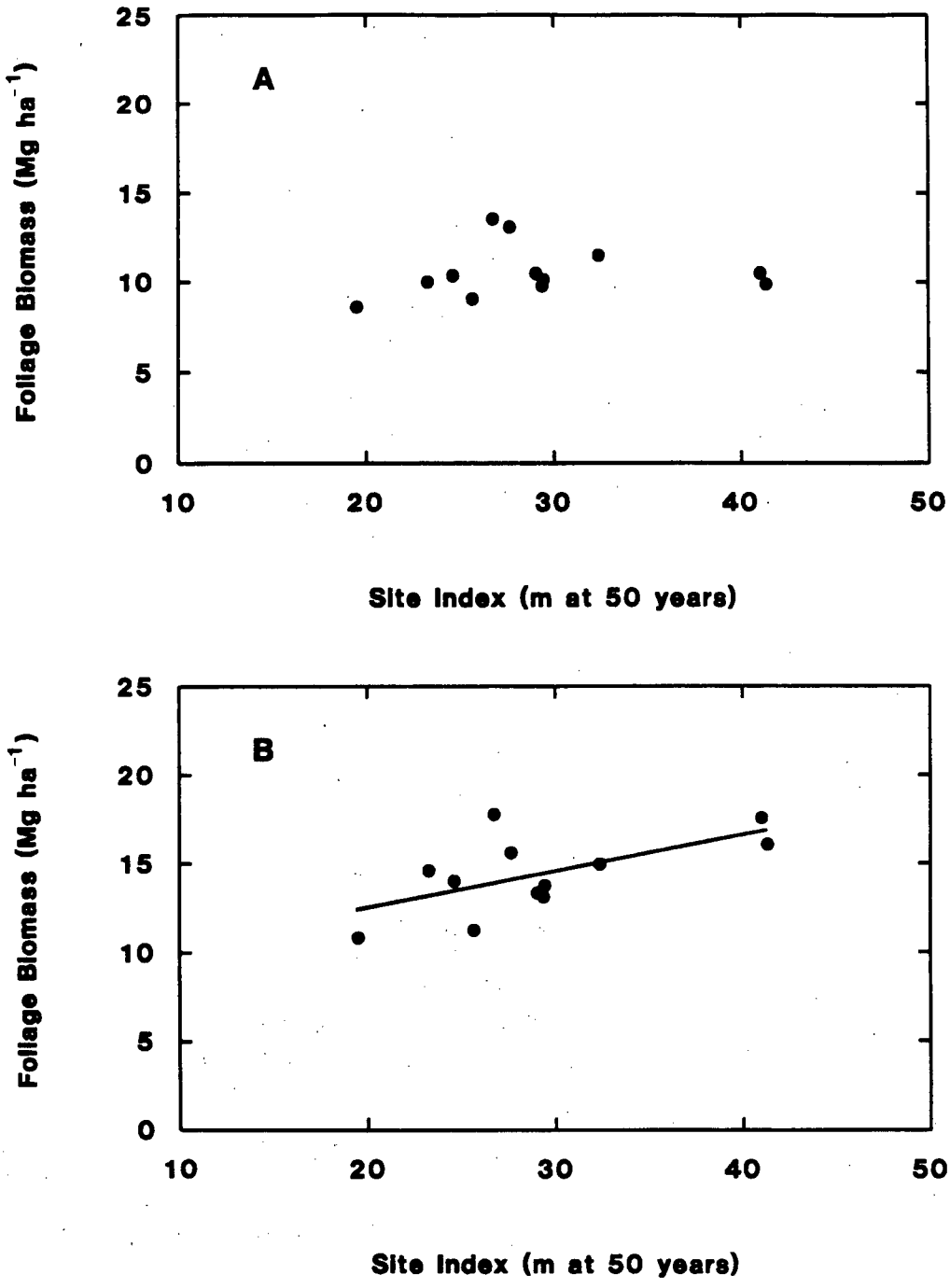

Figure 6.1. The relationship between foliage biomass (Mg ha^{-1}) and site index (m at 50 years) based on (A) the foliage biomass regression model developed in this study and (B) the model of Gholz *et al.* (1979).

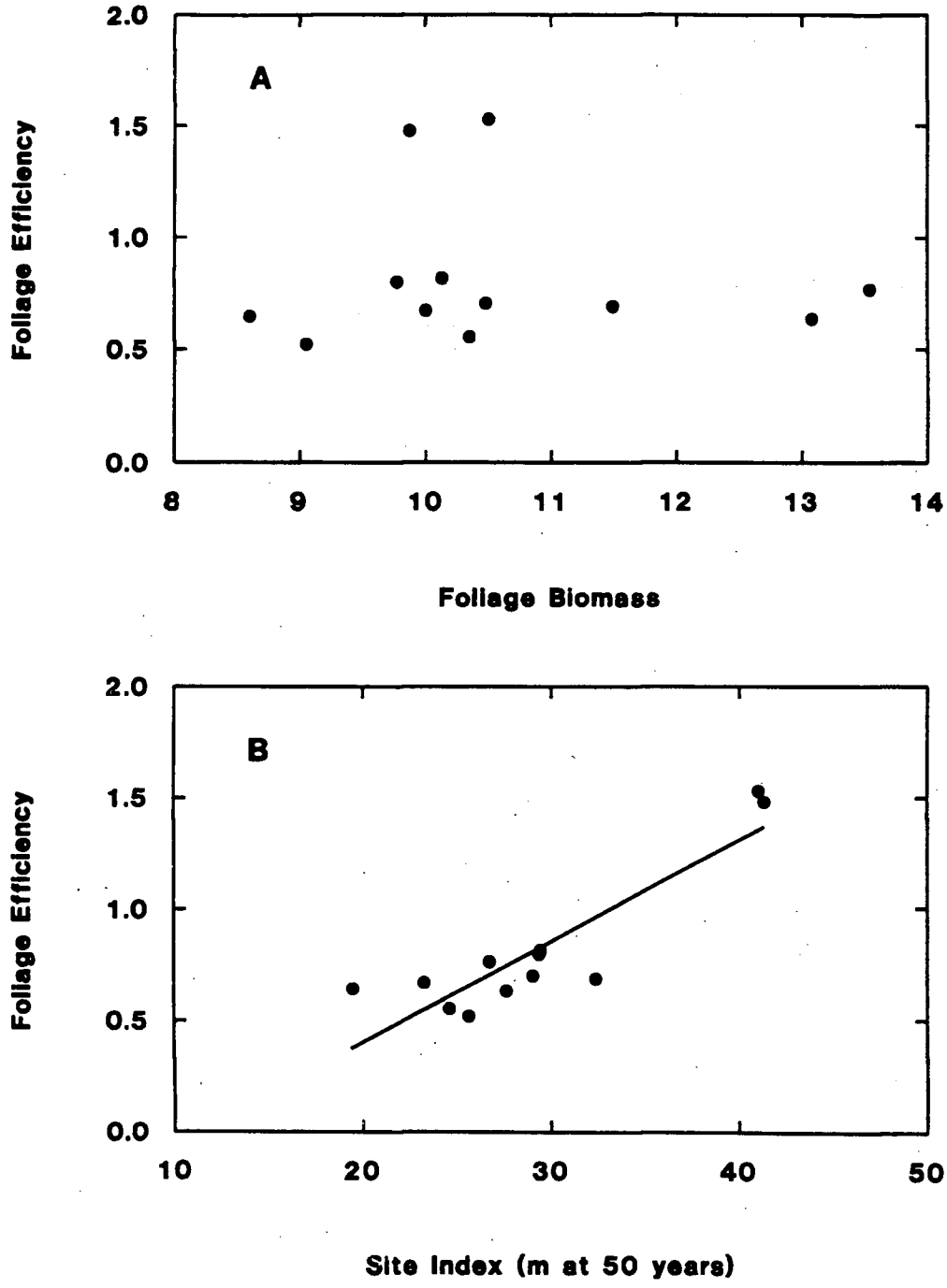

Figure 6.2. The relationships between foliage efficiency (Mg yr^{-1} Mg^{-1}), calculated from total aboveground production (ANPP) and (A) foliage biomass (Mg ha^{-1}) and (B) site index (m at 50 years).

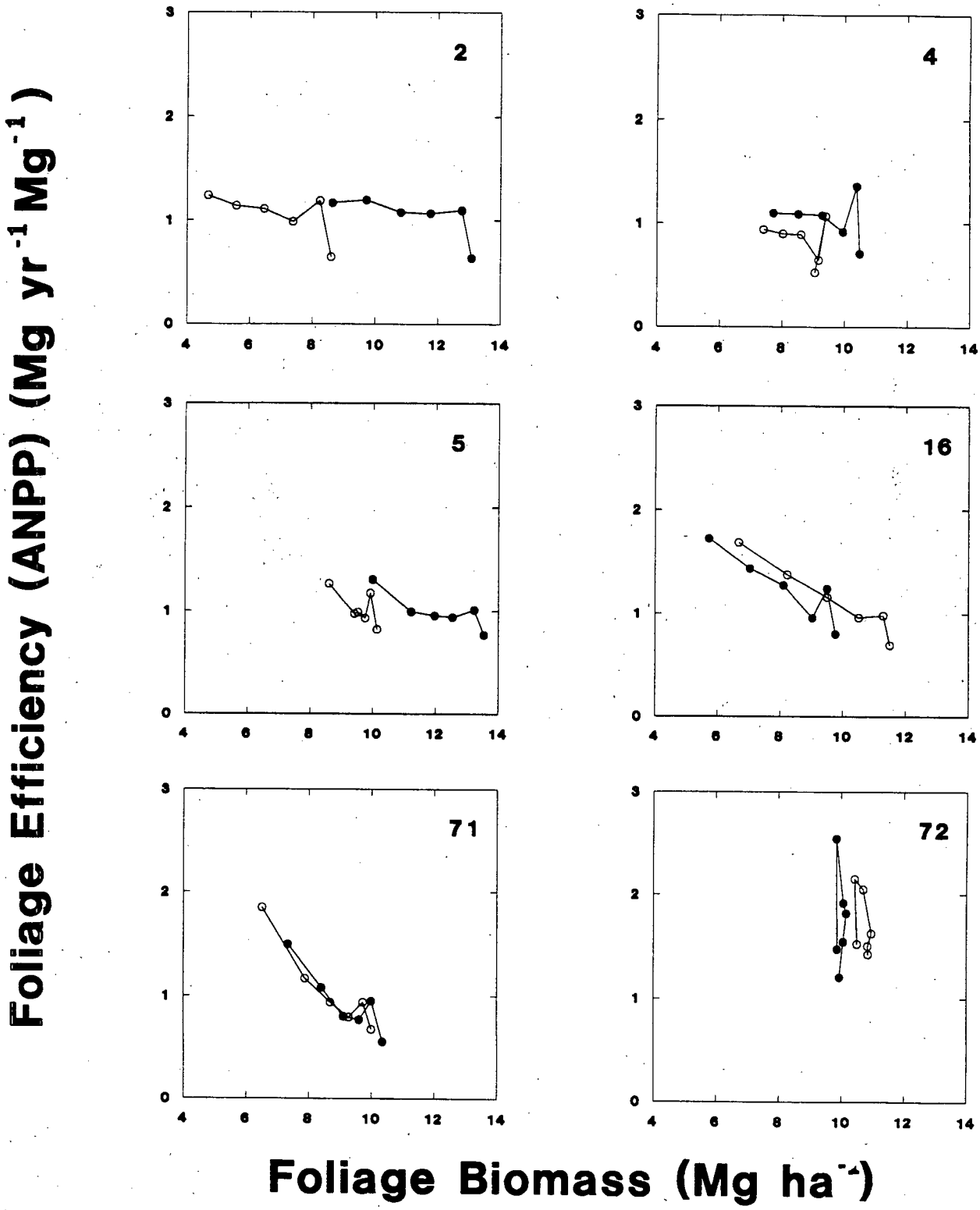

Figure 6.3. Foliage efficiency (ANPP) (Mg yr^{-1} Mg^{-1}) plotted against foliage biomass (Mg ha^{-1}) for each of the 12 plots. Installation numbers are in upper right corner of each graph. Legend as in Figure 4.6.

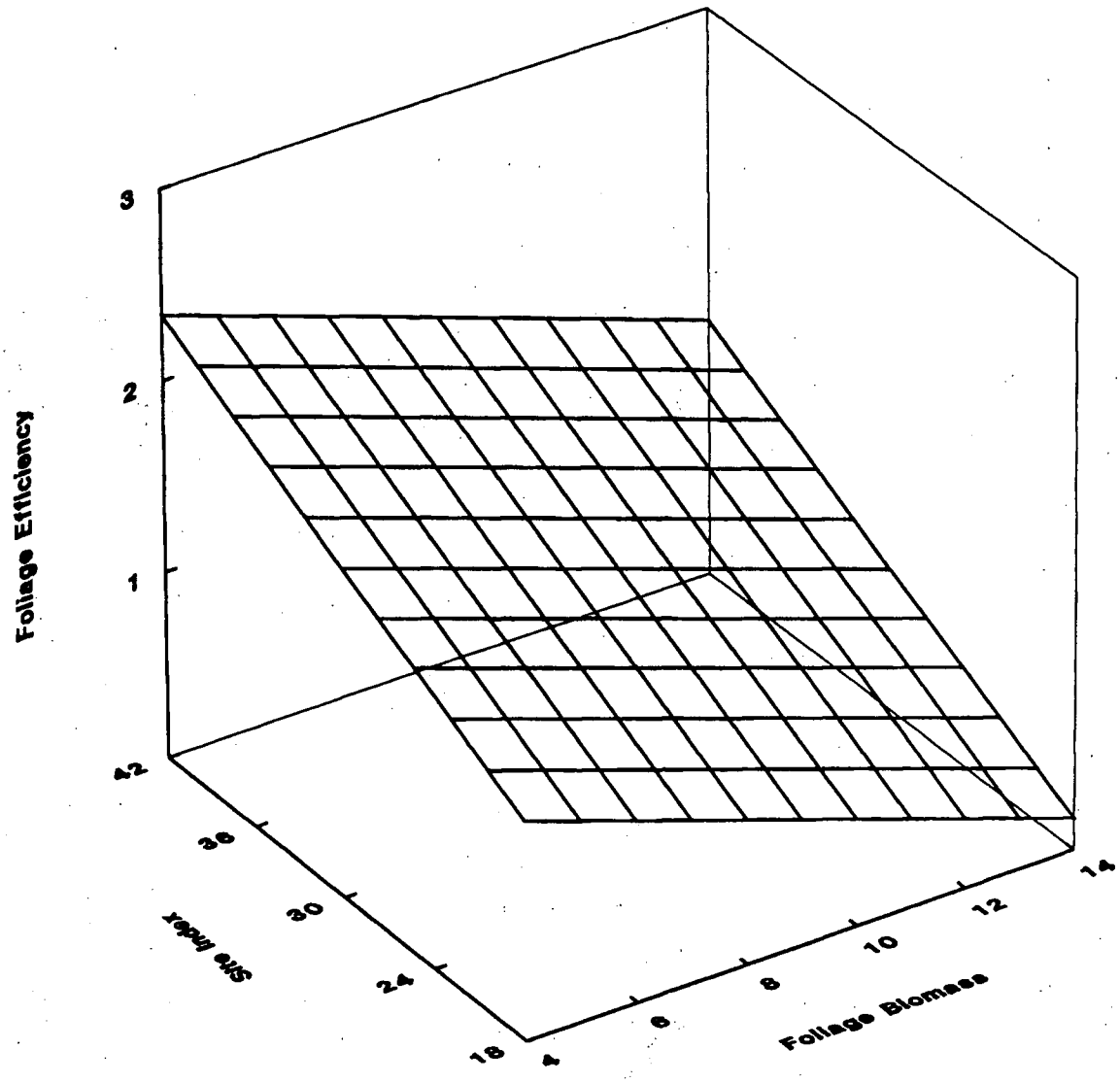

Figure 6.4. Graphical presentation of Equation 6.1, which predicts foliage efficiency (ANPP) (Mg yr^{-1} Mg^{-1}) as a function of site index (m at 50 years) and foliage biomass (Mg ha^{-1}).

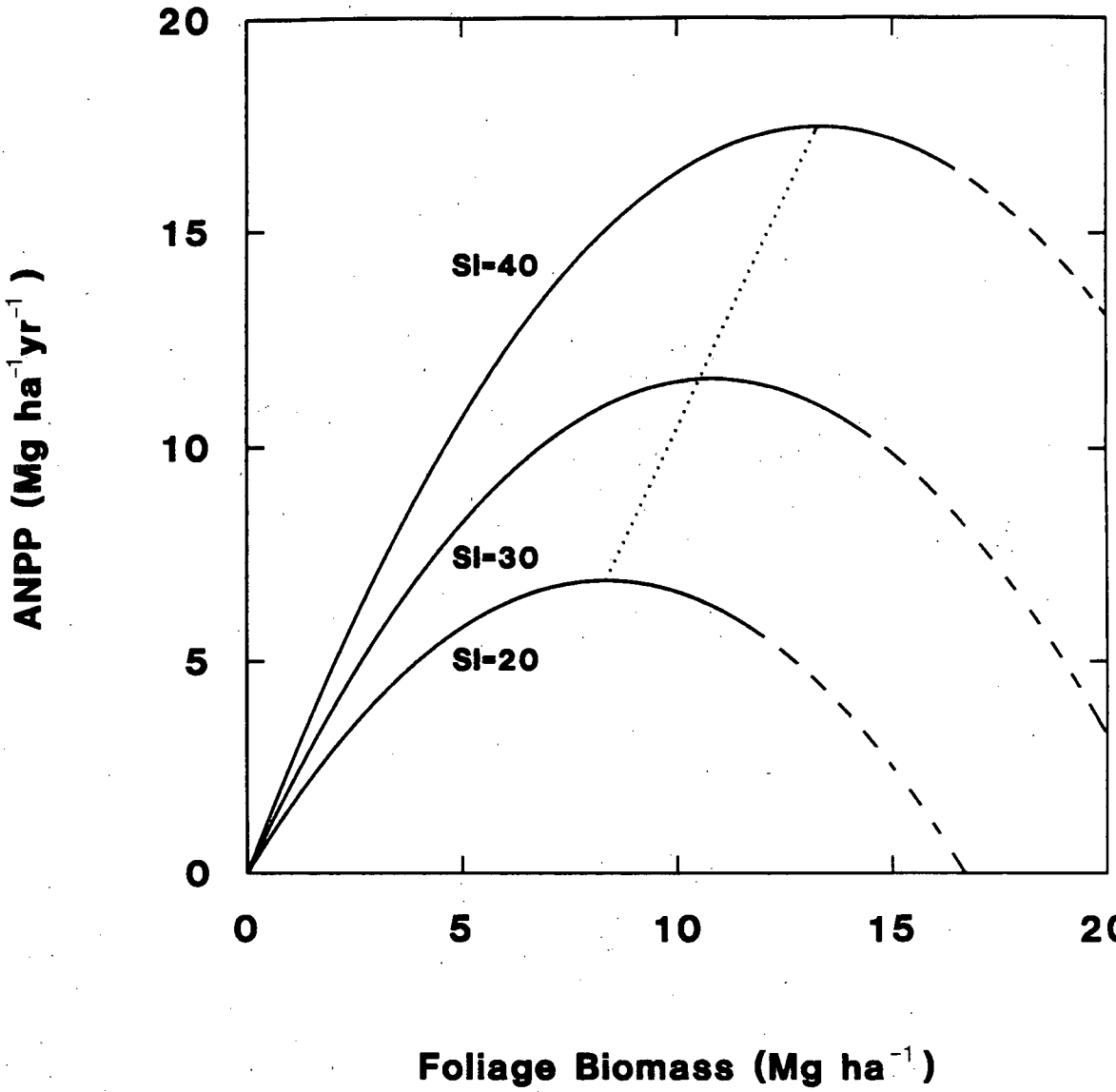

Figure 6.5. Aboveground production (ANPP) as a function of foliage biomass and site index (Equation 6.3, n=72). Natural stands will probably not occur much beyond the site-specific optimum foliage biomass (see Figure 6.6 and Discussion).

figure, as discussed in Section 6.4.2). The function also suggests that this optimum foliage biomass increases with site index, e.g. 8.3 and 13.3 Mg ha^{-1} for site index 20 and 40, respectively. From equation 6.3, the optimum foliage biomass FB_{opt} can be calculated as a function of SI, such that

$$FB_{opt} = 3.398 + 0.247 * SI \qquad [6.4]$$

This equation can be used to establish the difference between actual and optimum foliage biomass. Foliage biomass in eight of the 12 plots appears to be converging towards the site-specific optimum (Figure 6.6). Two plots are diverging from the optimum foliage biomass, and the two plots of Installation 72 have stable foliage biomass below the expected optimum.

6.3.3 Production allocation versus site index

The proportion of total aboveground biomass, which is represented in each of the main aboveground biomass components, changes with site index for all components except stembark (Table 6.1 , Figure 6.7). Foliage and branch biomass represent a larger proportion of total aboveground biomass on sites with lower site index than on sites with higher site index. The proportion of total biomass in stemwood and coarse root biomass increases with increasing site index. Similar trends are observed in the change of proportions of total aboveground production allocated to the main biomass components (Table 6.1, Figure 6.8). As site index increases, a smaller proportion of total aboveground production is allocated to foliage and an increasing proportion to stemwood and stembark. Coarse roots and branches showed no significant change in allocation.

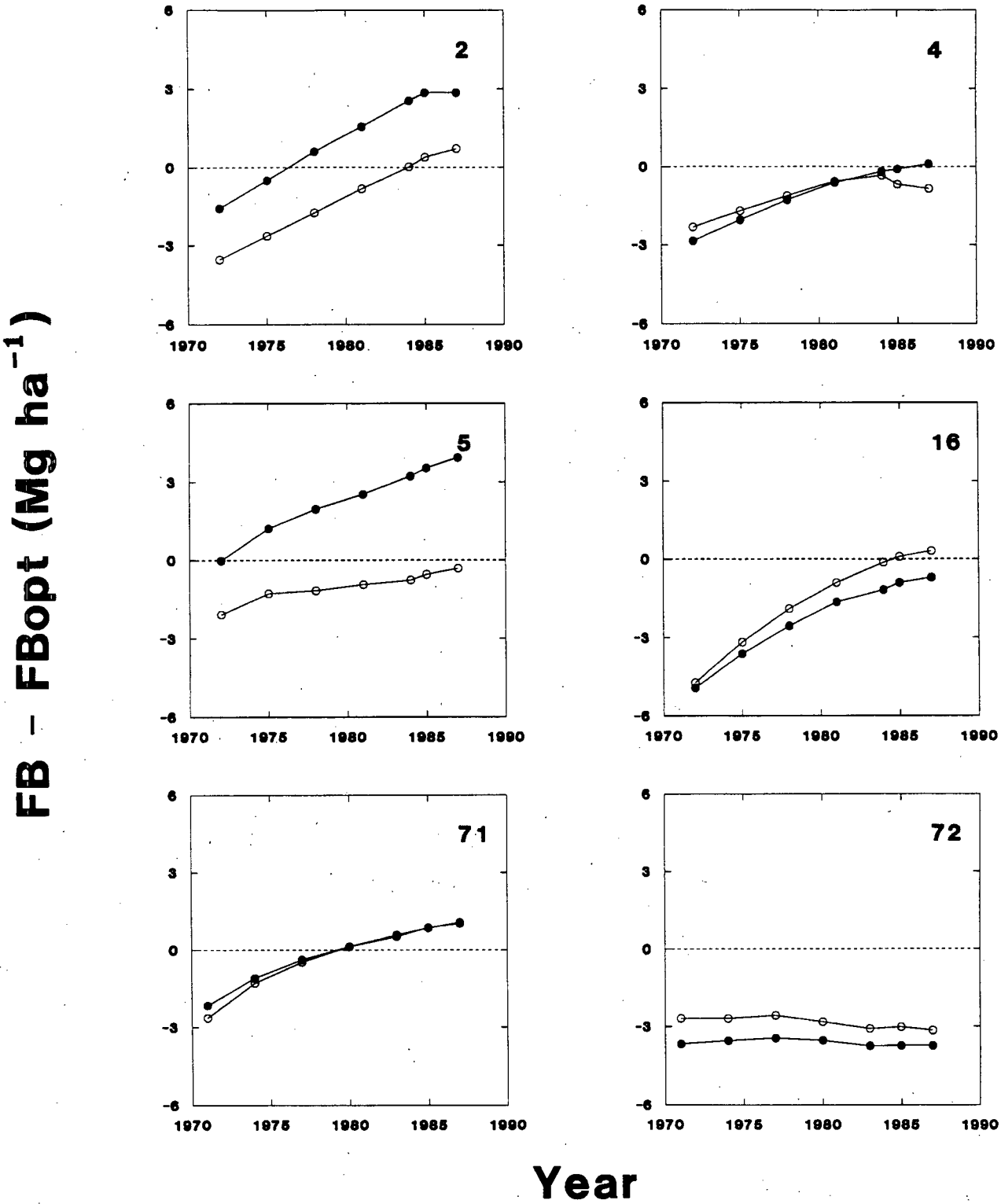

Figure 6.6. The difference between actual foliage biomass (FB) and site-specific optimum foliage biomass (FB_{opt}) for each of the 12 plots. Installation numbers are in upper right corner of each graph. Legend as in Figure 4.6.

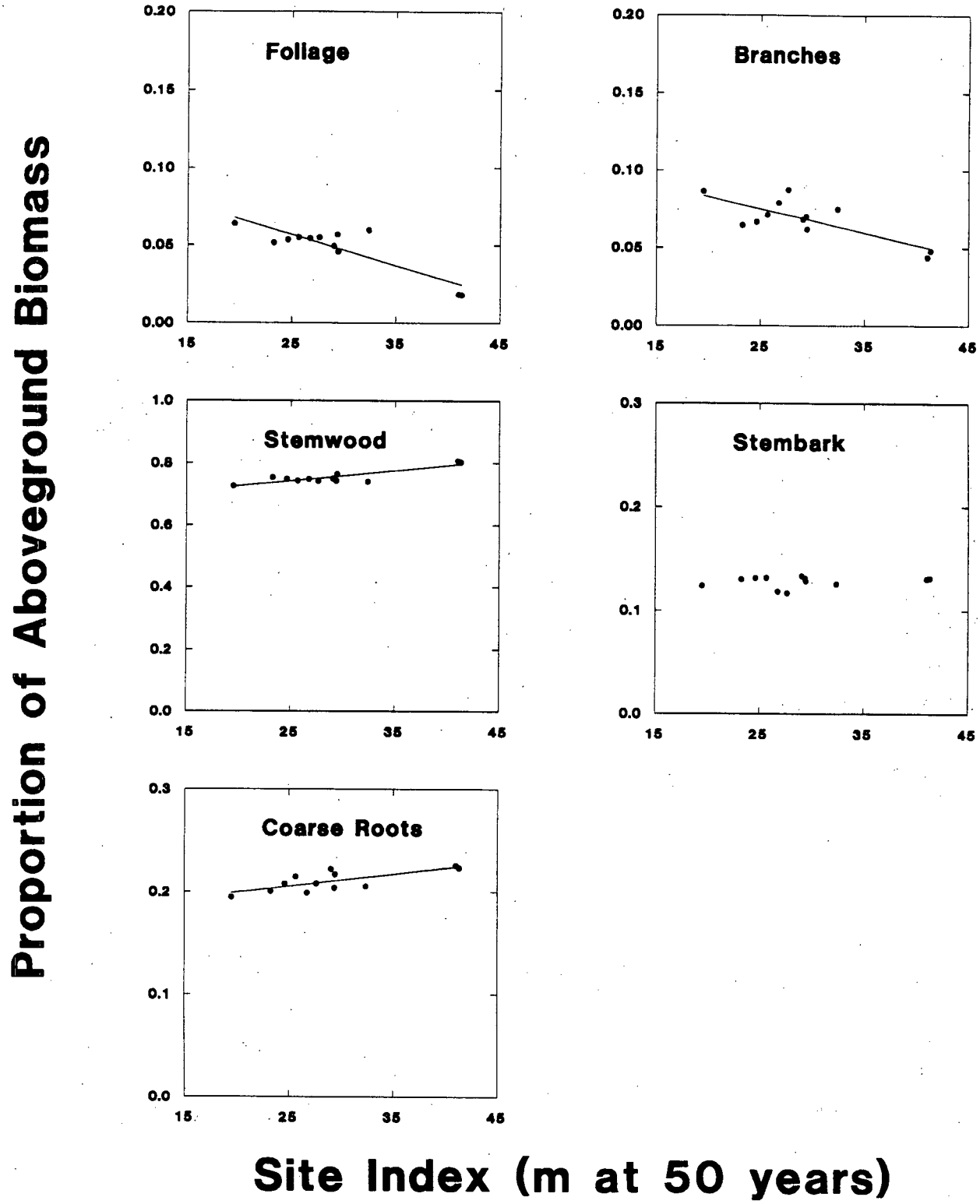

Figure 6.7. Proportions of aboveground biomass allocated to foliage, branches, stemwood, stembark, and coarse roots plotted against site index.

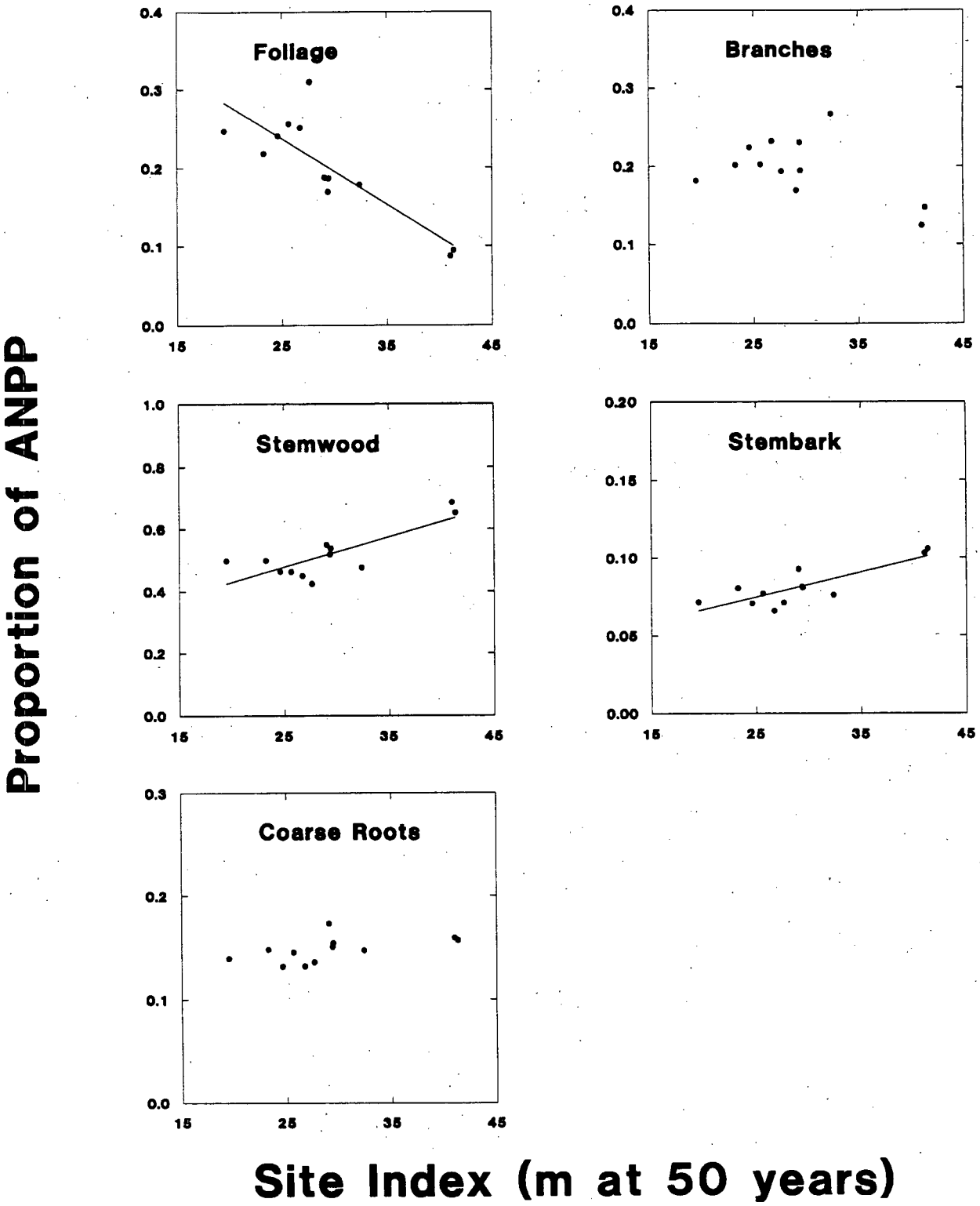

Figure 6.8. Proportions of aboveground production allocated to foliage, branches, stemwood, stembark, and coarse roots plotted against site index.

Total production is partitioned between aboveground and belowground stand components. Belowground production in this study is the sum of coarse, small (2-5mm), and fine (0-2mm) root production. Fine and small root production data are only available for 5 of the 12 plots (cf. Chapter 5).

As has been discussed in Chapter 5, there are two measures of fine root turnover: production and mortality. In a steady state system, the two estimates of fine root turnover should be approximately equal, otherwise fine root biomass would either disappear or increase indefinitely. The estimates of root production and mortality obtained in this study differed in some plots, with mortality estimates exceeding those of production (Figures 5.14 and 5.15) for reasons explained in Chapter 5. Therefore, results of belowground allocation are reported for both root production and root mortality estimates.

Annual aboveground production (ANPP) increases significantly with site index (r^2=0.791, p<0.001, n=12) (Figure 6.9, open circles). Estimates of total production (TNPP) have been obtained by adding four different estimates of belowground production to ANPP (Figure 6.9 A-D, filled squares). The increase of TNPP with increasing site index is statistically significant for both production and mortality-based estimates of belowground allocation (p=.035 to .038 and p=.053 to .062, respectively).

The proportion of total production allocated belowground ranged from about 0.25 to about 0.5, depending on site conditions and computational method used (Table 6.2). This proportion tended to decrease with increasing site index, regardless whether the estimates of belowground allocation were derived from fine and small root production or mortality estimates, and regardless of the computational method used (Table 6.3). This decrease of the proportion of total

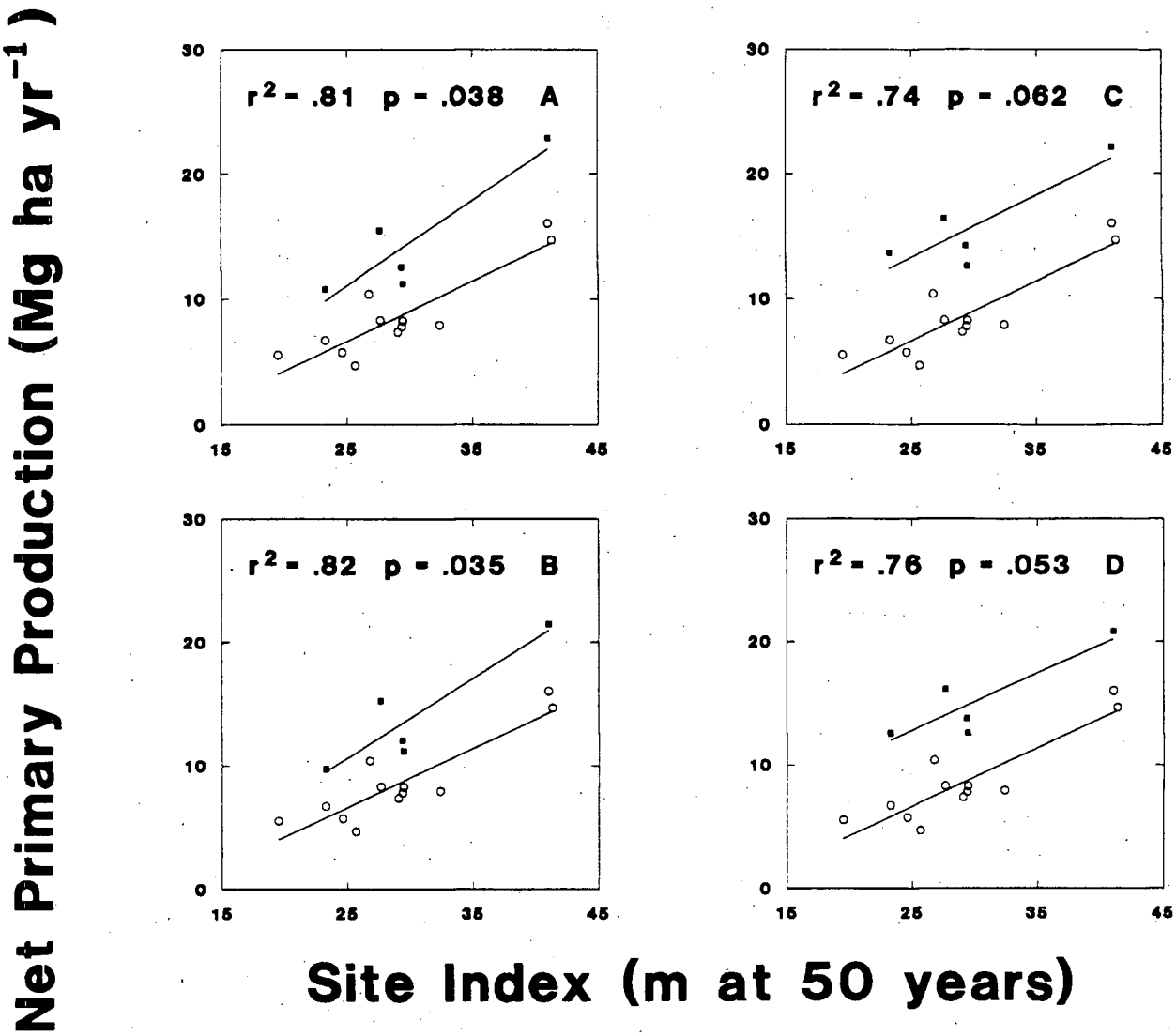

Figure 6.9. Aboveground (○, ANPP) and total (■, TNPP) annual production increase with site index. The statistics (r^2, p) refer to the relationship between TNPP and site index (n=5). The relationship between ANPP and site index is highly significant (r^2=.791, p<.001, n=12). Fine and small root turnover estimates are based on A: Production DM-method, B: Production AC-method, C: Mortality DM-method, D: Mortality AC-method. See text for further explanations.

production allocated belowground with increasing site index was significant for mortality derived estimates of fine and small root turnover (AC method) ($p=0.038$). If fine and small root turnover was calculated from mortality estimates derived with the DM method, the decrease in the proportion of total production allocated belowground was less significant ($p=0.054$). If the proportion of total production allocated belowground was calculated from root turnover estimates based on fine and small root production data, the same trend was observed but neither computational method yielded a significant relationship.

Table 6.1 The relationship between site index and the proportion of total biomass and total production allocated to foliage, branches, stemwood, stembark, and coarse roots. For all models n=12. r^2 = coefficient of determination, p = significance.

Component	Intercept	Slope	r^2	p
BIOMASS				
Foliage	0.106	-0.0020	0.753	<0.001
Branches	0.113	-0.0015	0.587	0.004
Stemwood	0.660	0.0033	0.756	<0.001
Stembark	0.121	0.0002	0.071	0.401
Coarse Roots	0.175	0.0012	0.573	0.004
PRODUCTION				
Foliage	0.448	-0.0084	0.696	<0.001
Branches	0.280	-0.0028	0.226	0.118
Stemwood	0.236	0.0097	0.633	0.002
Stembark	0.035	0.0016	0.675	0.001
Coarse Roots	0.119	0.0010	0.278	0.078

Table 6.2 The proportion of total production allocated belowground for five Douglas-fir stands. Fine and small root production (P) and mortality (M) estimates have been derived with two computational methods: Decision Matrix (DM) and All Changes (AC).

			Production-based		Mortality-based	
Inst.	Plot	SI	DM	AC	DM	AC
2	6	27.6	0.461	0.454	0.492	0.486
5	10	29.4	0.260	0.259	0.342	0.342
16	2	29.4	0.374	0.350	0.450	0.432
71	14	23.3	0.375	0.308	0.506	0.465
72	14	41.0	0.300	0.255	0.280	0.233

Table 6.3 The relationship between site index and the proportion of total production allocated belowground for four different estimates of belowground production. Fine and small root turnover estimates derived from production- or mortality-based estimates using the decision matrix (DM) and all changes (AC). For all models n=5. r^2 = coefficient of determination, p = significance.

Method	Intercept	Slope	r^2	p
Production-based:				
DM	0.520	-0.005	0.216	0.430
AC	0.488	-0.005	0.190	0.464
Mortality-based:				
DM	0.810	-0.013	0.761	0.054
AC	0.821	-0.014	0.807	0.038

6.4 DISCUSSION

6.4.1 Foliage biomass versus site index

During stand development, foliage biomass of forest stands reaches a site-specific maximum value after canopy closure, which in temperate coniferous forests averages approximately 10 Mg ha^{-1} (Turner and Long 1975). The stand age at which this plateau of foliage biomass is reached depends on factors such as site quality and stand density (Turner and Long 1975). The total amount of foliage biomass in a stand at the time of stabilization is thought to depend on site conditions such as soil moisture and soil nutrient availability (Grier *et al.* 1986).

Foliage biomass regressions which use dbh as the independent variable are not able to predict a stabilization of stand foliage biomass, and will instead predict continuing foliage biomass accumulation as stand basal area increases. None of the models investigated in Chapter 3 which use dbh alone, or a derivative thereof, had an inflexion point at greater stem diameters, which means that foliage biomass per tree predicted by such models continues to increase with increasing diameter. In contrast, models which use sapwood basal area or dbh plus a competition index as independent variables can potentially predict the stabilization of foliage biomass after canopy closure.

The relationship between foliage biomass and site index was not significant when foliage biomass was calculated using the regression model developed in this study, which uses a competition index as the independent variable in addition to dbh. In contrast, foliage biomass estimates obtained with the regional model of Gholz *et al.* (1979) increased significantly with increasing site index. A possible explanation for this difference is that the regional model predicts a continuing increase of foliage biomass with greater stand basal area. Because stand basal area in the twelve stands is highly correlated with site index (r^2=.686, p=0.001), the

correlation between site index and foliage biomass also becomes significant. In contrast, the GSI-based model predicts that foliage biomass stabilizes in some plots, despite continuing increases in stand basal area. The two regression models also differ in that the regional model consistently predicted higher foliage biomass values for each of the plots, and it predicted a greater range of values (10.8 to 17.7 Mg ha^{-1}) than the the GSI-model (8.6 to 13.5 Mg ha^{-1}). The GSI-based model has been derived from destructively sampled trees from plots in the immediate vicinity of the stands to which the regression model was applied. The regional model overpredicted foliage biomass of the sample trees by an average of 55.7% (Table 3.16) and is therefore not suitable for the prediction of foliage biomass of the stands used in this study. Warnings against using regression models which are based on dbh only for the prediction of stand foliage biomass have been presented earlier (Marshall and Waring 1986). Furthermore, in studies that use such models, all variables that are correlated with basal area will also be correlated with foliage biomass (Satoo and Madgwick 1982, p.64).

6.4.2 Foliage efficiency (ANPP) versus site index and foliage biomass

Foliage efficiency (ANPP) of a plant or tree canopy decreases with increasing biomass of the entire canopy because the amount of light that reaches its lower portions diminishes due to self-shading (Cannell 1979). This inverse relationship between foliage biomass and efficiency, calculated from total aboveground production, was not detected in this study when only data from the 12 stands and one measurement period were analysed (Figure 6.2A). Foliage efficiency increases with site index (Figure 6.2B) and the relationship displayed in Figure 6.2A is therefore confounded with site index.

Analysing the data from each plot separately showed that in five of the 12 plots, foliage efficiency decreased significantly with increasing foliage biomass. In five additional plots, foliage efficiency was negatively correlated with foliage biomass, but the relationship was not statistically significant. In the two plots of Installation 72, foliage biomass did not change over time and the observed variation in foliage efficiency is probably related to other factors, such as climatic variability. The two plots of each Installation tend to show very similar patterns (Figure 6.3) of changes in foliage efficiency with changing foliage biomass. Foliage biomass is confounded with time, and the observed similarities in the pairs of plots of each Installation could be interpreted as an expression of the influences of site or regional climate.

The regression model (Equation 6.3) which predicts foliage efficiency from foliage biomass and site index accounts for 56.5% of the variation in the 72 data points (Figure 6.4). Climatic variability, and other factors which affect foliage efficiency but are not represented in the model, account for the remaining variation. This model also explains the lack of correlation between foliage efficiency and foliage biomass observed in Figure 6.2. Equation 6.3 (Figure 6.5) should not be extrapolated beyond the range of the data. At low stand foliage biomass values, very little self-shading will occur and foliage efficiency will not increase further but will asymptotically approach some maximum value as most of the foliage approaches light saturation. At very high foliage biomass values, an increasing proportion of the foliage would have to be maintained at light levels which are inadequate to support positive net-photosynthesis. While it is often stated that foliage which is a net sink for carbon will be shed (Cannell 1979) or will adapt to the low light intensities by reducing respiration rates (Loomis and Gerakis 1975), the small growth improvement following pruning of the lower 25 to 30% of live branches has been attributed to the removal of a net carbon sink (Stein 1955).

6.4.3 Optimum foliage biomass in Douglas-fir stands

Scientists concerned with crop production have shown that there is an optimum foliage biomass or leaf area at which production is maximized (Watson 1958, Zavitkovski *et al.*1974). Respiration increases with greater foliage biomass while the rate of increase in photosynthesis diminishes due to increasing self-shading. Waring *et al.*(1980) showed that in five Douglas-fir stands of different densities, basal area growth rate was highest at a leaf area index of approximately 7. In their study, leaf area was calculated from sapwood basal area assuming that this relationship is not affected by stand density, an assumption that has since been demonstrated to be incorrect (Brix and Mitchell 1983, Keane and Weetman 1987, Long and Smith 1988).

The results of this study suggest that there is an optimum foliage biomass at which aboveground production is maximized (Figure 6.5). They further demonstrate that this optimum foliage biomass increases with site index, i.e. the optimum amount of foliage biomass is greater for a better site than for a poorer site. There are at least two explanations for this observation. In Douglas-fir, a determinant species, the distance between whorls increases with site index because of greater height growth rates at better sites. Increasing the vertical spacing of foliage biomass allows for greater intrusion of diffuse light into the lower parts of the canopy, which results in greater total photosynthesis (Kira 1975, Cannell 1979, Jarvis and Leverenz 1983). The light extinction coefficient, which determines reductions in light intensity as a function of foliage biomass, is affected by the spatial arrangement of the foliage (Monsi and Saeki 1953).

A second argument is that in Douglas-fir, foliage nitrogen concentrations are positively correlated with site index (R.E. Carter and K. Klinka, pers. comm.), as has been observed with other conifers such as black spruce (Gagnon 1964). Foliage

with higher N-concentration has a greater photosynthetic efficiency and compensation points at lower light intensities (Kuroiwa 1960, Brix 1981). The optimum foliage biomass will therefore increase with greater soil nitrogen availability.

Equation 6.3 has been used to predict the optimum foliage biomass as a function of site index for each of the 12 plots. Figure 6.6 shows that most of the 12 plots of this study asymptotically approach the site-specific optimum foliage biomass. However, two plots are clearly above the expected optimum foliage biomass. Installation 2 Plot 6 and Installation 5 Plot 8 have stand densities of 3000 and 3400 stems per hectare, respectively. These two plots also have the highest component of western hemlock and western redcedar: 33.5 and 24% of basal area, in Installation 2, Plot 6, and Installation 5, Plot 8, respectively. Because no regression models for the prediction of western hemlock or western redcedar foliage biomass have been developed in this study, the regional models of Gholz *et al.* (1979) were used to predict foliage biomass of these species. The higher than expected foliage biomass of these two plots may be attributable to overprediction by the regional models which are not sensitive to stand densities, as discussed above.

A stable but lower than expected foliage biomass was observed in Installation 72, the site with the highest site index (41 m@50) and also the highest stand age (70 years). In the two plots of Installation 72, foliage biomass was about 25% below the expected value. There are several possible explanations for this. The trees in these stands are very tall (45 to 55 meters) and during storm events their crowns will swing considerable distances. The resulting crown contact between trees is known to cause large branches or branch parts to be broken off, which can be a potentially significant cause of foliage loss (Grier 1988). The stands may therefore not be able to maintain the optimum amount of foliage biomass.

6.4.4 Production allocation versus site index

The change with site index in the proportion of total biomass represented in the major aboveground biomass components is to some extent due to the influence of the two plots of Installation 72. These two plots are older than the remaining ten plots and have a lower stand density (Table 4.3). When the data from these two plots are removed, the changes in distribution among aboveground biomass components with changing site index become non-significant. The slopes maintain the same direction in all five models, however. The variablity in the remaining data, the reduction of the sample size to ten and of the site index range to about half its original spread, all contribute to the non-significance of the reduced model.

The proportion of total aboveground production allocated to the major biomass components also changed with site index, although only changes in foliage, stemwood, and stembark were statistically significant. The three significant relationships were strongly influenced by Installation 72, because removing the data of this Installation resulted in non-significant slopes, although again, their direction did not change. Both biomass and production distribution are affected by stand age and stand density, the influence of which is not accounted for in the simple models which use only site index as the independent variable.

The quantification of belowground biomass and biomass production has always been very difficult, which is reflected in the paucity of information about this biomass component. Newbould (1967) suggested that belowground production should be calculated using the equation:

$$\frac{\text{Aboveground Production}}{\text{Aboveground Biomass}} = k \times \frac{\text{Belowground Production}}{\text{Belowground Biomass}} \qquad [6.4]$$

For a lack of better data, he also suggested that k be assumed to have a value of 1. More recently, Keyes and Grier (1981) have demonstrated that the proportion of total production allocated belowground changes with site quality, and that

therefore a constant ratio between aboveground and belowground production cannot be assumed. The results of this study strongly support the conclusions reached by Keyes and Grier (1981).

Figure 6.10 contains the data from the five stands of this study and the two stands investigated by Keyes and Grier. The differences between production and mortality estimates of fine and small roots obtained in this study have been discussed above. The decrease in the proportion of total production allocated belowground with increasing site index is apparent in both production- or mortality-based estimates of belowground production. The production-based estimate of fine and small root turnover calculated with the decision matrix is significant at the 10% level (p=0.087). The two mortality-based estimates are highly significant, p=0.003 and 0.002 for the DM- and AC-based methods, respectively. Considering the differences in geographic location and methods used, the similarity of the estimates of allocation obtained by Keyes and Grier (1981) and in this study is striking.

In this study, soil moisture regime (Green *et al.* 1984) of the twelve plots ranged from moderately dry to fresh and site index increased with improved soil moisture regime. Although Douglas-fir does not normally grow on wet or very wet sites, exceptions can be found as a result of off-site planting or due to other unusual circumstances. On wet sites, poor growth of Douglas-fir may result in a lower site index than on fresh sites (K. Klinka, pers. comm.). Growth limitations on these wet sites are different than those on drier sites which may, however, have the same site index. Some of the conclusions reached about the relationships between site index and carbon allocation may not apply to Douglas-fir stands on wet or very wet sites.

The results of this study emphasize that shifts in carbon allocation from above- to belowground stand components are an important and frequently ignored

adaptation of forest ecosystems to changes in site quality. Future predictions of stand responses to silvicultural treatments and environmental change require a better understanding of the role of shifts in carbon allocation in forest ecosystems.

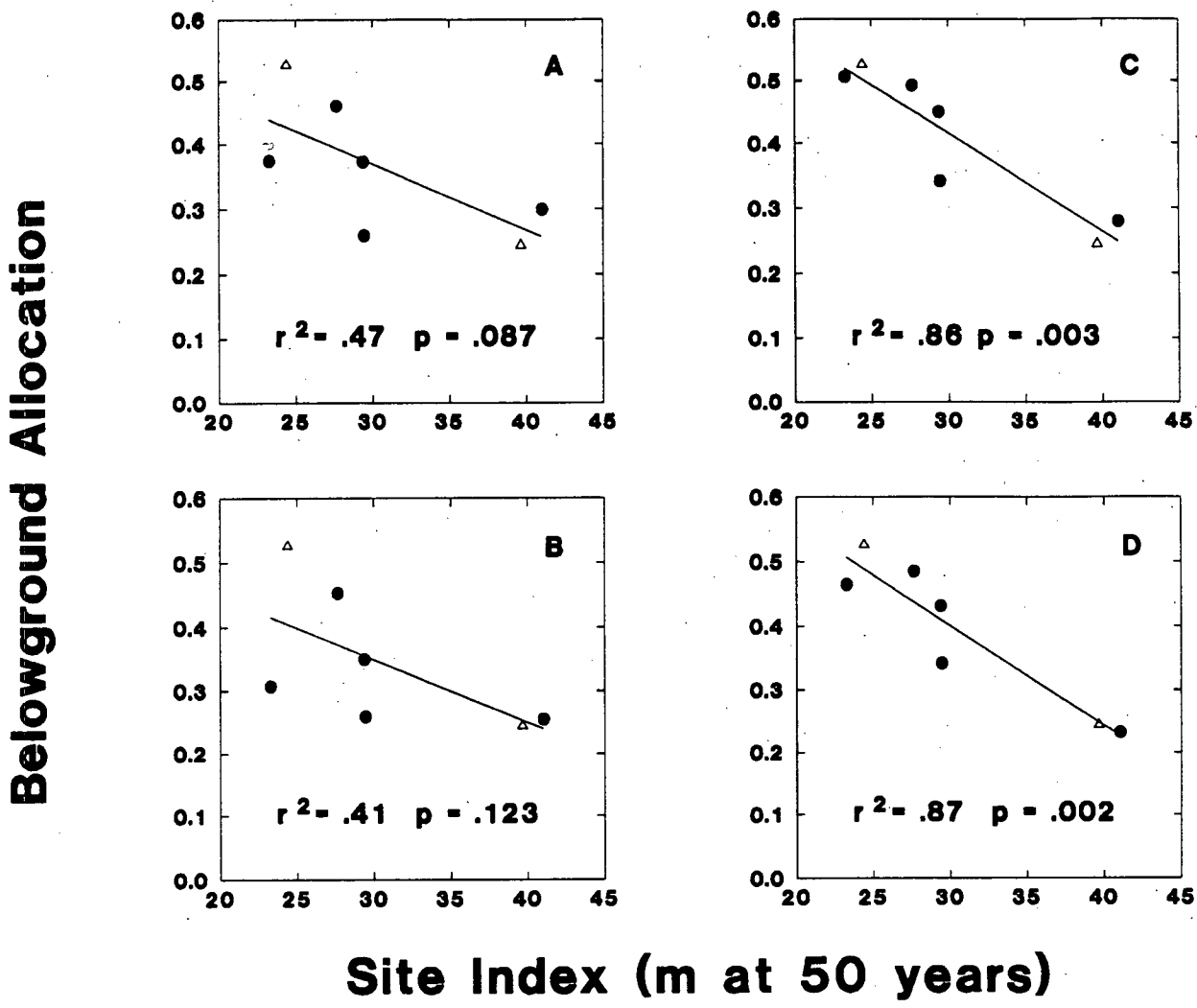

Figure 6.10 The partitioning of total production to above and belowground components for the 5 stands of this study (●) and the two stands of Keyes and Grier (1981) (Δ). Fine and small root turnover estimates are based on A: Production DM-method, B: Production AC-method, C: Mortality DM-method, D: Mortality AC-method. See text for further explanations.

7. SUMMARY AND CONCLUSIONS

1) Regression models for the prediction of aboveground biomass components of Douglas-fir that include a competition index in addition to dbh, are significant improvements over models which use dbh only. Of the four competition indices tested, the Growing Space Index (GSI) (Lin 1974) was the best independent variable in addition to dbh for the prediction of foliage, branchwood, and stemwood biomass.

2) Foliage biomass predicted with the GSI model appears to reach a steady state in some Douglas-fir stands, despite the continuing increase in basal area in these stands. Foliage biomass regression models based on dbh only do not predict this stabilization of foliage biomass.

3) In 1985, aboveground biomass in 12 Douglas-fir stands, with site index 19.5 to 41.3 m at 50 years and age 32 to 70 years, ranged from 135 to 573 Mg ha^{-1}. The aboveground biomass was distributed among the major components as follows: foliage 2 - 6%, branches 4 - 9%, stemwood 73 - 81%, and stembark 12 - 13%. Coarse root biomass was equal to 20 - 23% of the aboveground biomass.

4) In the period between 1985 and 1987, annual aboveground production (ANPP) in these stands ranged from 4.7 to 16.0 Mg ha^{-1} $year^{-1}$. Aboveground production was distributed among the major components in the following proportions: foliage 9 - 31%, branches 12 -23%, stemwood, 42 - 68%, stembark 7 - 11%. Coarse root production was equal to 13 - 16% of the aboveground production.

5) Live fine root (0-2mm) biomass showed a similar seasonal pattern of variation in all five stands that were sampled. A maximum value was reached in May or June, and a minimum value in August or October.

6) Biomass of living fine roots (0-2 mm) in May 1985 ranged from 1.82 to 7.91 Mg ha^{-1}, and that of living small roots (2-5 mm) ranged from 0.59 to 4.10 Mg ha^{-1}.

7) Different estimates were obtained for production and mortality in both fine and small roots. Estimates derived using the decision-matrix ranged from 1.12 to 5.14 Mg $ha^{-1}year^{-1}$ for fine root production, and from 2.15 to 4.89 Mg $ha^{-1}year^{-1}$ for fine root mortality. Small root production and mortality estimates ranged from 0.51 to 2.22 and from 0.88 to 2.13 Mg $ha^{-1}year^{-1}$, respectively. The differences in fine root turnover estimates derived from fine root production and mortality data are probably attributable to the unusually dry conditions during the summer of 1985. In particular, the lower site index stands were not able to replace by the subsequent spring all living fine roots which had died during the summer.

8) A highly significant regression model (Equation 6.1), which uses stand foliage biomass and site index as independent variables, accounted for 56.5% of the variation in foliage efficiency (based on ANPP) observed in 72 data points which represented 12 plots and 6 measurement periods. The model suggests that foliage efficiency decreases with increasing stand foliage biomass and increases with increasing site index.

9) Based on the above model, it would appear that there is an optimum foliage biomass at which total aboveground production is maximized. This optimum foliage biomass appears to increase with increasing site index.

10) With increasing site index, a decreasing proportion of total production is allocated to belowground stand components. The site with the lowest site index allocated from 31 to 51% of total production to belowground components while the site with the highest site index allocated from 23 to 30%. The ranges in estimates are due to the differences between production and mortality estimates of fine and small roots, as discussed above.

11) The relationship between the proportion of total production allocated belowground and site index that was observed in the five stands of this study strongly supports a similar observation by Keyes and Grier (1981) in two Douglas-fir stands of high and low site quality.

12) Future predictions of the responses of forest ecosystems to environmental change and silvicultural treatments should be based on a quantitative understanding of shifts in carbon allocation patterns in forest stands.

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