COMPARATIVE STUDY OF NUTRIENT CYCLING IN THE SUBALPINE MOUNTAIN HEMLOCK ZONE OF BRITISH COLUMBIA

by

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ABSTRACT

This study was undertaken to compare the overstory above-ground biomass, net primary production, and nutrient cycle in three common types of subalpine coastal forests near Vancouver, B.C. Canada. Twelve sample plots, representing three plant associations of different moisture regime, were established along an elevation transect. The following parameters were determined on each plot: overstory litterfall biomass and its macronutrient content, overstory throughfall volume and its macronutrient content, above-ground tree biomass and its macronutrient content, tree bole wood increment, annual net primary production and its macronutrient content, mean depth of forest floor and its biomass. The quantity of macronutrients supplied in incident precipitation was measured in three forest openings in the vicinity of the sample plots. Litterfall was sampled for 24 months, while throughfall and incident precipitation were sampled during the summers of three consecutive years. Diameter increment for the last 20 years was measured on increment cores obtained from 95 randomly selected trees. Increment of tree boles was calculated from allometric volume equations and combined with data on litter production to provide the estimate of net primary production. Distribution of biomass and macronutrients in the above-ground tree layer was calculated by logarithmic equations prepared in a preliminary study.

Sample plots ranged in elevation from 1250 to 1450 m. Tree cover consisted of mountain hemlock and Pacific silver fir in

various proportions with some yellow-cedar at the top and some western hemlock at the bottom of the elevation transect. Mean age of trees on the sample plots ranged from 295 to 440 years.

The above-ground tree standing biomass on the sample plots was 389-731 t/ha, with the largest volumes on the mesic sites. The annual net primary production was 1.77-3.35 t/ha. The biomass of overstory above-ground litterfall was 1.48-3.02 t/(ha•a); the amount of macronutrients in litterfall was 24-41 kg/(ha•a). The largest litter production was on mesic sites. There was a considerable amount of epiphytic lichens in the litterfall (71-426 kg/(ha•a)).

The amount of nitrogen in incident precipitation was greater than in throughfall, indicating that the tree canopy extracted nitrogen from rainwater. More than 1 kg/ha of nitrogen was extracted from rainwater during the summer sampling period. In contrast, up to 3 kg/ha of potassium, 1 kg/ha of calcium and 10 kg/ha of sulphur were leached from the tree canopy during the 13 weeks summer sampling period. It is possible that the high value for sulphur reflects the presence of a pulpmill about 20 km southwest of the study area.

The results of the study were used to test the hypothesis that differences in phytosociological characteristics occurring on a topographic sequence along relatively short elevation transects are accompanied by sufficiently large changes in patterns of ecosystem function to distinguish these sites on a functional basis. Analysis of the data supported this hypothesis.

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CHAPTER 1

INTRODUCTION

With the exception of occasional natural disasters such as fire, windthrow, landslide and insect kill, the high-elevation forests in the subalpine regions of coastal British Columbia have remained relatively undisturbed until recently. However, logging activities in these forests have increased substantially over the past two decades, and in many places the forest has been clearcut right up to the timberline.

In some regions harvesting of coastal subalpine forests has already occurred on a large scale. Clearcuts covering many square miles have appeared in many places.

Relatively little is known about subalpine forest ecosystems in British Columbia: their stability, resilience, and suitability for conversion to managed, productive forests. Descriptive studies of these forests have been reported by Krajina (1959, 1965) and his students Peterson (1964) and Brooke (1965, 1966, 1969), culminating in a treatise on the subalpine plant communities of southwestern coastal British Columbia (Brooke, Peterson and Krajina 1970). However, productivity and biogeochemical cycling of elements were not studied and there is a paucity of this type of information in the literataure.

Large areas of the coastal subalpine forests of British Columbia are in a mature to over-mature stage; tree ages of 500 years or more are not uncommon. The timber volume in some cases may be over 1000 m^3/ha, tree height over 50 m and tree diameter at breast height between 1 and 1.5 m. Apparently many of these ecosystems have not been altered by any drastic changes for hundreds of years. Many are in a steady state (or approaching it) in which the characteristics of the ecosystem are either not changing or their rate of change is too slow to be measured.

The limited geographic extent of these ecosystems, the lack of data about their dynamics, their apparently increasing economic importance in a world that is demanding more and more fiber and the ample evidence that conventional, low-elevation approaches to harvesting and management frequently have produced less than desirable consequences led to the study reported in this thesis. The study was one component of a broader investigation, the results of which will be reported elsewhere (e.g. Yarie 1978, Nuszdorfer 1979, Kimmins *et al*. in preparation).

1.1. Objectives

The main objectives of this study were:

1. To quantify the most important nutrient pathways of the overstory biogeochemical cycle (Switzer and Nelson 1972) (such as mineral uptake by net primary production and mineral elements returned with above-ground litterfall and throughfall) in undisturbed and mature types of the three most widespread plant associations in the Subalpine Mountain Hemlock Zone (Krajina 1965) in the vicinity of Vancouver, British Columbia. Nutrient dynamics resulting from annual root mortality were not included in the study.

2. To estimate the input of nutrients by atmospheric fallout to these plant associations.
3. To estimate the net primary productivity and true increment of trees in these plant associations.
4. To test the hypothesis that differences in plant species composition (as reflected in biogeoclimatic classification of subalpine forest ecosystems proposed by Brooke *et al.*, 1970) among three sites located on a short elevation transect are accompanied by sufficiently large changes in patterns of ecosystem function to distinguish these sites on a functional basis.
5. To test the hypothesis that the same plant association (sensu Brooke *et al.*, 1970) occurring on two different parent materials cannot be distinguished by different patterns of ecosystem function (at least for the parameters measured). In other words, identical plant associations have identical or very similar patterns of ecosystem function, independent of some environmental differences between them.
6. To test the hypothesis that the functional classification of world ecosystems proposed by Rodin and Bazilevich (1967) can also be usefully applied on a local scale, in classifying the plant associations along a topographic transect within one biogeoclimatic zone (Subalpine Mountain Hemlock Zone).

To fulfil these objectives the following major steps were undertaken:

1. Three plant associations were identified (primarily by their plant species composition) and sample plots were established along an elevation transect (Fig. 1.1). These three plant associations had soils derived from parent material of volcanic origin. One of the plant associations was replicated on a different geologic material (plutonic) giving a fourth study site.
2. A detailed description of the sample plots was made, which included their size, a list of plant species and mensurational data (dbh, height and crown length) for all trees on the sample plots.
3. Increment cores were taken to determine age and dbh increment for a selected sample of trees on the sample plots.
4. Volume, biomass, and nutrient content were calculated for all standing trees on the sample plots.
5. Tree bole volume increment of standing trees and immobilization of mineral elements in this increment were calculated.
6. Tree litterfall and throughfall were monitored for 24 months. The resulting data were processed to yield estimates of the biomass of annual litterfall and the amount of nutrients transferred annually by throughfall and litterfall.
7. Net primary production and the nutrient content of net primary production were calculated.

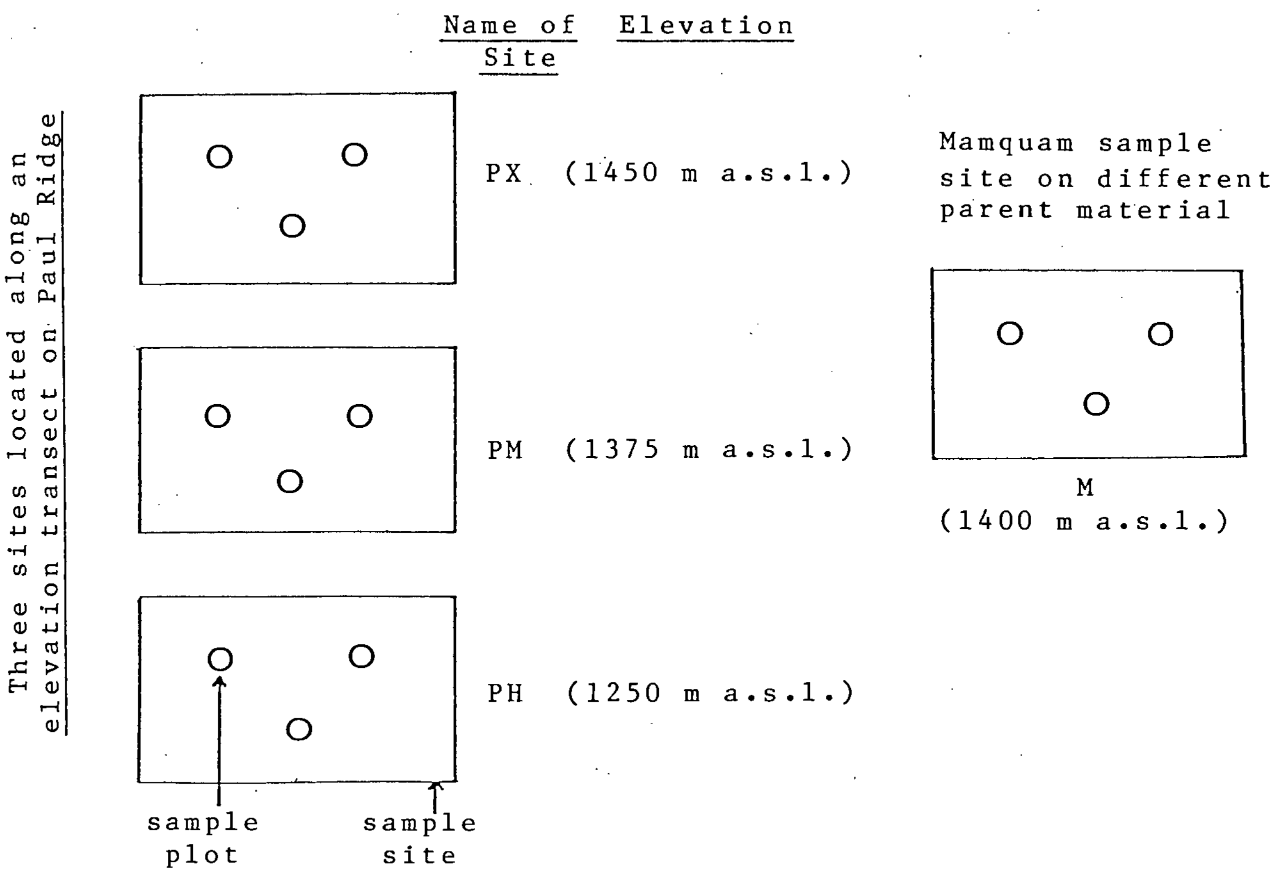
8. The four sample sites were then characterized and compared in terms of litter biomass, quantity of mineral elements within litter, and throughfall.

1.2. Design of the study

Four sample sites were selected to represent the three plant associations (Krajina 1969). Three of the sites were ordered along the topographic sequence in such a way that they differed in the following environmental parameters:

1. elevation (1250 - 1450 m)
2. length of snow duration (3 to 4 weeks difference from bottom to top of the sequence)
3. hygrotope (xeric to hygric)

The soil parent material of the fourth site differed from that of the other three. This design can be represented diagramatically as follows:



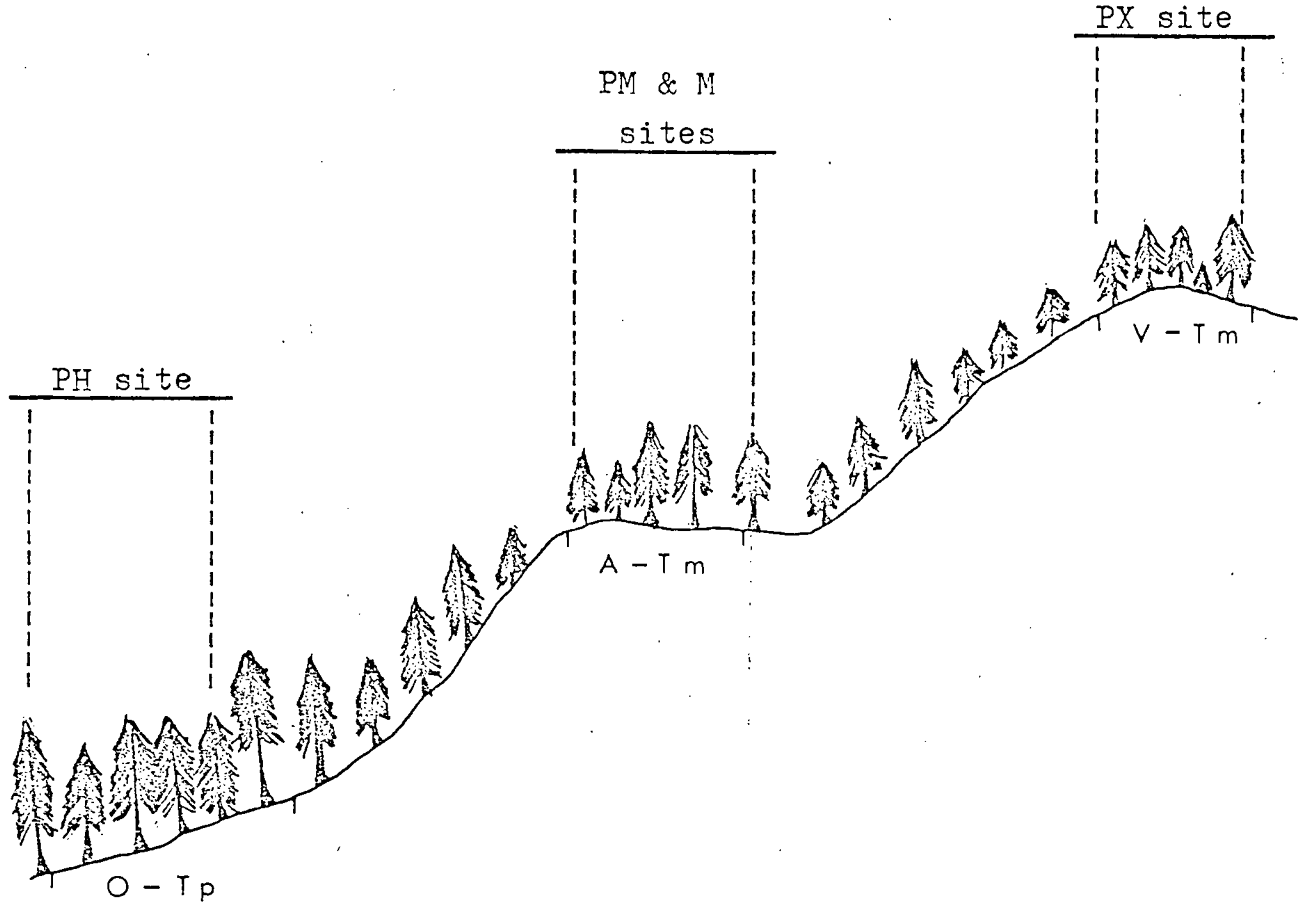


Figure 1.1. Diagram showing the location of the plant associations that were studied along the elevation transect.

Xeric site	V - Tm	Vaccinio-Tsugetum mertensianae (Brooke <u>et</u> <u>al</u>. 1970)
Mesic site	A - Tm	Abieto-Tsugetum mertensianae (Brooke <u>et</u> <u>al</u>. 1970)
Hygric site	O - Tp	Oplopanaco-Thujetum plicatae (Brooke <u>et</u> <u>al</u>. 1970)

1.3 Units used in the thesis

All results in this thesis are reported in metric units. The results from older publications in Chapter 2 - Literature review, were converted to metric units. The nomenclature of units follows National Standard of Canada (1976) and Selected metric units and conversion factors for Canadian forestry (1974). All units used throughout this thesis and their conversion to British units are defined in these two publications.

CHAPTER 2

LITERATURE REVIEW

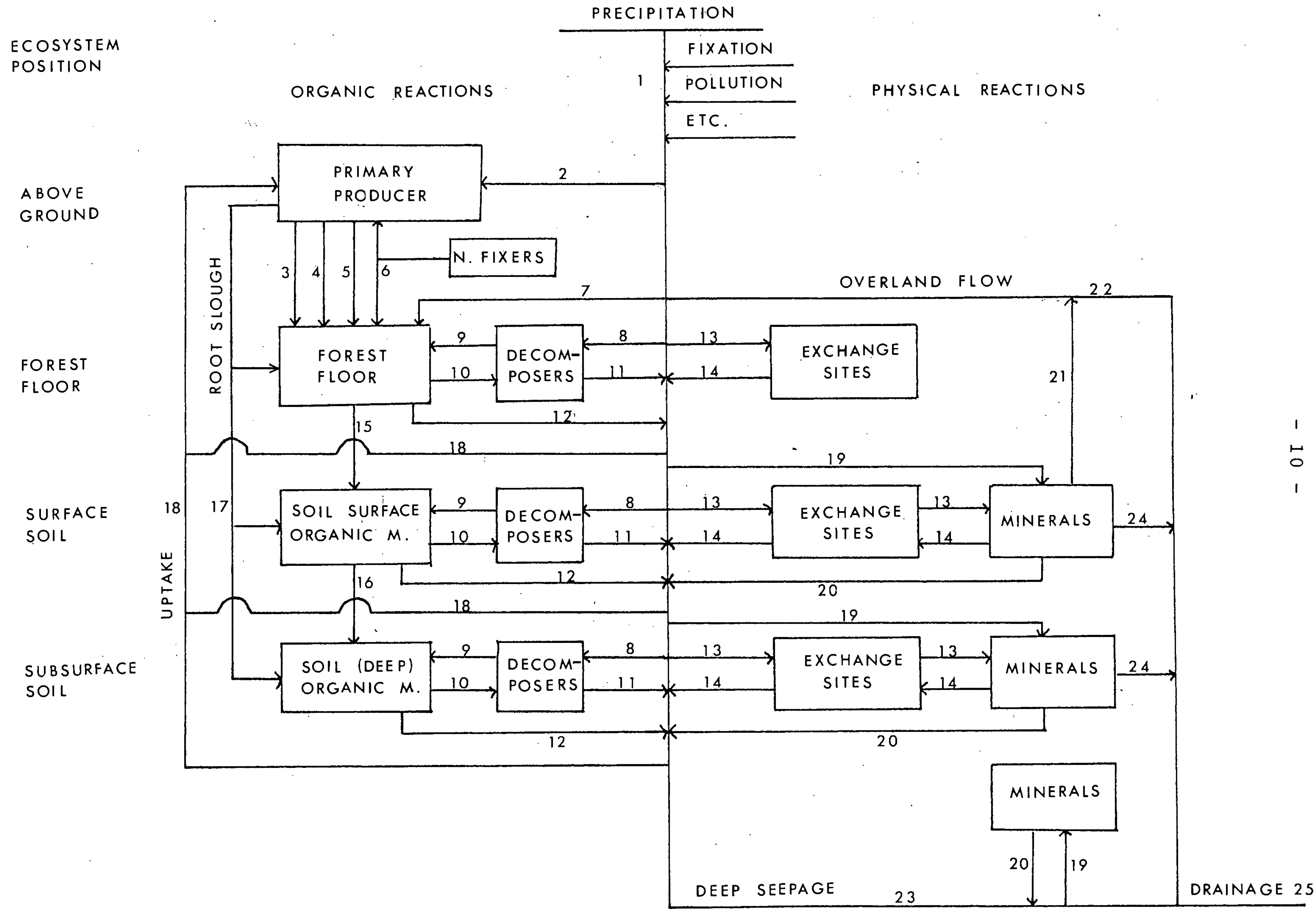
The first published discussion of the exchange of mineral elements between soil and plant biomass was perhaps that of Liebig (1840). This was followed during the second half of the 19th century by several other researchers who studied the uptake of ash elements by plants. Perhaps the most important papers from that period came from Ebermayer (1876, 1882) and Weber (1876, 1881). The subsequent development of studies on nutrient turnover is well reviewed by Rodin and Bazilevich (1967).

During the last decade a great number of publications concerned with the cycle of chemical elements in biological systems have appeared. However, relatively few of these have been concerned with the entire nutrient cycle of a forest ecosystem (e.g. Duvigneaud and Denaeyer-DeSmet 1967, Cole et al. 1967, Curlin 1971, Gessel et al. 1973, Switzer and Nelson 1972, Johnson and Riser 1974, Malkonen 1974, Turner and Singer 1975, Foster and Morrison 1976). Most students of forest biogeochemistry have limited their studies to only one or a few ecosystem compartments or pathways of nutrient transfer. The reason for this limitation is easily understood if one considers the complexity of the nutrient cycle in a forest ecosystem, as shown in the nutrient cycling flow diagram presented in Figure 2.1. There are 10 major compartments and 24 pathways in this model. To quantify all these pathways and compartments is a formidable task even for a large and experienced group of researchers.

Figure 2.1. A visual model of pools and pathways of mineral cycling in a forest ecosystem. (modified after Gessel *et al.* 1973)

Key to the transfers in the elemental cycling flow diagram. (modified after Turner 1975)

1. Atmospheric inputs, physical (e.g., precipitation, N-fixation, pollution, fertilization, etc.).
2. Ion absorption and/or interception by the aerial portion of the primary producer.
3. Litterfall.
4. Stemflow.
5. Leaf wash.
6. Biological N-fixation.
7. Ion input from the atmosphere.
8. Ion immobilization.
9. Decomposer death.
10. Organic matter consumption by decomposers.
11. Ion mineralization by the decomposers.
12. Direct ion release from the organic matter.
13. Held to ion exchange sites (both mineral and organic).
14. Release from ion exchange sites (both mineral and organic).
15. Organic transport from the forest floor to surface mineral soil by leaching and organisms.
16. Organic transport within the soil primarily by organic colloidal leaching.
17. Root sloughing.
18. Uptake by primary producers.
19. Ion fixation and precipitation.
20. Mineral weathering.
21. Surface erosion.
22. Overland flow.
23. Deep seepage.
24. Drainage loss.
25. Drainage out of ecosystem.



PRECIPITATION
FIXATION
POLLUTION
ETC.
ECOSYSTEM POSITION
ORGANIC REACTIONS
PHYSICAL REACTIONS
ABOVE GROUND
FOREST FLOOR
SURFACE SOIL
SUBSURFACE SOIL
PRIMARY PRODUCER
N. FIXERS
ROOT SLOUGH
UPTAKE
OVERLAND FLOW
FOREST FLOOR
DECOM-POSERS
EXCHANGE SITES
SOIL SURFACE ORGANIC M.
MINERALS
SOIL (DEEP) ORGANIC M.
DEEP SEEPAGE
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My study was concerned with net primary production, litterfall, throughfall, input from the atmosphere and nutrient relocation within foliage in subalpine forest ecosystems. The literature review is therefore limited to publications relevant to these topics.

2.1. Net primary production of forest ecosystems

The methods for estimating net primary production of forest ecosystems are summarized by Newbould (1967), Whittaker and Woodwell (1971), Whittaker and Marks (1975), and Chapman (1976).

There are two major methods. In the first, the biomass of the community must be estimated twice (at times t_1 and t_2) with sufficient accuracy to assure a reliable estimate of the biomass increment ΔB. Plant losses by death and shedding (L) and to consumer organisms (G) must be estimated for the same time period, and then the net primary production (Pn) can be calculated as:

$$Pn = \Delta B + L + G$$

In the second method, plants are measured only once (at the end of the growing season). Separation of the biomass into current year organs and older parts and stem analysis of perennial stem and branch biomass yields estimates of the amount of biomass formed over the past year. The apparent growth increment (B_2N) in this procedure corresponds to (Pn-LN-GN) where:

LN - litter from newly formed biomass

GN - loss through consumption by heterotrophic organisms, from newly formed biomass

B_2 - biomass of a plant community at time t_2 ($= t_1 + \Delta t$)

The net production is then estimated:

$$Pn = B_2N + LN + GN$$

B_2N alone would be an underestimate of the real net production, whereas (B_2+L+G) would be an overestimate (Newbould 1967).

Most studies of the net primary productivity of forests are based on direct measurements of sizes and weights of plants and plant parts (Newbould 1967, Whittaker and Woodwell 1971). There are at least three methods of synthesizing such measurements into production estimates: mean-tree, production ratio, and regression analysis (Whittaker and Marks 1975). The regression analysis approach is most often used and gives the most accurate results. In this method some readily measured parameter such as stem diameter or tree height is correlated with the biomass of various tree components (tree bole, bark, branches, foliage) as well as the whole tree biomass. These relationships are then used in combination with appropriate mensurational data to calculate the biomass and production of the whole forest stand.

A model that has been widely employed in the regression analysis approach is based upon the law of allometric growth:

$$\log Y = a + b \log X$$

Where: Y = weight of the standing crop, or some component of the standing crop or production

X = some readily measured parameter of the standing crop

a and b are constants.

This type of expression has been used to relate measurements such as basal area, diameter at breast height (dbh) or height to weight, volume or produciton (Ovington and Madgwick 1959, Whittaker and Woodwell 1968, Satoo 1970, Turner and Singer 1975, and others).

In some cases (Yoda 1968, Krumlik 1974, Madgwick and Satoo 1975, Gholz et al. 1976, and others) a more satisfactory estimate can be obtained by including measurements of both diameter and height in the regression:

$$\log Y = a + b \log (D^2H)$$

If the estimate of the total standing crop is obtained from an allometric regression by taking the sum of the antilogs of the predicted values for the individuals, it will be biased and give an underestimate of the true value. Baskerville (1972) and Mountford and Bunce (1973) suggest multiplication by a factor $e^{s^2/2}$ to correct for this bias:

$$\hat{y} = e^{(\hat{\mu} = 6^2/2)} \qquad \text{(Baskerville 1972)}$$

where $\hat{y}$ = the estimated mean in arithmetic units of the (skewed) Y distribution

6^2 = sample variance of the logarithmic equation

or

$$W = e^{s^2/2} \sum_{i=1}^{N} e^{a} + bx_i \qquad \text{(Mountford and Bunce 1973)}$$

where W = total standing crop

S^2 = estimated variance about the regression line.

x = some readily measured parameter of the standing crop.

a and b are constants.

The equations of Baskerville (1972) and Mountford and Bunce (1973) have identical meaning even though they are written in different terms.

Kira and Shidei (1967) give an example of the accuracy of biomass estimation obtained by the allometric method in comparison with the direct determination of biomass (i.e. weighing, physical size measurements, etc.). (Table 2.1). Values obtained by the allometric method are very close to the values determined directly; the difference varies from -4.5% to +11.5%.

Table 2.1. Comparison of the values of above-ground biomass determined directly and by calculation for a clear-felled plot (10 x 40 m) in Khao Chon rain forest, Southern Thailand (Ogawa et al. 1965)

	Stem t/ha	Branch t/ha	Total wood t/ha	Leaf t/ha	Total shoot t/ha	Leaf area index ha/ha
Determined directly	292	104	396	7.8	404	10.7
Calculated	279	116	395	8.2	403	11.2
Relative error %	-4.5	11.5	-0.25	5.1	-0.15	4.7

The annual net primary production in fully formed biogeocoenoses (30-80 years old) in the coniferous and mixed forest subzone of the Soviet Union varies between 7 and 20 t/ha (Rodin and Bazilevich 1967). In the warm temperate regions of the Japanese Archipelago the annual net primary production of broadleaf evergreen forests ranges between 10 and 30 t/ha of dry matter, with the highest frequency at 15-20 t/ha (Kira and Shidei 1967). Pine forests have a somewhat lower rate, with a peak at 10-15 t/(ha•a), while deciduous broadleaf forests in the cool temperate zone have the lowest net production, at only 5-10 t/(ha•a). Coniferous forests in subarctic and subalpine regions have a higher production with a peak of 10-15 t/(ha•a) (Kira and Shidei 1967, Tadaki *et al*. 1970). Evergreen forests, whether coniferous or broadleaf, apparently are more productive than deciduous forests.

The net primary production of forests of the Pacific Northwest falls within the range indicated by Kira and Shidei (1967) and by Rodin and Bazilevich (1967). Plant communities dominated by 450 year-old Douglas-fir* in the cool-temperate western hemlock forest zone of western Oregon had above-ground net primary production from 6.3 to 10.1 t/(ha•a) (Grier and Logan, 1977). Comparable values were 10.3 t/(ha•a) for a 100-120 year-old western hemlock-Sitka spruce stand in the Sitka spruce zone, 12.7 t/(ha•a) for a 90-110 year-old Douglas-fir-western hemlock stand in the western hemlock zone, and 13.0 t/(ha•a) for a 100-130 year-old noble fir-Douglas-fir stand in the Pacific silver fir zone of western Oregon (Fujimori *et al*. 1976).

The absolute amount of net primary production varies in relation to the age, quality and stocking of the forest stand also in relation to biogeoclimatic and local ecological conditions. The maximum net primary production of conifers usually occurs between the ages of 40 and 70 years. The

* Latin names of plant species are in Appendix 1.

proportion of net primary production that goes into foliage remains fairly stable at approximately 38-45% (Rodin and Bazilevich 1967).

2.2 Turnover of nutrients in litterfall and throughfall in forest ecosystems

A great number of studies have examined nutrient turnover in litterfall and throughfall. Comprehensive reviews of litterfall studies were published by Viro (1955), Bray and Gorham (1964), and Rodin and Bazilevich (1967). Comprehensive reviews of throughfall and foliar leaching have been presented by Rodin and Bazilevich (1967) and by Tukey (1970), respectively.

2.2.1. Litter production

Most of the litterfall studies have been undertaken in forests located in low and medium elevation (under 1000 m) (Bray and Gorham 1964). Few studies have been conducted on litterfall in subalpine forests at high elevations.

Annual above-ground litter production ranges from 1 t/(ha•a) in arctic-alpine forests to 11 t/(ha•a) in equatorial forests (Bray and Gorham 1964). Rodin and Bazilevich (1967) reported values of total litterfall for coniferous forests in cool temperate regions of between 2 and 7 t/(ha•a). Some recent values for litterfall in the Pacific Northwest appear to be in close agreement with this range (Table 2.2). The amount of litterfall depends on stand composition, age, climate, nutrient status and silvicultural treatment (Bray and Gorham 1964), but is not dependent on the amount of standing tree biomass (Rodin and

Basilevich 1967) and may not be dependent on the successional stage of the forest (Hurd 1971).

In the majority of mature forests of the northern coniferous region the biomass of total litterfall is equal to 1.5-2% of perennial plant biomass (Rodin and Bazilevich 1967). This proportion is increased up to 9% in young forest plantations and varies between 5 and 10% in mountain pine forests (Rodin and Bazilevich 1967). A distinct relationship may be established between the quantities of litterfall, net primary production, and the green part of the biomass (Rodin and Bazilevich 1967). There is the possibility that above-ground litterfall might serve as a simple and convenient index to net primary production (Bray and Gorham 1964).

The proportion of different litterfall components varies greatly from place to place. Results of eight studies, reviewed by Bray and Gorham (1964) indicated that leaf material contributed 60-76% of litter, branches 12-15%, bark 1-14%, and fruit 1-7%. According to Rodin and Bazilevich (1967), the green parts account for 40-50%, perennial above ground parts for 30-40%, and roots 5-20%.

Return of 11 nutrient elements with litterfall in coniferous and mixed forest varies widely, between 40 and 230 kg/(ha•a) (Rodin and Bazilevich 1967). Table 2.3 gives some values for nutrients returned to the forest floor in litterfall in the Pacific Northwest of U.S.A. and Canada.

Table 2.2. Mean annual litter production of some forest stands in the Pacific Northwest area of the U.S.A. and Canada

Author	Location	Altitude m	Age (approx.)	Forest type	Litterfall kg/(ha•a)
Tarrant *et al.* 1951				Pacific silver fir western hemlock	1772+ 1048+
Cole *et al.* 1967	Washington	210	36	Douglas-fir	3112
Hurd 1971	southeast Alaska			western hemlock/ Sitka spruce	2941
Abee and Lavender 1972	Oregon	610	450	western hemlock	5131
		975	450	western hemlock/ Pacific silver fir	4530
		1311	450	Pacific silver fir	6916
Kimmins 1975	British Columbia	100	90	Douglas-fir/ western hemlock-salal -moss -swordfern	 3906* 4389* 5142*
Turner and Singer 1975	Washington	1200	175	Pacific silver fir/ western hemlock	3017

* Amount of litterfall was stated for a 24 month period, and interpolated for a 12 month period

+ needle litterfall only

Table 2.3. Annual nutrient quantities returned to the forest floor in litterfall by some Pacific Northwest forest stands (kg/(ha•a)) and some other forest stands

Age	Altitude m	N	P	K	Ca	Mg	Author
		22.2	2.1	4.3	16.2	1.0	Tarrant *et al.* 1951[1]
		8.1	1.1	2.0	6.3	0.7	Tarrant *et al.* 1951[2]
36	210	13.6	0.2	2.7	11.1	3.5	Cole *et al.* 1967[3]
	457	21.9	3.9	6.4	71.5	1.1	Abee and Lavender 1972
	762	32.7	5.6	9.8	63.1	1.1	Abee and Lavender 1972
175	1200	16.3	2.0	7.3	39.7	2.3	Turner and Singer 1975
		15.1	1.0	4.0	10.0	2.0	Chandler 1943[4]
		36.0	2.6	3.5	32.3	4.6	Chandler 1943[5]
		-	-	4.7	17.8	2.0	Grier and Cole 1972[6]

1 Pacific silver fir, foliage litter only
2 Western hemlock, foliage litter only
3 The Mg value is from Turner and Singer (1975)
4 Hemlock, foliage only, New York State
5 Balsam fir, foliage only, New York State
6 location Washington State. Other locations as in Table 2.2.

The green, annually-alienated parts of plants contain the greatest proportion of the mineral elements (up to 90%) in the above-ground litterfall. Because the mineral elements of the green parts make such a significant contribution to litterfall, the basic features of the return of mineral elements to the soil may be assessed from data for the leaf litterfall alone without particular loss of accuracy (Rodin and Bazilevich 1967).

Litterfall is unevenly distributed throughout the year. In coniferous forests of the cool temperate zone, most of the litter falls during autumn and winter. Abee and Lavender (1972) observed in the old Douglas-fir stands in Oregon that the needle cast was greatest in the fall, decreased during the winter, and gradually increased during spring.

Methods for the estimation of litter production are discussed by Newbould (1967), Medwecka-Kornas (1968), and Chapman (1976). Medwecka-Kornas (1968) suggests circular traps and plots to decrease the edge effect. The size and shape of the litter traps used by different investigators has varied greatly. Most investigators have used square litter traps of varying size: 1.22 x 1.22 m (4 x 4 ft) were used by Chandler (1943); 0.61 x 0.61 m (2 x 2 ft) by Owen (1954); 0.457 x 0.457 m (18 x 18 in.) by Cole _et al._ (1967), Grier _et al._ (1972) and Turner and Singer (1975); 0.508 x 0.508 m (20 x 20 in.) by Abee and Lavender (1972); 0.5 x 0.5 m by Cromack and Monk (1975), and 1 x 1 m by Johnson and Risser (1974) and by Kimmins (1975). Rectangular traps 0.305 x 0.61 m (1 x 2 ft) were used by Hurd (1971), and circular traps with a diameter of 0.53 m were used by Gosz _et al._ (1972).

2.2.2. Throughfall

Leaching is defined as the removal of substances from plants by the action of aqueous solutions, such as rain, dew, mist, and fog (Tukey 1970). Throughfall (crownwash) is the solution that has passed through the canopy of the stand; hence, its nutrient content is the sum of input by precipitation plus nutrients leached from the canopy (leaves and twigs) and/or the removal of dust and tree organic matter from the surface (Turner 1975). Loss from the solution may occur by foliar re-absorption (Rapp cit. by Turner 1975, Carlisle *et al*. 1966).

Not all the rainwater that falls on tree crowns reaches the forest floor. Part of it evaporates from the foliage, branches and tree trunks. This phenomenon is called interception. The proportion of rainwater lost by interception depends on the tree species, tree age, density, amount of rainfall, and wind velocity, and may account for up to 80% of the rainfall in the case of young dense coniferous stands and small amounts of precipitation (Ovington 1954). A summary of rainfall interception for certain conifers in North America was prepared by Helvey (1971) and in England by Ovington (1954), while Hoover (1971) discussed the snow interception and redistribution in the forest. A mathematical model for predicting rainfall interception in forests was developed by Rutter *et al*. (1975).

Tree canopies function also as a filter to catch dust and aerosols, and on foggy days vapor condenses on foliage and twigs and drips to the forest floor. The amount of rainwater and nutrients under a set of plastic nets and in an open collector were compared by Nihlgard (1970). He found that in spite of approximately equal amounts of rainwater, the concentration of nutrients, and therefore the amount of nutrients, was much higher in the rainwater under the plastic nets than in the incident rainfall (Table 2.4.)

Table 2.4. Average values in kg/ha (sampling period 8 months) of the nutrients in the incident rainfall (1) and in the rainwater under a plastic net (2) (Nihlgard 1970)

	Precip. quantity	N	P	S	K	Ca	Mg
1	276	2.13	19	2.2	0.29	0.99	0.20
2	291	5.17	72	8.4	1.00	5.47	1.60

Another experiment of this kind was undertaken by Schlesinger and Reiners (1974). Their apparatus consisted of pairs of polypropylene buckets. One bucket of each pair contained plastic artificial foliage selected to structurally resemble balsam fir (Abies balsamea (L.) Mill.). The results of this experiment are summarized in Tables 2.5 and 2.6. The division of throughfall nutrients between surface wash and actual leaching still remains unanswered.

A few examples of the concentration of chemical elements in throughfall are given in Table 2.7. Some common values for the amount of chemical elements reaching the forest floor in the throughfall are presented in Table 2.8.

Table 2.5 Volume (mL) and cationic concentrations (mg/L) of precipitation captured by open buckets and foliar interception collectors at 1372 m on Mt. Moosilauke, N.H. (Schlesinger and Reiners 1974)

Collector	Volume	Ca	Mg	Na	K
open	6 821	0.21	0.06	0.19	0.11
foliar	30 558	0.39	0.08	0.20	0.15

Table 2.6 Deposition of five cations in µg/day captured by open and foliar collectors at 1372 m on Mt. Moosilauke. Collectors were mounted for periods of a week at monthly intervals from December through August (Schlesinger and Reiners 1974)

Collector	Ca	Mg	Na	K
open	20	6	18	11
foliar	166	36	88	63

Some aspects of throughfall sampling are discussed by Kimmins (1973), such as the variability of volume and cation concentration among throughfall samples, different methods of throughfall sampling, and the influecne of the length of the collection period on the data variability. He concluded that the use of fixed collectors in heterogenous forests results in high spatial variance of throughfall parameters; therefore, excessively large numbers of collectors are required to obtain

Table 2.7. Concentrations of macronutrients in throughfall (mg/L)

N	P	K	Ca	Mg	Reference
-	0.12	6.3	4.0	-	Tamm 1951
-	0.05-1.0	0.2-42.8	1.0-128.8	0.5-12.5	Madgwick and Ovington 1959
0.2	0.18	1.1	0.4	0.18	Abee 1973[1]

[1]Pacific silver fir stand at elevation of 1311 m. Values are average for 2 years.

Table 2.8. Mean annual amount of elements in throughfall (in kg/(ha·a))

N	P	K	Ca	Mg	Reference
-	-	22.6	24.1	8.8	Madgwick and Ovington 1959
8.8	1.3	28.1	17.2	9.4	Carlisle *et al.* 1966
8.5	0.1	9.9	9.0	3.0	Nihlgard 1970
10.6	0.6	26.9	7.0	2.0	Eaton *et al.* 1973
1.5	0.3	10.7	3.5	-	Cole *et al.* 1967
3.4	2.7	21.7	4.4	2.1	Abee and Lavender 1972
1.3	0.1	11.5	5.4	2.1	Turner and Singer 1975
-	-	7.8	6.1	1.3	Kimmins 1975[1]
-	-	19.5	12.2	3.7	Kimmins 1975[2]

[1]salal plot, the lowest throughfall value given

[2]salmonberry plot, the highest throughfall value given

reasonably accurate and precise data. The number of collectors may be reduced using the "roving collector method". The major problem of this method and its reduced number of collectors is that while it may result in small standard errors as compared with the fixed collector method, it may be associated with less accurate estimates of the means.

2.2.3. Stemflow

Stemflow is the solution that is channelled down from the branches ot the stem and then flows down the bole of the tree. The nutrient content of stemflow is thus derived from incident precipitation, crown wash, and the washing of the tree trunk. The proportion of nutrients deposited on the forest floor by stemflow is usually, but not always, small. Nutrients in stemflow accounted for 1-4% of the total in the study of Foster and Gessel (1972), 5-10% of the throughfall in the study of Eaton et al. (1973), and 5-30% of the throughfall, depending upon the nutrient, in the study of Abee and Lavender (1972). Stemflow is generally a minor part of the return to the forest floor, but its importance varies with the species and the age of the stand. Stemflow is usually higher in nutrient concentration than throughfall (Turner 1975).

2.2.4 Total return to the forest floor

The total return of chemical elements to the forest floor is the sum of litterfall, throughfall, and stemflow. Examples for the Pacific Northwest are given in Table 2.9.

Table 2.9 Total return of elements to the forest floor (litterfall, throughfall, and stemflow, where studied) in kg/(ha•a)

N	P	K	Ca	Mg	Reference
16.4	0.6	15.8	18.5	-	Cole et al. 1967
30.7	7.5	29.8	71.7	3.2	Abee and Lavender 1972
17.6	2.1	18.8	45.1	4.4	Turner and Singer 1975

2.3 Input of nutrients to forest ecosystems

There are several different sources of input of nutrients to an ecosystem, such as wet precipitation and dry atmospheric fallout, the lateral movement of nutrients through the soil from adjacent areas, nitrogen fixation, faunal migration, and the weathering of soil minerals. In this study, only the inputs in precipitation and atmospheric fallout were considered.

A comprehensive review of the composition of atmospheric precipitation was published by Erickson (1952 and 1955). The input of nutrients through bulk fallout is very significant. In a study done in England, Carlisle et al. (1967) calculated that rainfall nutrients would more than replace the macronutrients in stems of oak on woodland managed on 12 years' rotation. This may not be the case in all ecosystems, since the input to the forest ecosystem studied by Carlisle et al. (1967) is considerably higher than average values for the Pacific Northwest (Cole et al. 1967, Turner and Singer 1975, Zeman 1973, Feller 1975, Kimmins

1975) (Table 2.11). But even in the areas with low values of aerial nutrient input, these nutrients represent a significant proportion of elements immobilized annually within tree biomass. Some values of the concentration of macronutrients in incidental rainfall are given in Table 2.10. The mean amount of macronutrients supplied by the incidental rainfall annually can be found in Table 2.11. These figures are probably underestimates since samples did not include dust and aerosols (see pages 22-23, Tables 2.4, 2.5, and 2.6).

2.4 Internal cycling: the transfer of nutrients within tree biomass

Redistribution and recycling of mineral elements within plant biomass have been observed and described by several researchers (Switzer and Nelson 1972, Johnson and Riser 1974, Malkonen 1974, Turner 1975, Turner and Singer 1975). Switzer and Nelson (1972) proposed the term "biochemical cycle" for this internal transfer of nutrients.

Nutrients are transferred from older to younger tissue. This transfer is apparently greatest when nutrients are potentially limiting to growth. Turner (1975) found that with increasing stand age and forest floor accumulation an increasing proportion of annual growth nutrient requirement was being supplied through internal redistribution. A 22-year-old Douglas-fir stand had a forest floor biomass of 20.5 t/ha, and about 70% and 85% of the annual N and P requirements, respectively, were taken from the soil. The remainder was supplied by redistribution. In the 95-year-old Douglas-fir stand

Table 2.10. Concentrations of macronutrients in incident rainfall (mg/L)

N	P	K	Ca	Mg	Reference
-	-	0.11	0.21	0.06	Schlensinger and Reiners 1974
-	0.04	0.3	0.5	-	Tamm 1951
-	-	0.5	2.7	0.22	Paterson 1975
0.61	-	-	-	-	Tabatabai and Laflen 1976
-	0.05-0.5	0.05-3.5	0.2-9.8	0.5-0.9	Madgwick and Ovington 1959
0.09	-	0.06	0.2	0.06	Feller 1975
0.07	0.01	0.02	0.21	0.06	Zeman 1973

Table 2.11. Mean annual amount of chemical elements in incident rainfall (kg/(ha·a))

N	P	K	Ca	Mg	Reference
9.5	0.4	3.0	7.3	4.6	Carlisle _et al._ 1966
9.1	0.4	3.9	12.5	5.4	Carlisle _et al._ 1967
-	-	2.8	10.7	4.2	Madgwick and Ovington 1959
8.2	0.07	1.9	3.5	0.9	Nihlgard 1970
1.8	0.05	0.4	0.9	0.2	Eaton _et al._ 1973[1]
6.2	-	-	-	-	Tabatabai and Laflen 1976
1.1	T*	0.8	2.8	-	Cole _et al._ 1967
1.3	0.4	0.8	0.6	0.1	Turner and Singer 1975
-	-	1.1	3.7	0.7	Kimmins 1975
1.7	0.4	0.9	7.2	2.2	Zeman 1973
5.2	-	1.3	4.8	1.3	Feller 1975

[1] for the period of June 1 to October 28, 1969

* trace

the forest floor biomass was 80.7 t/ha, and 42% and 62% of the annual N and P requirements, respectively, were obtained from the soil, the remainder being supplied by redistribution (Turner 1975).

Nutrient redistribution seems to be related to nutrient availability rather than tree age. Turner (1975) altered the patterns of nitrogen redistribution by changing its availability. Redistribution was increased by nitrogen stress created after a sawdust-sucrose mixture was added to the forest floor. On the other hand, urea (46% N) fertilization reduced redistribution.

Internal nutrient cycling deserves thorough study to elucidate its role in forest productivity.

CHAPTER 3

DESCRIPTION OF STUDY AREA

3.1. Location and description of sample plots

The study area is located in southwestern coastal British Columbia, about 55 km north of Vancouver and 10-14 km east of Squamish. Twelve sample plots were established, divided between two major localities. One group (9 sample plots) was located on Paul Ridge in the extreme southwestern corner of the Garibaldi Provincial Park (Appendix 9). These plots were on an elevation transect approximately 1.5 km long which was located on a west facing slope (Fig. 3.1.). The second group (3 plots) was located about 8.5 km southeast from the first group, just south of the Garibaldi Provincial Park boundary, on the east boundary of McMillan-Bloedel timber lease no. 3068. The area is about 3 km north of Mamquam River and 4 km east of Skookum Creek (Appendix 9). The size of the plots was approximately 0.1 ha (exact size of plots is given in Table 3.4).

3.1.1. Paul Ridge Plots

The first group of plots is referred to as the P-plots (from Paul Ridge). The nine P-plots were in three groups of three, each group being in a different plant association (see section 3.4 - Vegetation). These were located along an elevation transect and differed in moisture regime or hygrotope (sensu Krajina 1969). Sample plots of the highest sampling area were located on small ridges; the soil was therefore well drained. Sample plots of the medium elevation area were located on relatively flat terrain with moderately well drained soil and

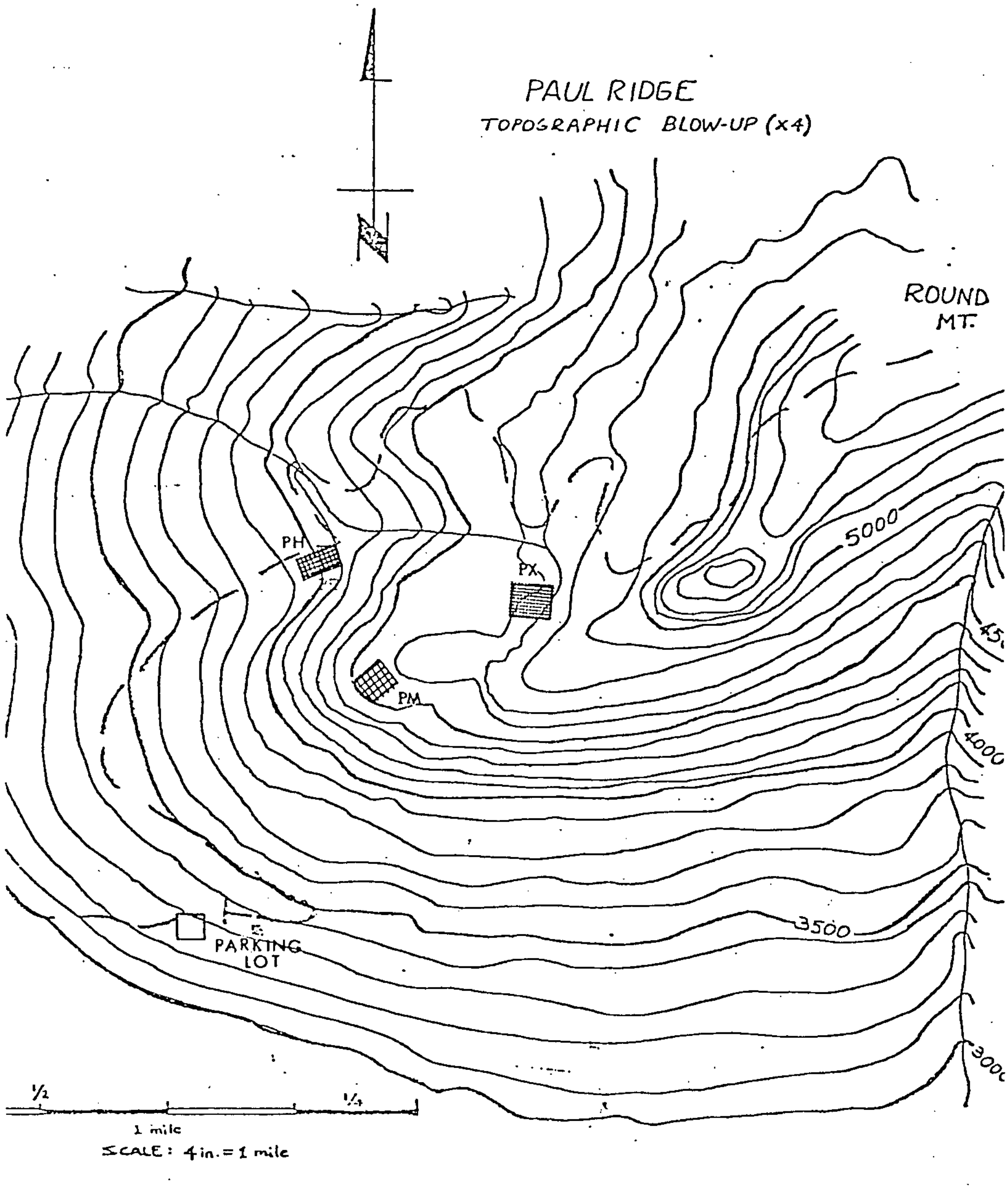


Fig. 3.1. Location of PX, PM and PH sampling areas on Paul Ridge

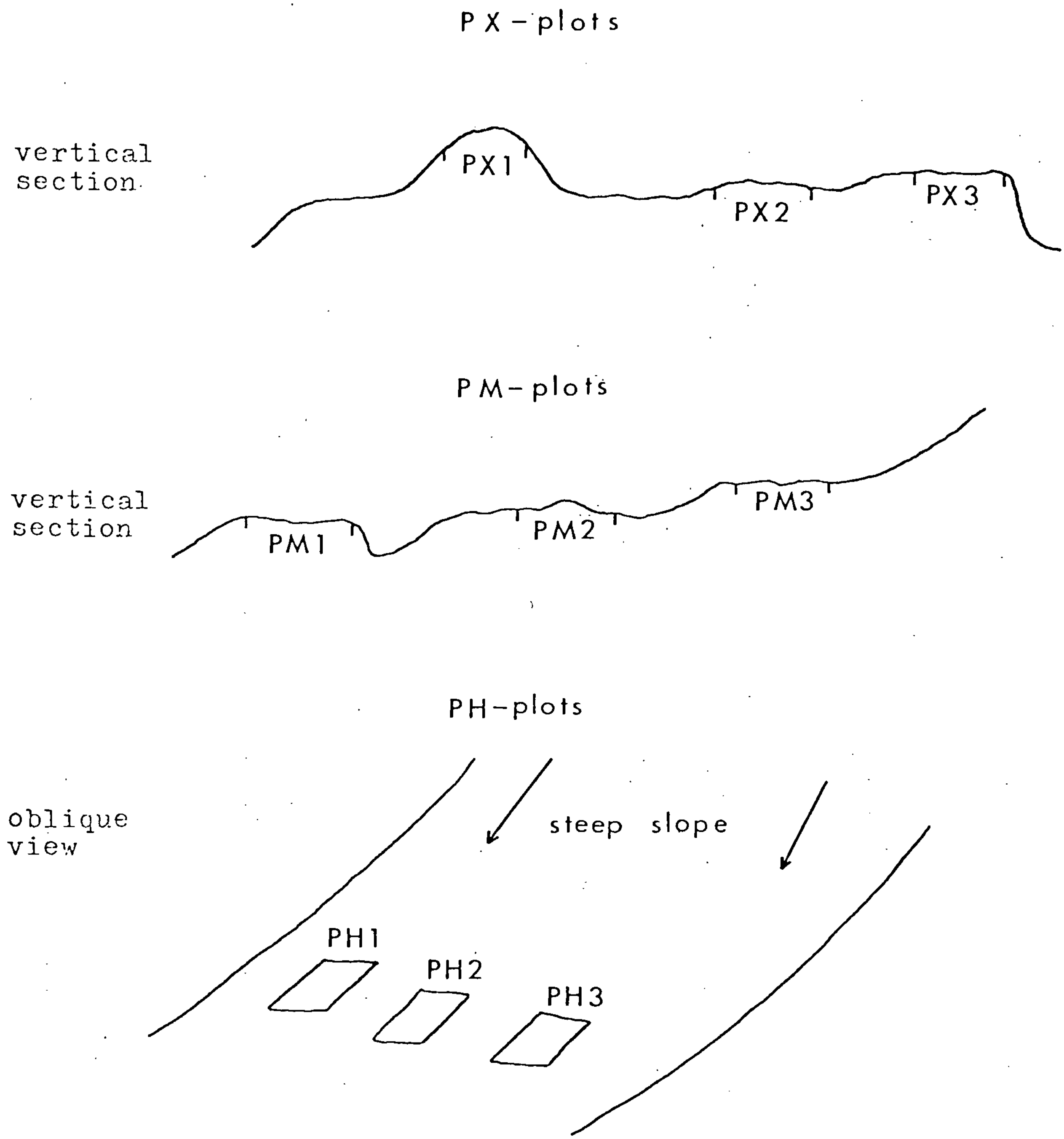


Figure 3.2. Topographic location of sample plots.

without the influence of seepage. Sample plots at the bottom of the elevation transect were located on the lower portion of a slope. The soil which was rather poorly drained, received seepage water from the upper part of the slope. There was a very similar type of soil parent material throughout the whole elevation transect.

The three plots at the top of the elevation transect were 1450 m above sea level; they are referred to as PX1, PX2 and PX3 (X stands for xeric, but the hygrotope can be characterized as subxeric to submesic rather than xeric, sensu Krajina 1969). The three plots on the central part of the transect were 1375 m above sea level; they are referred to as PM1, PM2 and PM3 (M stands for mesic hygrotope). The three plots at the bottom of the transect (1250 m above sea level) are referred to as PH1, PH2 and PH3 (H stands for hygric hygrotope).

The geography and physiography of southwestern Garibaldi Park are described in detail by Brooke _et al_. (1970). The topography of individual sample plots is depicted in Figures 1.1 and 3.2. The maximum distance between two plots within one plant association was 200 m; most plots were 20-50 m apart.

3.1.2 Mamquam plots

This group of three plots is refered to as the M-plots (Mamquam). The study area corresponds to the middle part of the Paul Ridge elevation transect in vegetation composition, elevation (1400 m), hygrotope and snow duration. It was located on a different soil parent material (see section 3.3.1. of this chapter). The maximum distance between plots is 165 m.

3.2 Climate

The climate of the Subalpine Mountain Hemlock Zone, where the study area is located, has been described by Brooke, Peterson and Krajina (1970) and by Krajina (1959 and 1965). The characteristic features are high precipitation, mainly in the form of snow during winter, prolonged accumulation of heavy snow cover (up to 7 m of snow with snow cover lasting as long as 10 months per year), frequent heavy fog (low cloud) during fall and winter, short cool summers with maximum mean monthly temperature between 10 and 15° C, long winters with minimum mean monthly temperature between -2 and -6° C and the lowest temperature rarely below -15° C due to the warming effect of the ocean. There is a characteristic dry season during summer, usually in July or August.

Four weather stations were established within the study area in July 1975 and climatic data were obtained for a period of 24 months; only 19 months of data were available (August 1975 to February 1977) at the time of writing. The weather stations were located as follows:

1. Forest microclimatic station on Plot PX1 at 1450 m
2. Forest microclimatic station on Plot PM1 at 1375 m
3. Forest microclimatic station on Plot PH1 at 1250 m
4. Clearcut climatic station at 1100 m, approximately 1 km SW from the PH-plots.

The weather stations on plots PX1, PM1, and PH1 measured and recorded air temperature and humidity under the tree canopy, approximately 2 m above the ground. The weather station on the clear-cut recorded air temperature and humidity in the open area, also approximately 2 m above the ground. Measurements were obtained throughout the year, with instruments being elevated during the winter to maintain them above the snow pack. The rain gauge with antifreeze added during the frost period, was located at the clearcut climatic station. There was no weather station on the Mamquam site because of extremely difficult access during winter months.

The distribution of precipitation on Paul Ridge is summarized in Fig. 3.3. The highest monthly precipitation occurred in late fall/early winter (October to December) mainly in the form of rain. The total water equivalent of precipitation from October 1, 1975 to September 30, 1976 was 2668 mm (105.04").

The mean monthly temperatures calculated from the records of the three forest microclimatic stations are presented in Figure 3.4. All three sites have very similar temperature regimes although the mesic site seems to be slightly warmer during summer and the xeric site (the highest in elevation) slightly cooler during winter than the other two sites. This corresponds with the observation on snowmelt. During the 3 years when the snowmelt was observed (1974, 1975 and 1976) the hygric plots were the first ones to be snow free (by the end of June), followed by mesic and xeric sites, where snow persisted till the end of July.

In the winter of 1975-76 there was an exceptionally heavy snow accumulation and a late snowmelt. The first snow appeared on October 5, 1975 while continuous snow cover developed between October 14 and 18 and persisted till August 1976. There were

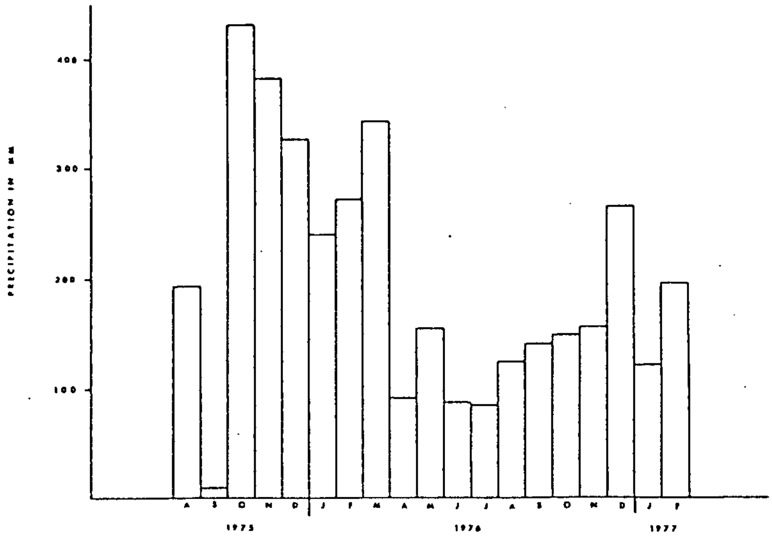


Figure 3.3. Quantity of atmospheric precipitation (in mm) on Paul Ridge during the period of August 1975 to February 1977.

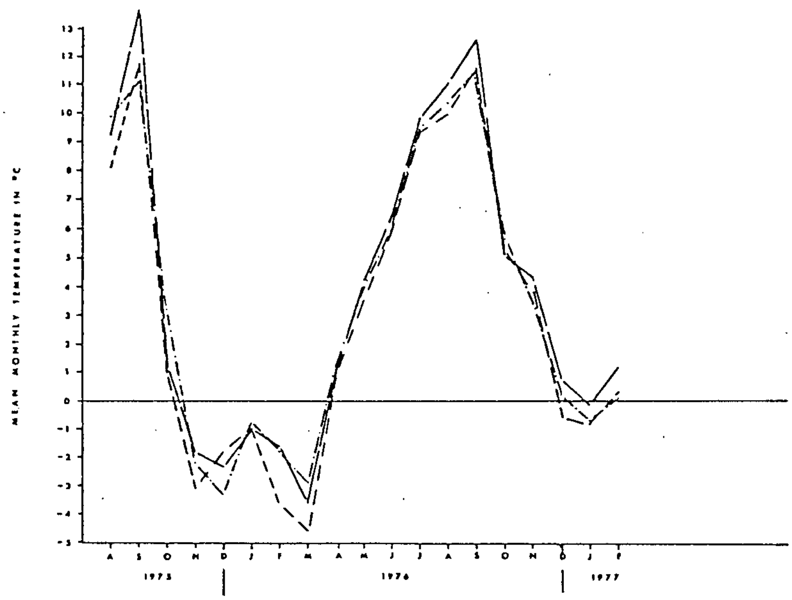


Figure 3.4. Mean monthly temperatures below the forest canopy on PX, PM and PH sites (in °C) between August 1975 and February 1977.

- - - - - - - -	PX
————————	PM
-·-·-·-·-	PH

still a few snow patches on the PX plots and on the Mamquam site on August 21, 1976. The snow-free period in 1976 was very brief; the first snow again appeared on October 5. The area is usually snow-free for 3-41/2 months on the PH plots and for about 3 months on the PX plots.

The mean monthly relative humidity beneath the forest canopy was between 70 and 80% throughout most of the year. The relative humidity on the PM and PH plots was almost identical and on PX plots it was 3-5% lower.

3.3. Geology and soil

3.3.1. Geology and soil parent material

The geology of the area has been described by Roddick (1965) and Mathews (1957, 1958). According to Roddick (1965), about 80% of the area is underlain by plutonic rocks which engulf pendants of volcanic, metamorphic and sedimentary rocks. Quaternary volcanic rock types in the Garibaldi area rest on a foundation of Cretaceous quartz diorites, metavolcanic and metasedimentary rocks. The volcanics include largely dacite rocks associated with andesites and basalts. The plagioclases of many of the diorites are somewhat more calcic than those of basalts, and orthopyroxene is the most common mafic mineral of the dacites (Mathews 1957).

Two soil pits were dug on each of the sample plots. Several rocks from the C-horizon were collected and identified by Dr. W. R. Danner, Department of Geological Sciences, University of British Columbia. His report with a brief discussion is included as Appendix 2. Only a brief summary is given here.

The rocks collected on the 12 sample plots appear to belong to at least four groups (ordered according to abundance):

1. Garibaldi volcanic flow rocks which are mostly dacite.
2. Rounded coarse grained hornblende-quartz diorites.
3. A few dense and heavy porphyritic rocks which may be parts of dense Garibaldi flows.
4. A few dark green schistose rocks which may represent metamorphosed older volcanic rocks.

The soil on the Mamquam plots seems to be derived mainly from quartz diorite. The predominant type of rocks on the Paul Ridge plots appears to be a grey Garibaldi dacite of volcanic origin with some intermixed quartz diorite, porphyry, feldspar, and schist. The mixture of various rock types in the C-horizon is typical for transported soil parent material: glacial till in this case.

Mathews (1958b) gives the following chemical analysis of dacite debris from Diamond Head, Garibaldi Park and of quartz diorite from the vicinity of Cheakamus station, north of Squamish (Table 3.1).

Table 3.1. Chemical analysis of dacite debris from Diamond Head, Garibaldi Park and of quartz diorite from the vicinity of Cheakamus station, north of Squamish (Mathews 1958a,b)

	Location	
Chemical	Diamond Head Percent Composition	Cheakamus station Percent Composition
SiO_2	63.94	65.29
Al_2O_3	16.48	16.86
Fe_2O_3	3.38	1.96
FeO	1.29	2.24
TiO_2	0.46	0.46
MnO	0.23	0.14
CaO	5.38	5.18
MgO	2.53	2.06
K_2O	1.42	1.12
Na_2O	3.64	3.18
H_2O (-105° C)	0.16	0.12
H_2O (+105° C)	0.98	1.43
CO_2	Nil	Nil
P_2O_5	0.09	0.17
Sum	99.98	100.21

The mineral composition of dacite debris and quartz diorite from the same locations is in Table 3.2.

Table 3.2. Mineral composition of dacite debris form Diamond Head, Garibaldi Park and of quartz diorite from the vicinity of Cheakamus station, north of Squamish (Mathews 1958a,b)

	Location	
Mineral	Diamond Head Percent Composition	Cheakamus station Percent Composition
Quartz	22.67	27.93
Orthoclase	8.39	6.62
Albite	30.78	26.89
Anorthite	24.44	24.58
Corundum	-	1.41
Diopside	1.29	-
Hypersthene	5.70	7.13
Magmetite	3.58	2.84
Ilmenite	0.87	0.87
Apatite	0.21	0.39
H_2O+	0.98	1.43
H_2O-	0.16	0.12
Hematite	0.91	-

The rocks analyzed by Mathews (1958a,b) were not obtained from the sample plots, but from a reasonably close locality. It is assumed that the composition of dacite and quartz diorite from the sample plots would not differ greatly from the analyses given by Mathews (1958a,b). It is probable, therefore, that the chemistry of parent material on Mamquam plots and Paul Ridge plots is fairly similar. The slight difference in mineral composition would probably result in slightly faster weathering on Paul Ridge plots, because of lower amount of quartz, absence of corundum and higher amount of more readily weathered minerals (albite, orthoclase).

3.3.2. Soil

Soils of the southwestern corner of Garibaldi Provincial Park were described by Brooke (1966) and by Brooke, Peterson and Krajina (1970).

On each of the 12 sample plots two soil pits were dug. Soil profiles were described and soil samples were analyzed by Kimmins, Watt and Stathers in 1974 (unpublished data).

3.4 Vegetation

The vegetation of the Subalpine Mountain Hemlock Zone was described by Peterson (1964), Brooke (1966), and Brooke, Peterson and Krajina (1970). Studies concerned with successional dynamics of the subalpine vegetation were done by Brink (1959, 1964).

The tree layer on all sample plots consisted of mountain hemlock and Pacific silver fir, the proportion of each species varying from plot to plot. In addition there was some yellow cedar on PX1 and PX2 and some red cedar on PH1. PH-plots had a mixture of mountain and western hemlock and their hybrids (Table 3.5).

A summary of the mensurational data from the plots is presented in Tables 3.3 and 3.4 and in Appendix 3. Trees on all sample plots can be characterized as mature to overmature, with the mean age per plot ranging from 295 to 440 years (Appendix 6). The maximum age measured was 620 years.

The mean tree height was smallest on the PX1 plot, (only 12 m). The tallest trees were on the PH2 plot, where mean tree height was 36.2 m; the tallest tree on this plot measured 53.5 m (Table 3.3). The smallest mean tree diameter was on the PX2 plot (27.9 cm), while the largest mean diameter was on the M1 plot (67 cm); the biggest tree on this plot had a diameter of 141 cm. The timber volume of the mean tree varied from 0.48 m^3 on plot PX2 to 6.43 m^3 on plot PH2 (Table 3.3). The timber volume per hectare ranged from 523 m^3 on plot PX1 to 1354 m^3 on plot M1. The number of trees per hectare varied from 180 on plot PH2 to 1275 on plot PX2 (Table 3.4). The diameter, height, and volume of the mean tree for each tree species on each sample plot is given in Appendix 3.

The proportion of individual tree species on each sample plot is presented on Table 3.4. On plots PX1 and PX2 there was a higher proportion of mountain hemlock than Pacific silver fir in terms of both stems per hectare and timber volume per hectare. There was also a small proportion of yellow cedar on these two plots. Plot PX3 had a higher proportion of Pacific silver fir in terms of stems per hectare, but the hemlock trees were of larger dimensions and therefore they contributed the bulk of the timber volume per hectare. Plots PM1 and PM2 had a higher proportion of mountain hemlock than Pacific silver fir in terms of stems per hectare and timber volume per hectare. On the plot PM3, as well as on all PH and M plots, Pacific silver fir dominated mountain hemlock both in terms of stems per hectare and volume.

Table 3.3. Mean and maximum tree diameter, height, basal area, and timber volume for 12 sample plots.

Plot	n	D (cm)	H (m)	BA (m^2)	VOL (m^3) [1]
PX1	169	28.1 (1.2)* 5.6 74.7	11.9 (0.5) 2.0 24.5	0.081 (0.006) 0.002 0.438	0.514 (0.049) 0.003 3.325
PX2	116	27.9 (1.1) 7.6 70.9	13.2 (0.5) 2.0 23.5	0.073 (0.006) 0.005 0.394	0.478 (0.046) 0.004 2.854
PX3	52	43.5 (3.5) 7.9 99.1	17.0 (1.1) 3.0 31.0	0.197 (0.027) 0.005 0.771	1.588 (0.237) 0.009 7.814
PM1	64	44.9 (1.9) 15.0 76.5	24.3 (1.0) 6.0 35.0	0.177 (0.014) 0.018 0.459	1.888 (0.169) 0.053 5.470
PM2	48	45.9 (2.1) 18.0 75.9	25.6 (1.0) 10.0 34.5	0.182 (0.015) 0.026 0.453	2.034 (0.199) 0.119 5.041
PM3	33	55.9 (3.7) 15.2 88.4	29.6 (2.0) 6.0 43.0	0.281 (0.030) 0.018 0.614	3.875 (0.460) 0.054 9.201
PH1	45	45.9 (3.3) 13.2 96.0	26.4 (1.9) 5.5 52.0	0.202 (0.027) 0.014 0.724	2.782 (0.433) 0.031 10.980
PH2	25	66.1 (5.0) 23.9 110.0	36.2 (2.8) 9.0 53.5	0.390 (0.051) 0.045 0.950	6.433 (0.991) 0.232 16.588
PH3	34	62.7 (3.7) 15.5 114.3	33.2 (1.8) 6.0 48.0	0.344 (0.038) 0.019 1.026	4.801 (0.575) 0.052 12.930
MM1	29	67.0 (5.3) 24.6 141.0	30.9 (1.5) 13.5 44.0	0.413 (0.065) 0.048 1.561	5.276 (0.852) 0.290 19.507
MM2	28	62.2 (4.1) 25.4 109.5	30.6 (2.0) 11.0 44.5	0.339 (0.040) 0.051 0.941	4.589 (0.644) 0.238 12.050
MM3	25	65.2 (4.8) 35.6 119.9	30.2 (1.7) 15.0 45.0	0.377 (0.057) 0.099 1.129	4.699 (0.701) 0.627 12.247

* Mean (SE)
Min Max

[1] Estimated using B.C.F.S. equations

n - number of trees on sample plot
D - diameter at breast height
H - tree height
BA - basal area at breast height
VOL - total timber volume

Table 3.4. Some basic statistics for the sample plots

		No. of trees on a plot (stem/ha)			Plot Area	Timber Volume[1]		Basal Area
Plot	SP	per species	%	total	(ha)	by species (m^3/ha)	plot total (m^3/ha)	(m^2/ha)
PX1	H	512	50	1018	0.166	436	523	82.5
	PF	452	45			62		
	YC	54	5			25		
PX2	H	813	64	1275	0.091	457	609	93.1
	PF	418	33			132		
	YC	44	3			20		
PX3	H	190	36	520	0.100	480	826	102.4
	PF	330	64			346		
PM1	H	463	69	673	0.095	855	1272	119.2
	PF	210	31			417		
PM2	H	276	60	457	0.105	500	930	83.2
	PF	181	40			430		
PM3	H	38	12	311	0.106	206	1206	87.5
	PF	273	88			1000		
PH1	H	92	29	319	0.141	199	888	64.5
	PF	227	71			689		
PH2	H	43	24	180	0.139	319	1157	70.1
	PF	137	76			838		
PH3	H	56	29	190	0.179	239	912	65.3
	PF	134	71			673		
MM1	H	71	28	257	0.113	552	1354	106.0
	PF	186	72			802		
MM2	H	116	46	250	0.112	368	1147	84.7
	PF	134	54			779		
MM3	H	35	16	216	0.116	238	1013	81.2
	PF	181	84			775		

[1]Estimated using B.C.F.S. volume equations

SP - tree species
H - mountain hemlock on PH plots also western hemlock and hybrids.
PF - Pacific silver fir
YC - yellow-cedar

The abundance/cover and vigor of plant species in the understory layer is presented in Table 3.5. Plant community sampling followed the standard releve method as described by Mueller-Dombois and Ellenberg (1974) and Brooke *et al.* (1970). The understory layer was best developed on the PH plots and least developed on the M-plots. PH plots also had the highest diversity of plant species present in the understory layer. On PX plots the understory layer was dominated by *Rhododendron albiflorum** and *Vaccinium* species, with coverage around 80-90%. On PM plots the understory layer was dominated by *Vaccinium* species and by *Rubus pedatus*, with coverage around 40-50%. The M-plots had a poorly developed understory layer dominated by *Vaccinium* species, with coverage between 30 and 40%. PH plots had a well developed understory layer with coverage between 90 and 100%; the characteristic species were *Vaccinium membranaceum*, *V. alaskaense* and *V. ovalifolium*, *Rubus pedatus*, *Veratrum viride*, *Streptopus amplexifolius*, *Tiarella unifoliata*, *Viola glabella*, *Valeriana sitchensis*, *Gymnocarpium dryopteris*, *Dryopteris austriaca*, and *Athyrium filix-femina*. In addition to these species there were *Streptopus roseus* on the PH1 and PH2 plots, *Streptopus streptopoides* and *Clintonia uniflora* on the PH3 plot and *Oplopanax horridum* on the PH2 and PH3 plots.

Only the most abundant bryophytes and lichens were identified and listed. The same procedure was followed for epiphytes; a number of epiphytic species were present on the sample plots.

* See Appendix 1 for list of plant species.

Alectoria spp. and *Hypogymnia* spp. were the most abundant, but *Ptilidium californicum* and some species of *Usnea* were also present.

Brooke, Peterson and Krajina (1970) described two subzones and 13 plant associations within the Subalpine Mountain Hemlock Zone. If their system for classifying plant associations is applied to the sample plots described in this study, then the PX plots are most similar to the plant association Vaccinio (membranacei)-Tsugetum mertensianae of the Parkland subzone (Brooke *et al*. 1970), PM and M plots are most similar to the Abieto (amabilis)-Tsugetum mertensianae plant association, variant abaieto-tsugetosum mertensianae of the Forest subzone, and the PH plots are most similar to the Oplopanaco-Thujetum plicatae plant association, abietetosum amabilis subassociation of the Forest subzone. Brooke *et al*. (1970) classified the Vaccinio (membranacei)-Tsugetum mertensianae as a submesic habitat, Abieto (amabilis)-Tsugetum mertensianae as mesic, and Oplopanaco-Thujetum plicatae as a hygric habitat with temporary seepage influence. These hygrotope designations appear to be appropriate for the corresponding sample plots.

Table 3.5. Plant species on the sample plots and species ratings

Layer	Species	PX1	PX2	PX3	PM1	PM2	PM3	M1	M2	M3	PH1	PH2	PH3
A	Abies amabilis	5.1	6.2	7.2	7.3	7.3	8.3	8.3	7.3	8.3	8.2	8.3	8.3
	Tsuga mertensiana	9.2	8.2	8.2	8.3	8.3	6.3	6.3	7.3	5.3	)6.2	)6.3	)6.3
	Tsuga heterophylla										)	)	)
	Thuja plicata										+.2		
	Chamaecyparis nootkatensis	+.2	+.2										
B	Rhododendron albiflorum	9.2	8.2	9.2	+.1	3.2							
	Vaccinium membranaceum	5.2	6.2	5.2	6.3	6.3	7.3	2.2	2.2	3.2	4.3	3.3	2.3
	Vaccinium alaskaense	4.2	4.2	3.2	3.3	4.3	3.3	+.1	+.1	+.2	2.3	3.3	2.3
	Vaccinium ovalifolium	4.2	3.2	2.2	4.3	4.3	4.3	+.1	+.1	+.2	3.3	3.3	2.3
	Vaccinium deliciosum	3.2	4.2	2.2									
	Sorbus sitchensis		+.1		+.1	1.1	3.2				2.2	2.2	+.2
	Abies amabilis	2.+	2.1	1.1	1.1		5.2	3.1	2.1	4.2	1.2	3.2	3.3
	Tsuga mertensiana	1.+	1.1	1.1	3.1		3.2	3.1	1.1	1.2	1.2	)2.2	)2.2
	Tsuga heterophylla										1.2	)	)
	Chamaecyparis nootkatensis	1.+	+.1										
	Sambucus pubens					+.2							+.2
	Ribes bracteosum										2.3	2.3	1.3
	Oplopanax horridum											3.3	5.3
	Vaccinium parvifolium					2.1	+.1						
C	Phyllodoce empetriformis	1.1	4.1	3.2									
	Cassiope mertensiana		+.1	+.1									
	Rubus pedatus	3.1	5.2		5.2	4.2	7.3				4.3	3.3	4.3
	Pyrola secunda	1.1	3.1		1.2	2.2							+.3
	Veratrum viride				+.2	+.2	1.2				3.3	3.3	3.3
	Streptopus streptopoides					+.2	+.+						3.3
	Athyrium filix-femina					+.2	+.2				3.3	3.3	3.3
	Luzula parviflora						+.2						
	Streptopus amplexifolius						+.2				3.3	2.3	3.3
	Dryopteris austriaca						+.2				3.3	3.3	3.3
	Blechnum spicant						+.2					+.1	
	Streptopus roseus										3.2	3.3	
	Tiarella unifoliata										4.3	3.3	3.3
	Viola glabella										3.2	2.3	2.2
	Valeriana sitchensis										3.3	2.3	2.2
	Rubus spectabilis										2.3	1.2	3.3
	Osmorhiza chilensis										1.2		
	Abies amabilis						3.2				1.2		
	Tsuga mertensiana										1.2		
	Gymnocarpium dryopteris										2.3	4.3	3.3
	Listera cordata										1.2		
	Cinna latifolia										+.2		
	Caltha leptosepala										+.2		
	Clintonia uniflora												2.2
	Chamaecyparis nootkatensis	+.1	+.1								+.2		
D	Dicranum scoparium	8.2	9.2	9.2	8.2	8.2	5.2	4.2	3.2	3.2			
	Rhytidiopsis robusta	4.2	3.2	3.2	2.2	3.2	2.2	1.2	+.2	+.2	1.3	3.2	3.2
	Pleurozium schreberi	1.2	1.2	+.2									
	Dicranum fuscescens	2.2	1.2	+.2	+.2						3.3	3.2	3.2
	Rhytidiadelphus loreus	+.2	+.2	+.2									
	Bazzania spp.	+.2											
	Cladonia bellidiflora	+.1	+.1	+.2									
	Brachythecium spp.		+.2										
	Lophozia spp.		+.2										
	Rhytidiadelphus squarrosus										3.3	2.2	
	Mnium spp.										1.3		
	Lepidozia reptans										1.3		
	Rhizomnium nudum											2.2	2.2
	Rhizomnium magnifolium											2.2	2.2
	Pohlia nutans											2.2	2.2
	Plagiothecium undulatum											2.2	1.2
	Hypnum spp.											1.2	
	Plagiothecium denticulatum											2.2	2.1
	Ptilidium californicum	1.2											
E	Alectoria spp.	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2	5.2
	Hypogymnia spp.	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2
Fungi	Boletus spp.	1.3	1.3	+.2	+.3	+.3	+.3	+.3	+.3	+.3	+.2	+.2	+.2

Table 3.5, continued. Species ratings used in Table 3.5

(after Brooke *et al.* 1970)

Species ratings for individual plots are based on the Domin-Krajina scale (see Krajina 1933) and are given by two figures (e.g. 1.2) that represent species significance and vigor, respectively.

Species significance (combined scale for abundance and dominance):

- \+ Very sparsely present, dominance very small
- 1 Sparsely present, dominance small
- 2 Very scattered, dominance small
- 3 Scattered to plentiful, dominance less than 1/20 of plot surface
- 4 Often present, dominance 1/20 to 1/10 of plot
- 5 Often present, dominance 1/5 to 1/4 of plot
- 6 Any number of individuals, dominance 1/4 to 1/3 of plot
- 7 Any number of individuals, dominance 1/3 to 1/2 of plot
- 8 Any number of individuals, dominance 1/2 to 3/4 of plot
- 9 Any number of individuals, dominance over 3/4 of plot

Vigor ratings (from Peterson 1964):

- 0 Vigor nil (plant dead)
- \+ Vigor poor
- 1 Vigor fair
- 2 Vigor good
- 3 Vigor excellent

Plots are arranged horizontally in the tables by decreasing elevation from left to right.

Species are arranged vertically into 5 layers:

- A layer--trees
- B layer--shrubs and woody plants 30 cm to 2 m in height
- C layer--herbaceous plants and small woody plants less than 30 cm in height
- D layer--bryophytes and lichens
- E layer--epiphytes

Table 3.6. Gross volume of timber (m^3/ha) in three plant associations.

Plant association	M.h.	P.s.f.	Volume of timber (m^3/ha) Y.c.	W.h.	W.r.c.	Sum
*Vaccinio-Tsugetum mertensianae	300[1] (210-363)[2]	113 (25-311)	47 (23-69)	---	---	470[3] (309-522)
*Abieto-Tsugetum mertensianae	625 (405-770)	278 (126-745)	20 (0-81)	---	---	924 (754-1150)
*Oplopanaco-Thujetum plicatae	129 (0-321)	284 (38-477)	---	489 (135-1340)	23 (0-83)	1098[4] (801-1977)
PX-plots	458 (436-480)	180 (62-346)	15 (0-25)	---	---	653 (523-826)
PM-plots	520 (206-855)	616 (417-1000)	---	---	---	1136 (930-1272)
M- plots	386 (238-552)	785 (755-802)	---	---	---	1171 (1013-1354)
PH-plots	252[5] (199-319)	733 (673-838)	---	---	---	986 (888-1157)

1 Mean
2 Range of volume
3 Includes minor species
4 May include some Douglas fir and Sitka spruce
5 Hybrids of mountain and western hemlock

* From Brooke <u>et</u> <u>al</u>. 1970

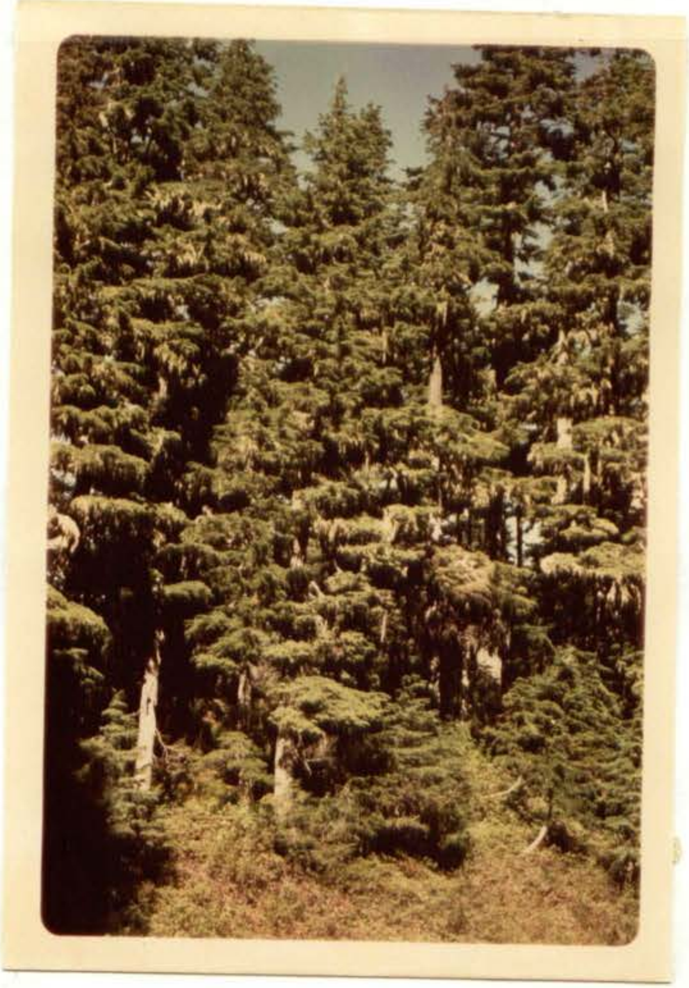


Figure 3.5.: Xeric site - plot PX1. Note the amount of epiphytic lichens on trees.

Figure 3.6.: Xeric site - plot PX2. The shrubs are white rhododendron and Vaccinium species.

Figure 3.7.: Xeric site - plot PX3

Figure 3.8. : Mesic site - plot PM1

Figure 3.9. : Mesic site - plot PM1

Figure 3.10.: Mesic site - plot PM2

Figure 3.11.: Mesic site - plot PM3

Figure 3.12.: Mesic site - plot M2. Picture taken on July 2, 1972. Note the amount of litter on top of the snow cover.

Figure 3.13.:

Mesic site - plot M3 Picture taken in August, 1972.

Figure 3.14.: Hygric site - plot PH1.

Figure 3.15.: Hygric site - plot PH1. The herb layer is well developed.

Figure 3.16.: Hygric site - plot PH2. Devil's club and lady fern are abundant on this site.

Figure 3.17.: Climatic station on hygric site.

Figure 3.18.: Pair of litter and throughfall collectors.

Figure 3.19.: Litter collector damaged by snow weight.

Figure 3.20.: Rain collectors on the open ridge.

Figure 3.21.:
Throughfall collector.

CHAPTER 4

METHODS

4.1 Field sampling

The following parameters were determined or samples were collected in the field:

- size of sampling plots for the purpose of converting all measurements obtained per plot into units per hectare.
- dbh, height and crown length of trees on the sample plots to calculate timber volume and above ground tree biomass.
- increment cores to determine tree age and annual dbh increment.
- overstory litterfall to estimate net primary production and nutrient turnover.
- throughfall to estimate nutrient turnover.
- incident precipitation to estimate input of nutrients to an ecosystem.
- foliage to determine foliar chemistry for the purpose of comparing foliar nutrient concentration between Paul Ridge and Mamquam sample locations.

4.1.1. Plot area

The area of each sample plot was measured using a transit (USHIKATA, model TRACON S25). Each plot was divided in basic geometric figures (e.g. triangle, square, or rectangle) the dimensions of which were measured, and used to calculate the total area of the plot.

4.1.2. Tree mensuration

All trees on the sample plots were numbered, and their dbh, height and crown length were measured. A steel dbh tape was used for measuring diameter, which was taken at 1.3 m above the ground. Tree height and crown lengths were measured with a RELASKOP.

All trees on the sample plots greater than 5.08 cm (2 inches) were ranked according to their dbh into 10.16 cm (4 inch) dbh classes. At the beginning I intended to take at least one increment core per dbh class for each tree species present on a plot in order to calculate total stem increment. However, this stratified sampling design was changed to a random sampling design. Many of the larger diameter trees had rotten cores, therefore the increase in the accuracy of the tree age estimate which would have been obtained by stratified sampling would have been lost due to incomplete cores. I did not consider it worthwhile to spend more effort to obtain more accurate estimates of dbh increment unless I could get similar estimates for the decrease of timber volume due to decay of tree cores and tree mortality. Tree mortality and decay were not accounted for and consequently the increase in tree bole volume is overestimated. On plots with greater dbh variability, a larger number of trees was sampled than on plots with rather uniform dbh. The two major tree species (mountain hemlock and Pacific silver fir) were sampled in proportion to their number of stems on the plots. Increment cores were taken from 23 trees on PX plots, 24 on PM plots, 26 on PH plots, and 19 on M-plots for a total of 92.

4.1.3. Overstory litterfall

Ten or 11 litterfall collectors were distributed randomly on each plot, and each was paired with a throughfall collector located nearby (Fig. 3.18). Thus, there were approximately 30 litterfall and 30 throughfall collectors per site type for a total of 120 collectors of each type in the entire study. The wooden sides of the 1 x 1 m litterfall collectors were 15 cm high, and the bottom of the collector was made of 1 mm nylon mesh. Collectors were oriented as close to horizontal as possible.

The number of litterfall and throughfall collectors is larger than the number of collectors used by most other researchers. Abee and Lavender (1972) used 8 litterfall and 4 throughfall collectors per plot of a size 0.20 ha. Johnson and Risser (1974) used 10 litterfall and 10 throughfall collectors per plot of a size 0.01 ha; Turner (1974) used 4 litterfall and 3 throughfall collectors per plot of a size 0.045 ha, and Malkonen (1977) used 8 litterfall collectors per plot of a size 0.16 ha.

Litter collectors were installed at the beginning of September 1974. The first litter collection was made at the end of that month followed by collections in July 1975, September 1975, July 1976, and September 1976. The reason for making only two collections per calendar year was the very long snow duration, from the beginning of October till the middle of July, and the paucity of litterfall during July and August. Litter was collected immediately after snowmelt and just before the first snowfall. Each winter a number of litter collectors were extensively damaged by the weight of the snow pack which, it was estimated, could have been as much as $2t/m^2$. The weight and movement of the snowpack deformed many of the collectors and altered their orientation which results in a slight underestimation of the amount of litter collected.

The prolonged storage of litter in the snowpack causes a further underestimate because of leaching and decomposition. Consequently, an attempt was made to estimate the amount of decomposition and leaching of mineral elements out of litter incorporated in snow. In winter, litter of known composition was enclosed in litterbags, which were periodically placed on the surface of the snow layer. These litterbags were progressively incorporated into the snowpack during the period of snow accumulation and subsequently exposed on the snow surface during the period of snowmelt. This work was unfortunately done in collaboration with a graduate student who in the middle of his project suddenly departed, and the results were lost. The preliminary results indicated that the litter weight may decrease by approximately 10% and great quantities of some mineral elements, particularly potassium, may be lost by leaching during the winter. This problem should be studied in the future; the partial results obtained clearly indicate that the decomposition of litter starts when litter is incorporated into the snow layer, before it reaches the forest floor.

4.1.4. Overstory throughfall

The throughfall collectors consisted of 12.70 cm (5 inches) diameter plastic funnels leading into 4.5 L plastic bottles (Fig. 3.21). A plug of glass wool was placed in the funnel to prevent larger particles from entering the collector, and to reduce microbial activity a few drops of chloroform were placed into each collector. Each collector was fixed on a wooden pole by rubber bands in such a way that the funnel edge was at least 50 cm above the ground to prevent contamination by particles splashing from the forest floor. The funnels were above the understory vegetation so that they did not collect understory throughfall.

Collectors were emptied after each major rain storm during the snow-free period. However, as mentioned in Chapter 3.2, the summer in the study area is characteristically dry, and the total number of collections was rather small: two collections in the fall of 1974, five in the summer of 1975 and two in the summer of 1976.

An attempt was made to monitor winter throughfall. As mentioned in Chapter 3.2, most of the annual precipitation occurs during November and December as a mixture of rain and snow with temperatures fluctuating around 0° C. This period was considered important for evaluating throughfall significance. Two collector designs were tested. The first type was a modification of an existing summer collector: the funnel was taped in a horizontal position to the upper end of a 2.4 m (8 foot) long bamboo pole that was supported by a sturdy wooden peg. It was connected by plastic tubing to a plastic bottle on the ground. The elevation of the funnel was to maintain it above the level of the snow, with the hope that the bottle would be progressively raised on the pole as the snow depth increased. This strategy was reasonably successful until temperatures dropped below zero when some of the bottles were ruptured by the freezing water, and some of the funnels were crushed by heavy blocks of snow sliding off tree branches. Fluctuations of temperature about the freezing point resulted in accumulation of alternating layers of snow and ice out of which it was virtually impossible to dig the bottles. When the snow had melted in July 1975, most of the plastic collectors were crushed and destroyed by the weight of the snow and most of the bamboo poles were broken by snow creep (Fig. 3.16).

When it became obvious in January 1975 that this collection strategy was a failure, a second type was tested, consisting of sturdy plastic buckets hanging on ropes between trees. Two of these collectors were tested on each of the Paul Ridge plots. Unfortunately this collector did not give satisfactory results either. Because it had no filter it collected litterfall as well as throughfall. When the samples were analyzed it was found that the concentration of elements in the throughfall was very closely related to the amount of litter collected with the throughfall. In other words, concentration was largely determined by the amount of nutrients leached out of litterfall.

The difficulty in designing a good winter collector together with difficult access during winter months resulted in the abandonment of attempts to measure throughfall during the winter, 1975-76. Only summer throughfall was measured. Stemflow was not studied.

4.1.5. Incident precipitation

To determine the amount of nutrients deposited by incident precipitation the same type of collector was used as for throughfall (Fig. 3.20). The incident precipitation was sampled at three locations: an open ridge in the vicinity of PX plots and clear-cuts in the vicinity of PH plots and M plots. In September 1974 two collectors were established at each of these locations. However, after the first two collections during the fall of 1974 it became obvious that due to a large between-collector variation in concentration of elements, two collectors were not sufficient to give reasonable results. Consequently, in July 1975 the number of collectors was increased to six per locality, and this number was used through the rest of the sampling period.

The incident rainfall was collected on the same dates as the throughfall.

4.1.6. Foliar chemistry

To determine the concentration of nutrients in foliage of different ages, needles were sampled from the lowest living branch of two trees on each of the Paul Ridge plots. The same trees were sampled in 1975 (August and September) and in 1976 (September).

4.2. Laboratory analyses

4.2.1. Tree increment

The increment cores were measured on an ADDO-X dendrochronometer. Whenever possible, diameter increment for the last 20 years and the total number of annual rings were measured.

4.2.2. Litterfall

Litter was air dried and sorted into six categories:

1. foliage
2. epiphytic lichens
3. twigs and branches
4. seeds and cones
5. understory litter (mainly leaves from *Vaccinium* spp. shrubs)
6. other plant litter (such as wood and bark from tree boles, etc.)

Each litter category was then weighed, and ground in a Wiley mill to pass a #40 mesh. Understory litter was excluded since this transfer pathway was studied by Yarie (1978). Samples were sealed in polyethylene bags to await chemical analyses.

In litter collections number 1 and 2 (September 1974 and July 1975) foliage litter from each litter collector was analyzed separately to give estimates of sample variability. Epiphytic lichens, twigs and branches, seeds and cones, and other plant litter were bulked within each sample plot, and one sample per plots was taken for chemical analyses. In litter collections 3, 4, and 5, (September 1975, and July and September 1976) foliage litter was also bulked, and only one sample of foliage per plot was analyzed. The bulking of samples for chemical analyses was necessary to reduce the number of analyses performed; information on the variability of concentration of elements had to be sacrificed.

The difference between air-dry and oven dry (105° C) moisture content was determined on 70 randomly selected samples and found to be an average of 8.87% (SE + 0.11%). Appropriate corrections were made to the nutrient concentration data.

The content of macronutrients (N, P, K, Ca, Mg) was determined in all samples or bulked samples. The ash content was determined for the litter set number 1 only (September 1974).

The method used for determining N and P content was a modified Kjeldahl digestion (Twine and Williams, 1971) using selenium as a catalyst with subsequent analysis for N and P using a Technicon Auto-Analyzer. Between 0.15 and 0.25 g of sample was added to a boiling tube containing 5 mL of digestion mixture and selenized Hengar granules to facilitate even boiling. The tubes were placed in a 77-place heating block and digested at 80-100° C for 12 h, then slowly raised to the boiling temperature (about 330° C, Williams and Twine, 1967) of the digestion mixture and held there until completely colourless and transparent (overnight). Glass balls placed over the mouths of the tubes acted as reflux condensers, washing undigested material spattered on to the walls of the tube back down into the digestion mixture. When the digests were cool they were diluted to 100 mL with deionized distilled water and left to stand overnight to permit settling of any undigested solids. The supernatant digestate was decanted into plastic bottles to await analysis. Nitrogen was determined using an ammonia cartridge of a Technicon Auto-Analyzer, which makes use of the Berthelot reaction (reaction of ammonia with sodium phenate and sodium hypochlorite to yield a blue indophenol complex that is quantified in a colorimeter). Phosphorus was determined using an ortho-phosphate cartridge of a Technicon Auto-Analyzer. This involves formation of a reduced phosphomolybdate complex, which is quantified in a colorimeter.

Analysis for K, Ca, and Mg was conducted on a Varian Techtron Atomic Absorption Spectophotometer (Model AA5) following dry-ashing. One gram of sample was weighed into a silica crucible and ashed in a muffle furnace at about 200° C for 11/2-2 h, followed by 475° C ± 5° C for 12 h. The weight of ash for each sample was determined and then taken up in 5 mL of 20% HCl. A further 15 mL of hydrochloric acid was then added, and the crucible heated on a sand bath to facilitate solution. The content of the crucible was then transferred to a volumetric flask, made up to 100 mL, and transferred to a plastic bottle for storage prior to analysis. An air-acetylene flame was used for determinations of K and Mg, while an acetylene-nitrous oxide flame was used for determination of Ca.

Because there are a number of interferences possible in the method used, the following investigations were undertaken:

1. To check the influence of pyrophosphates and hydrated silica on determination of Ca, Mg, and K, 28 samples were processed as follows (Allan, 1969). The ash obtained from the

muffle furnace was dissolved in 5 mL of 20% HCl and slowly taken to dryness on a sand heater (to hydrolyze the pyrophosphates and to dehydrate the silica). This operation was repeated with a further 5 mL of 20% HCl. The residue was then dissolved in 20 mL of 20% HCl, and analyzed as before. No significant differences were found between the concentrations of Ca, Mg, and K obtained by this method and those obtained by the basic method, which was therefore used throughout the study.

2. To determine the chemical interference of phosphorus, two releasing agents were tested: strontium chloride and lanthanum chloride, the former at 3000 ppm and the latter at 10000 ppm (David, 1960). No significant difference was found in the concentration of Ca and Mg using either of these releasing agents compared to the basic method, which was therefore used throughout the study.

The first 100 samples of Ca were analyzed in both and acetylene-air flame and a acetylene-nitrous oxide flame. The latter gave considerably higher readings because of more complete ionization in a hotter flame, and it was therefore used throughout the study.

4.2.3. Throughfall and incident precipitation

Throughfall and incident rainfall samples were stored frozen prior to analyses. Samples were analyzed for ammonia (NH_4^+) nitrogen, nitrate (NO_3^-) nitrogen, phosphate (PO_4^{-2}) phosphorus, and sulphate (SO_4-2) sulphur on a Technicon Auto-Analyzer using standard methods described in the Technicon Auto-Analyzer Methodology. Analyses for potassium, calcium, and magnesium were conducted on a Varian Techtron Atomic

Absorption Spectrophotometer (Model AA5). An air-acetylene flame was used for determination of K and Mg concentrations, while an acetylene-nitrous oxide flame for determining Ca concentrations.

4.2.4. Foliar chemistry

The green foliage sampled from the lowest living branch for the purpose of determining foliage nutrient concentration was separated into three categories on Pacific silver fir: current foliage, previous year's foliage, and foliage older than 1 year. On mountain hemlock only two categories were distinguished: current foliage and foliage from previous year and older. The analyses for nutrient content were performed in the same way as for the litter.

4.3. Data processing and statistical analyses

4.3.1. Tree mensuration

The timber volumes on the sample plots were calculated using B.C. Forest Service (1976) volume equations for Vancouver Forest Inventory Zone (Zone C). The volume equations give gross volume in cubic metres for the entire stem, inside bark, including stump and top when d.b.h. and height are measured in metric units. The point of d.b.h. measurement must be 1.3 metres above germination point. The equation:

$$\log V = -4.337451 + 1.783500 \log D + 1.120230 \log H$$

was used for computing the timber volume of mountain hemlock and western hemlock trees. The equation:

$$\log V = -4.226202 + 1.782960 \log D + 1.103820 \log H$$

was used for computing the timber volume of Pacific silver fir trees. Equation:

$$\log V = -4.187127 + 1.777360 \log D + 1.032990 \log H$$

was used for computing the timber volume of yellow cedar trees. In these equations V is the volume of wood in the tree bole in cubic metres, D is diameter at breast height in centimetres, and H is tree height in metres.

Timber volume of all trees on a sample plot was calculated by summing volumes of individual trees. A timber volume per hectare was then calculated by multiplying the timber volume on a plot by the reciprocal of the plot area.

Biomass of trees on the sample plots was calculated according to equations from my M.Sc. thesis (Krumlik 1974). Biomass of individual tree components (bole wood, bark, small branches, big branches, twigs, and foliage) was calculated as a dependent variable from allometric equations using tree dbh, height, and crown length as independent variables. Individual tree biomass was calculated as the sum of tree components, while plot biomass was calculated as the sum of individual tree biomass.

Allometric equations used to calculate the biomass of tree components of hemlock trees were:

$\log WOOD = 2.3195 + 0.7455 \log D^2H + 0.0007769/2$

$\log BARK = 3.1089 + 1.0388 \log BA + 0.001017/2$

$\log BIGBRAN = 2.8004 + 3.0744 \log D + 0.001083/2$

$\log SMBRAN = 1.2410 + 0.0008643 \log DCL^2 + 0.008636/2$

$\log TWFO = 0.8851 + 1.5576 \log D^2H - 0.0362 D^2H + 0.0003567/2$

$\log TW = -1.2724 + 1.1630 \log DCL^2 + 0.0002752/2$

$\log FO = 0.5980 + 1.7174 \log D^2H - 0.0447 D^2H + 0.0008062/2$

Allometric equations used to calculate the biomass of Pacific silver fir trees were:

$\log WOOD = 2.0472 + 0.9526 \log D^2H + 0.001184/2$

$\log BARK = 1.3455 + 0.9669 \log D^2H + 0.01133/2$

$\log BIGBRAN = 2.6654 + 2.4928 \log D + 0.02003/2$

$\log SMBRAN = 0.8615 + 0.7597 \log D \cdot CL = 0.003452/2$

$\log TWFO = 0.8787 + 1.0376 \log D \cdot CL + 0.003293/2$

Meanings of abbreviations in these equations are:

WOOD - biomass of tree bole wood

BARK - biomass of tree bole bark

BIGBRAN - biomass of big branches, diameter of a branch is over 2.54 cm (1 inch)

SMBRAN - biomass of small branches, diameter of a branch is 0.64 - 2.54 cm (1/4 - 1 inch)

TW - biomass of twigs, diameter is smaller than 0.64 cm (1/4 of an inch)

FO - biomass of foliage

TWFO - biomass of twigs and foliage together

Biomass of a tree bole was calculated as the sum of wood biomass and bark biomass. Biomass of a tree crown was calculated as the sum of small and big branches biomass and twigs and foliage biomass. Biomass of a whole tree was the sum of tree bole biomass and tree crown biomass. For hemlock, biomass of twigs and biomass of foliage were calculated separately. For Pacific silver fir, only the combined biomass of twigs and foliage was calculated.

All of the above logarithmic equations include the correction factor $\widehat{G}^2/2$--sample variance of the logarithmic equation divided by 2 (Baskerville, 1972) as the last figure of the equation.

Biomass of tree bole wood calculated by the above listed equations was compared with biomass calculated by the B.C. Forest Service timber volume equations (Table 4.1). The volume of tree bole wood obtained by these equations was multiplied by wood specific gravity: 0.41 g/cm^3 for hemlock, 0.36 g/cm^3 for Pacific silver fir, and 0.42 g/cm^3 for yellow cedar (Forestry Handbook of B.C., 1971, pp. 716-717). On 10 out of 12 sample plots biomass of tree bole wood calculated by B.C. Forest Service volume equations was larger than biomass calculated by logarithmic equations of Krumlik (1974). The largest differences were around 20%. Biomass calculated by the B.C.F.S. volume equations includes stumps which accounts for approxiamtely 4% of the total.

4.3.2. Biomass nutrient content

The amount of macronutrients immobilized within the above-ground standing tree biomass was estimated by multiplying the biomass of each particular tree component by the mean concentration of a particular macronutrient in that component, using data from Krumlik (1974) (Table 4.2).

4.3.3. Net above-ground primary production

Annual net primary production was calculated as the sum of annual wood increment and annual litter production. The assumption was made that the biomass of crowns of mature and overmature trees on sample plots is in a steady state; Turner (1975, pp. 113) confirmed that the crown and foliage biomass of mature trees is in a steady state. The annual wood increment was calculated as follows. The difference between present dbh and dbh 20 years ago was measured on increment cores obtained from bored trees on each plot. It was assumed that the height growth during the period of the last 20 years was negligible. Present wood volume and wood volume 20 years ago was then calculated for sampled trees using the B.C. Forest Service volume equations. A mean wood volume increment for sampled trees was calculated, then multiplied by the number of trees per hectare and divided by 20 (period for which increment was measured), to obtain annual wood volume increment per hectare. The annual periodic increment of wood volume was multiplied by wood specific gravity of a particular tree species to estimate stemwood biomass increment.

Table 4.1. Biomass of tree stemwood calculated by two sets of logarithmic equations. Biomass 1 was obtained by my logarithmic equations (Krumlik 1974). Biomass 2 was obtained by B.C. Forest Service equations (1976). Data in tonnes/hectare

Plot	Tree Sp.	Biomass 1 t/ha	Biomass 2 t/ha	Difference t/ha
PX 1	M.h.	224.5	178.8	+45.7
	P.s.f.	20.3	22.3	-2.0
	Y.c.	-	10.5	-
	Sum	244.8	211.6	+33.2
PX 2	M.h.	252.6	187.4	+65.2
	P.s.f.	42.1	47.5	-5.4
	Y.c.	-	8.4	-
	Sum	294.8	243.3	+51.5
PX 3	M.h.	199.8	196.8	+3.0
	P.s.f.	112.3	124.6	-12.3
	Sum	312.1	321.4	-9.3
PM 1	M.h.	361.6	350.6	+11.0
	P.s.f.	130.5	150.1	-19.6
	Sum	492.1	500.7	-8.6
PM 2	M.h.	213.4	205.0	+8.4
	P.s.f.	133.6	154.8	-21.2
	Sum	347.1	359.8	-12.7
PM 3	M.h.	68.8	84.5	-15.7
	P.s.f.	309.9	360.0	-50.1
	Sum	378.7	444.5	-65.8
PH 1	M.h.	75.6	81.6	-6.0
	P.s.f.	211.2	248.0	-36.8
	Sum	286.8	329.6	-42.8
PH 2	M.h.	83.3	130.8	-47.5
	P.s.f.	255.3	301.7	-46.4
	Sum	338.6	432.5	-93.9
PH 3	M.h.	87.4	98.0	-10.6
	P.s.f.	206.8	242.3	-35.5
	Sum	294.3	340.3	-46.0
MM 1	M.h.	176.1	226.3	-50.2
	P.s.f.	251.7	288.7	-37.0
	Sum	427.8	515.0	-87.2
MM 2	M.h.	136.3	150.9	-14.6
	P.s.f.	244.9	280.4	-35.5
	Sum	381.2	431.3	-50.1
MM 3	M.h.	80.3	97.6	-17.3
	P.s.f.	243.2	279.0	-35.8
	Sum	323.5	376.6	-53.1
		ΣΣ 4121.8	ΣΣ 4506.6	ΣΣ -384.8

Biomass 1--calculated by logarithmic equations of Krumlik (1974)

Biomass 2--volumes of wood calculated by B.C. Forest Service volume equations were multiplied by wood specific gravity. Included biomass of stumps which represents approximately 4% of the total.

Table 4.2. Mean concentrations (in percent) of macronutrients in biomass components of sampled mountain hemlock and Pacific silver fir on Mamquam plot (Krumlik 1974)

Tree	N		P		K		Ca		Mg	
component	M.h.	P.S.F.	M.h.	P.s.f.	M.h.	P.s.f.	M.h.	P.s.f.	M.h.	P.s.f
Wood	0.05	0.05	0.02	0.01	0.07	0.06	0.07	0.06	0.02	0.01
Bark	0.18	0.24	0.06	0.04	0.09	0.13	0.31	0.49	0.02	0.03
Big Branches	0.12	0.15	0.03	0.02	0.07	0.09	0.16	0.31	0.02	0.02
Small Branches	0.17	0.22	0.04	0.03	0.09	0.12	0.18	0.29	0.03	0.03
Twigs + Foliage	-	0.74	-	0.10	-	0.33	-	0.44	-	0.07
Twigs	0.38	-	0.06	-	0.16	-	0.18	-	0.04	-
Foliage	0.85	-	0.11	-	0.30	-	0.31	-	0.08	-

Nutrient uptake by above-ground net primary production was calculated as the sum of the amount of nutrients immobilized in the increment of wood and amount of nutrients returned in litterfall. To estimate the increase in the amount of immobilized nutrients, the annual biomass increment of wood was multiplied by the concentration of a particular element in stemwood (Table 4.2.).

4.3.4. Overstory litterfall

Biomass of litter per 10 m^2 and the concentration of elements in the litter were obtained for each of the five litter collections made during the study. For the biomass of foliage litter and the amount of nutrients recycled in foliage litter, mean, standard error of the mean, and confidence limits were calculated. For other litter components, which were bulked within plots no measure of variability is available. To calculate the biomass of litter and the amount of nutrients recycled in litter per year, all five collections were summed, and the resulting value was divided by 2. This constitutes a small overestimate of litter, since the whole sampling period was 2 years and 2 weeks. It was not possible to calculate the variability of foliage litter nutrient content for the whole sampling period. In the first two collections, every foliage litter sample was analyzed. In the following three collections, foliage samples were bulked for chemical analyses. Because the sources of variability were not consistent for all collection periods, confidence limits were calculated separately for litter collections one and two and for collections three, four and five.

4.3.5. Nutrient content of throughfall and incident precipitation

The amount of nutrients returned in the snow-free period throughfall was calculated for 1974, 1975, and 1976. It was not possible to calculate the annual return because throughfall was not sampled during winter. The input of nutrients in incident precipitation was also calculated for summer sampling periods only. Leaf wash was calculated as a difference between throughfall and incident precipitation. Aerosol interceptors were not used.

4.3.6. Statistical comparison of study sites

One-way analysis of variance was used to compare mean dbh, tree height, stem wood volume, foliage litter biomass, and nutrient return in litterfall among sampling plots and among the four site-types. Duncan's Multiple Range Test was used to group means into homogeneous groups. Bartlett's test was used to test the equality of variances of different samples. Since the number of samples per plot for litterfall and throughfall is equal or almost equal (10 or 11 samples), the F ratio is insensitve to departures from the assumption of equal variances (Walpole, 1971).

CHAPTER 5

RESULTS AND DISCUSSION

5.1. Tree standing biomass and nutrient content

As already mentioned in Chapter 4.3., logarithmic regression equations from my M.Sc. thesis (Krumlik 1974) were used to calculate tree standing biomass on the sample plots. These equations were derived from a very small number of destructively sampled trees at the Mamquam plot (5 mountain hemlocks, 7 Pacific silver firs). In order to check on the reliability of these equations, the biomass of stem wood was also calculated using B.C. Forest Service (1976) equations for hemlock (western and mountain) and Pacific silver fir (Chapter 4.3.1, Table 4.1). The Forest Service equations for hemlock gave lower values on five plots and higher values on seven plots in comparison to the results from my equations for mountain hemlock; the difference was more than 10% on two of the former (PX1: 25%, PX2: 35%) and on five of the latter plots (the two largest deviations were PH2: 36% and M1: 22%). B.C. Forest Service equations are for both western and mountain hemlock. Trees at high elevations have greater taper. Equations derived primarily from lower and middle elevations may therefore be less accurate for high elevation trees. The stem wood biomass of Pacific silver fir calculated by the B.C. Forest Service equations was higher on all 12 plots compared with the results from my equations. On 10 plots the difference was larger than 10%; the largest difference was 15.5% (plot PH2).

The wood biomass of the whole plot calculated by the B.C. Forest Service equations was lower on 2 plots and higher on 10 plots, than estimates from my equations. On 3 plots the difference was less than 10%, on 7 plots the difference was between 10 and 20%, and on 2 plots the difference was higher than 20% (PX2: 21%, PH2: 22%). The standard error of B.C. Forest Service volume equations is 13% for hemlock and 10% for Pacific silver fir. If it is assumed that the B.C. Forest Service equations are correct, the wood biomass was overestimated by more than 13% on two plots, and underestimated by more than 13% on 5 plots utilizing my equations. It is very difficult to determine which set of equations is closer to the truth. My equations are derived from a limited number of trees in this particular area, whereas the B.C. Forest Service equations are derived from many hundreds of sampled trees in various elevations in south coastal B.C.

Equations used for calculating biomass of trees on sample plots may slightly underestimate wood biomass. Since wood biomass represents the biggest proportion of the above-ground tree biomass, this means that the above-ground biomass may be slightly underestimated on most plots. There is only a very small probability that the tree biomass data are overestimated except on plots PX1 and PX2 (Table 4.1).

To verify the data on macronutrient distribution in the above-ground tree biomass, the foliage concentrations obtained on the Mamquam plot (Table 4.2) were compared with foliage concentrations on Paul Ridge plots. The macronutrient concentration of wood and bark of a particular species is fairly

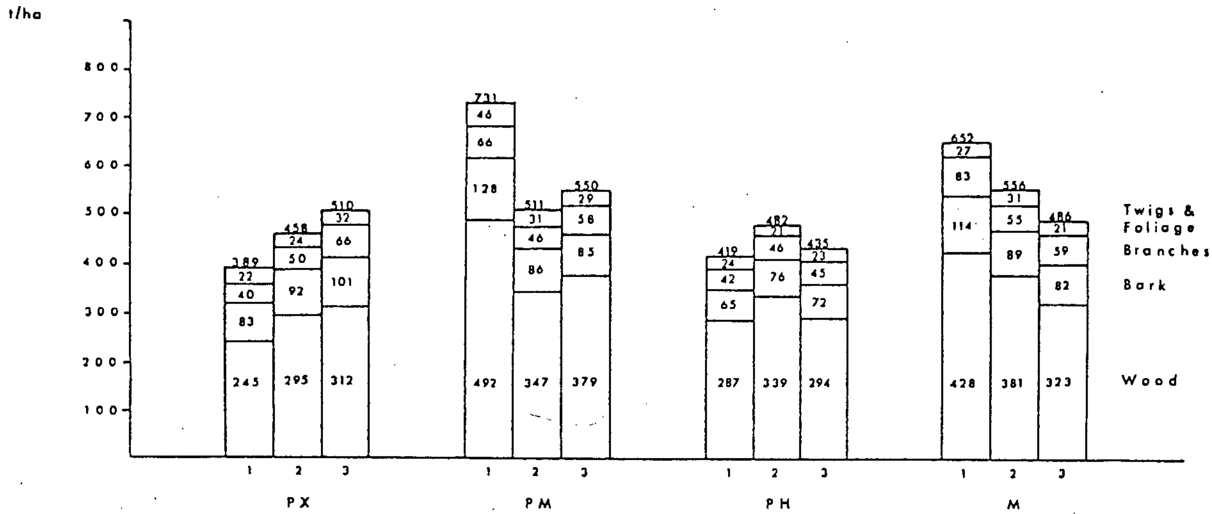


Figure 5.1. Distribution of above-ground tree biomass on sample plots (t/ha).

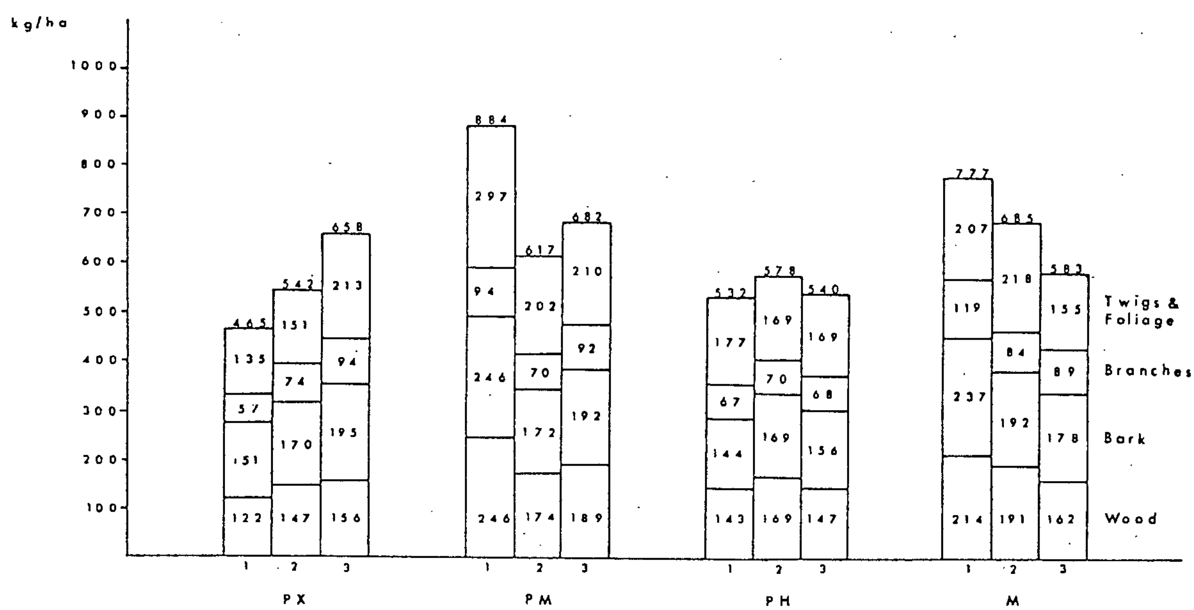


Figure 5.2. Distribution of nitrogen in the above-ground tree biomass (kg/ha).

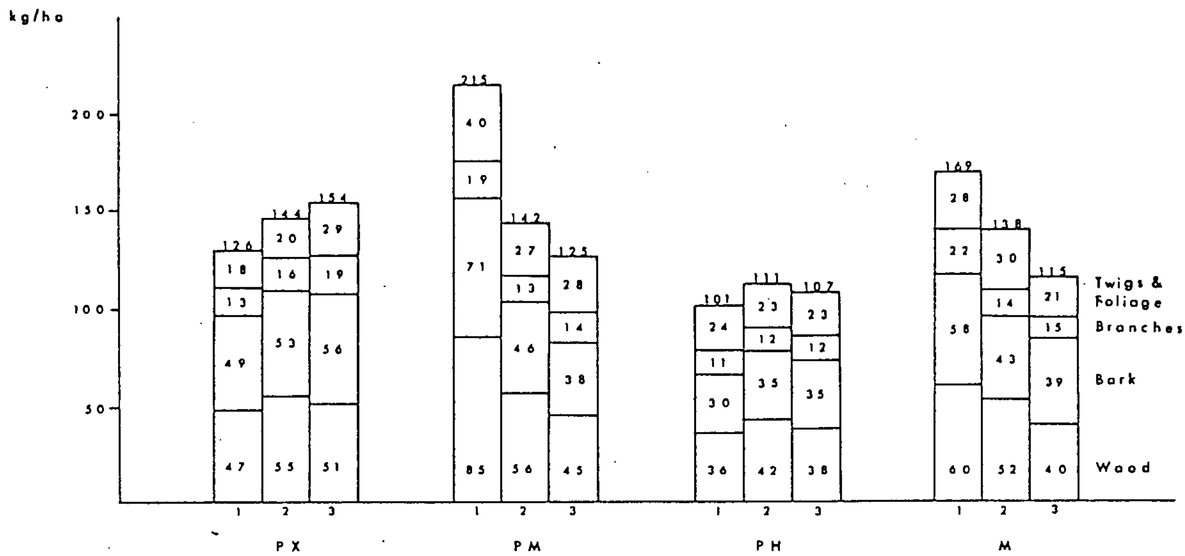


Figure 5.3. Distribution of phosphorus in the above-ground tree biomass (kg/ha).

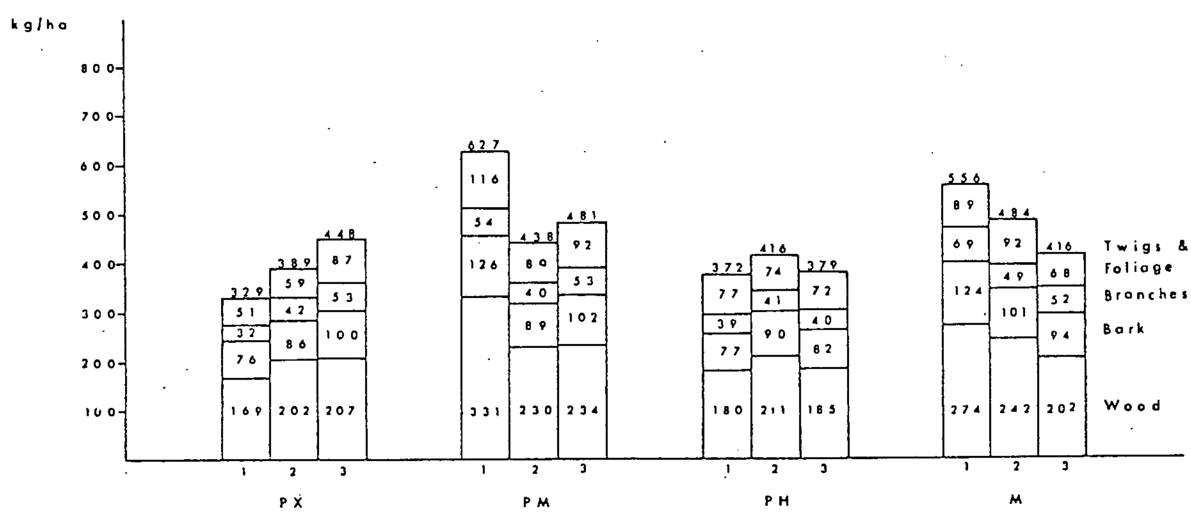


Figure 5.4. Distribution of potassium in the above-ground tree biomass (kg/ha).

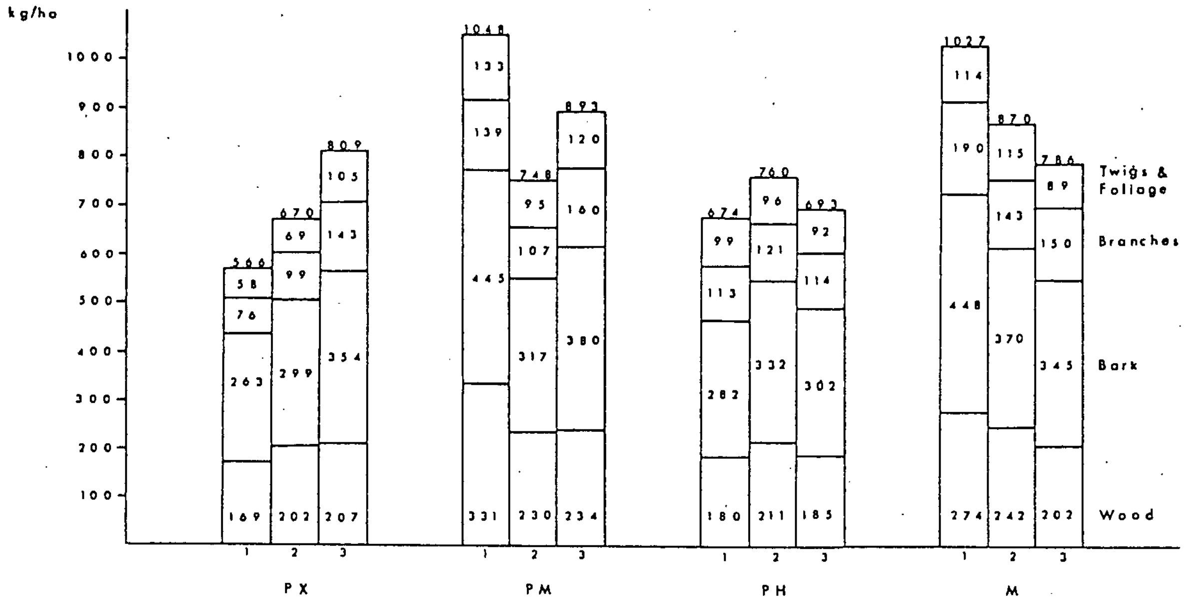


Figure 5.5. Distribution of calcium in the above-ground tree biomaes (kg/ha).

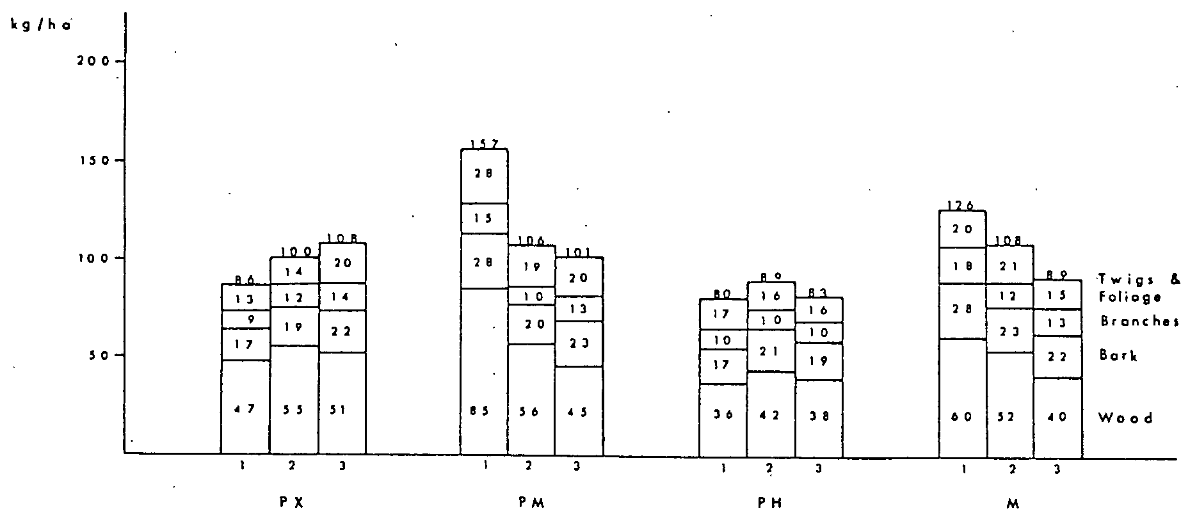


Figure 5.6. Distribution of magnesium in the above-ground tree biomass (kg/ha).

constant at various locations, but the foliage concentration is very prone to change. It was therefore assumed that if foliage macronutrient concentrations were similar then the macronutrient concentrations of wood and bark were similar too (Morrison, 1974). The foliar concentrations of sampled trees on the P-plots are summarized in Appendix 4. It must be emphasized that the foliage samples were obtained from the lowest living branch. If the macronutrient concentrations of hemlock foliage on the Mamquam plot and the Paul Ridge plots are compared, they appear to be fairly similar on the PX and PM plots and slightly higher on the PH plots. It therefore appears reasonable to use the macronutrient concentrations from the Mamquam plots for calculating macronutrient distribution on the Paul Ridge plots.

The above-ground tree biomass distribution and the macronutrient distribution in the above-ground tree biomass on 12 sample plots are summarized in Figures 5.1 - 5.6. More detailed data on macronutrient distribution by tree components and tree species are in Appendix 5.

The wood of tree boles accounts for the largest proportion of the above-ground tree biomass and foliage and twigs for the smallest proportion, reflecting the advanced age of the stand. Macronutrient distribution shows a different pattern. Twigs and foliage and tree bole bark contain the largest proportion of nitrogen, followed by wood and branches. Wood and bark contain the largest proportion of phosphorus, followed by twigs and foliage, and then branches. Wood contains the largest proportion of potassium and magnesium, followed by bark, twigs and foliage, and branches. Bark contains the largest proportion of calcium, followed by wood, branches, and twigs with foliage.

The quanitity of above-ground tree biomass and its macronutrient content are comparable with results of other authors. Turner and Singer (1975) measured the biomass and nutrient content of 175-year-old Pacific silver fir and mountain hemlock forest at an elevation of 1200 m in the Cascade Mountains of Washington state. The total above-ground tree biomass of 465 t contained 345 kg N, 63 kg P, 956 kg K, 1013 kg Ca, and 157 kg Mg. Turner (1975) reported the above-ground tree biomass of 95-year-old naturally regenerated Douglas-fir forest at an elevation of 210 m to be 348 t, and its macronutrient content to be 445 kg N, 80 kg P, 254 kg K, 333 kg Ca and 58 kg Mg. Hanley (1976) quantified the above-ground tree biomass of forests of northern Idaho. A 103-year-old grand fir-*Pachistima* forest (4 stands) had a biomass of 326 to 578 t/ha. A 100-110-year-old western hemlock-*Pachistima* forest (3 stands) had a biomass of 306-368 t/ha, while a 250-year-old stand of the same forest had a biomass of 341 t/ha. Studying the biomass of forests of Eastern Nepal, Yoda (1968) found that the above-ground tree biomass of a *Tsuga dumosa* forest growing at 2760 m was 629 t/ha, that of an *Abies spectabilis*-*Tsuga dumosa* forest at 2920 m was 503 t/ha, and that of *Abies spectabilis* forests at 3120, 3280, 3420 and 3530 m elevation was 496 t/ha, 399 t/ha, 420 t/ha, and 336 t/ha respectively.

If we use the 10-point scale of Rodin and Bazilevich (1967) which classifies ecosystems according to their productivity and nutrient turnover, the above-ground biomass of trees on the sample plots would qualify for class 9 to 10 (B_{9-10}). Similarly, the plots could be classified according to the amount of nutrients immobilized within the above-ground tree biomass as b_{6-7}.

The timber volume on the sample plots is close to or higher than the upper limit given for the appropriate plant associations by Brooke et al. (1970) (Table 3.6). The three PX plots, which were classified as examples of the Vaccinio-Tsugetum mertensianae plant association, have timber volumes of 523, 609, and 826 m^3/ha; Brooke et al. (1970) give a mean timber volume of 470 m^3/ha and an upper limit of 533 m^3/ha. The PM and M plots, which were all classified as the Abieto-Tsugetum mertensianae plant association, have timber volumes of 1272, 930, 1206 m^3/ha (PM plots) and 1354, 1147, and 1013 m^3/ha (M plots); Brooke et al. (1970) give a mean timber volume of 924 m^3/ha and an upper limit of 1150 m^3/ha. The PH plots, which were classified as examples of the Oplopanaco-Thujetum plicatae plant association, have timber volumes of 888, 1157, and 912 m^3/ha; Brooke et al. (1970) give a mean timber volume of 1098 m^3/ha and a range of 801-1977 m^3/ha.

Turner (1975) studied the increase in above-ground tree biomass with age. He found a very good correlation between wood and crown biomass and stand age; I found virtually no such correlation. However, the age of stands studied by Turner (1974) was from 9 to 95 years, a time period of rapid biomass increase. The age of my stands was from 295 to 434 years (Appendix 6), a time period of very small biomass change.

Individual tree biomass is very closely correlated to tree diameter, height and stem wood volume. Therefore, rather than trying to use statistical analyses to compare the biomass on the sample plots, mean tree dbh, height and stem wood volume were compared. One-way analysis of variance and Duncan's multiple range test were used to compare mean dbh, tree height and stem wood volume and to group means into homogeneous sets. The analyses were done in two stages. Firstly, the equality of mean dbh, height and stem wood volume among the three plots representing one ecosystem type were tested. Secondly, the equality of means between different ecosystem types were tested. The results of the first analysis are:

	DBH	H	VOL
PX	(1,2)(3)	(1,2,)(3)	(1,2)(3)
PM	(1,2)(3)	(1,2,3)	(1,2)(3)
PH	(1)(2,3)	(1)(2,3)	(1)(2)(3)
M	(1,2,3)	(1,2,3)	(1,2,3)

Plot PX3 has a mean dbh, tree height and stem wood volume that are significantly different ($p < 5\%$) from PX1 and PX2 which are similar to each other. Plot PM3 differs significantly from plots PM1 and PM2 in mean dbh and stem wood volume, but not in height. Plot PH1 differs from plots PH2 and PH3 in both mean dbh and height and three PH plots differ from each other in mean stem wood volume. Only the M plots are homogeneous in both terms.

The results of the second analysis are:

D	(PX) (PM) (PH) (M)
H	(PX) (PM) (M,PH)
VOL	(PX) (PM) (PH,M)

Each plant association (represented by a group of three plots) has a statistically significantly different ($p<5\%$) mean diameter, tree height and stem wood volume, with the exception of the M and PH plots, where the mean tree height and stem wood volume are statistically similar ($p<5\%$).

5.2. Estimate of the annual above-ground net primary production and nutrient uptake in net primary production.

Annual net primary production was calculated as the sum of annual stemwood increment and annual litterfall biomass (Chapter 4.3.3). This was done under the assumption that the crown biomass is in a steady state. The increment of tree bole bark was not taken into account. The litterfall included some large branches that were used to estimate branch biomass turnover.

The estimate of bole wood increment is based on a limited number of sampled trees. From each sampled tree only one increment core was taken, which means that the tree bole increment was estimated only in one direction. No attempt was made to estimate tree mortality or decrease in wood biomass resulting from internal stem decay or loss of plant biomass by grazing.

The estimate of annual net primary production presented here is based mainly on above-ground litterfall, which is considered by a number of researchers to be the major component and a good indicator of above-ground net primary production in mature forests (Bray and Gorham 1964, Rodin and Bazilevich 1967). Other components of net primary production were sampled less extensively.

The periodic increment of wood for the last 20 years and the age of sampled trees are summarized in Appendix 6. Due to the small number of sampled trees the standard error of the mean age and volume increment is rather large.

The mean annual net volume increment and the periodic annual net volume increment (calculated from the increment of the last 20 years) of the tree stemwood and the quantity of macronutrients immobilized annually in the stemwood biomass increment are summarized in Table 5.1. It is worthwhile to compare mean annual net increment with periodic annual net increment for individual plots. All except the PX plots show considerable smaller periodic annual net increment than mean annual net increment. This means that the increase of wood volume during the last 20 years is considerably slower than the average wood volume increase during the life of the stand for all plots except the PX plots, on which the periodic annual net increment is approximately equal to (plots PX1 and 3) or even bigger than (plots PX2) the mean annual increment. This is surprising considering that the mean age of trees on the PX plots is around 350 years. Figure 5.7 helps to understand the relationship between mean annual and periodic annual increment. PX plots at the age of about 350 years are still in the period of maximum growth. I consider this to be a very interesting discovery that deserves more detailed study in the future. Trees on PX plots seem to mature slower than on other plots; their growth curve is less steep and their net growth more prolonged.

The variation in periodic annual wood increment and mean annual wood increment on the different sample plots is shown in Figures 5.8 and 5.9, and the relationship between age on different sample plots in Figure 5.10.

Table 5.1. Mean annual net volume increment and periodic annual net volume increment (a period of the last 20 years) of tree stemwood. Immobilization of macronutrients in the periodic annual net increment of stemwood.

	Mean annual net volume increment $m^3/(ha \cdot a)$	Periodic annual net volume increment $m^3/(ha \cdot a)$	Periodic annual net increment: Biomass $t/(ha \cdot a)$	N	P	K	Ca	Mg
				----------	$Kg/(ha \cdot a)$	----------		
PX1	1.46	1.6	0.6	0.3	0.1	0.4	0.4	0.1
PX2	1.77	2.2	0.9	0.4	0.1	0.6	0.6	0.1
PX3	2.25	2.1	0.8	0.4	0.1	0.5	0.5	0.1
$\overline{PX}$	1.83	2.0	0.8	0.4	0.1	0.5	0.5	0.1
PM1	3.74	1.1	0.4	0.2	0.1	0.3	0.3	0.1
PM2	3.16	1.6	0.6	0.3	0.1	0.4	0.4	0.1
PM3	2.78	1.3	0.5	0.2	0.1	0.3	0.3	0.1
$\overline{PM}$	3.23	1.3	0.5	0.2	0.1	0.3	0.3	0.1
PH1	3.01	0.8	0.3	0.2	0.05	0.2	0.2	0.05
PH2	2.73	1.1	0.4	0.2	0.1	0.3	0.3	0.1
PH3	2.64	0.8	0.3	0.2	0.04	0.2	0.2	0.04
$\overline{PH}$	2.79	0.9	0.4	0.2	0.05	0.2	0.2	0.05
M1	3.21	1.9	0.7	0.4	0.1	0.5	0.5	0.1
M2	2.75	1.3	0.5	0.2	0.1	0.3	0.3	0.1
M3	2.63	1.5	0.5	0.3	0.1	0.4	0.4	0.1
$\overline{M}$	2.86	1.6	0.6	0.3	0.1	0.4	0.4	0.1

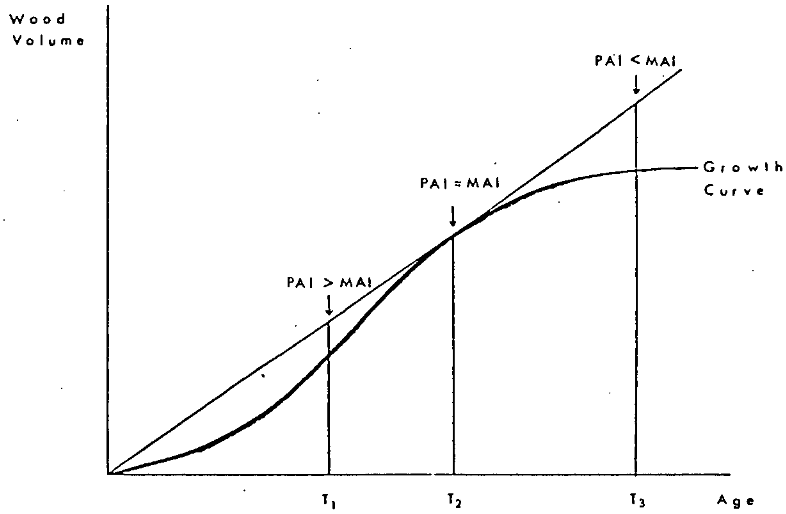


Figure 5.7. Relationship between tree growth and tree age. At time T_1 periodic annual increment is larger than mean annual increment; at time T_2 these two increments are equal; at time T_3 mean annual increment is larger than periodic annual increment. PX plots are at time T_2, or to the left of it; all other plots are to the right of T_2.

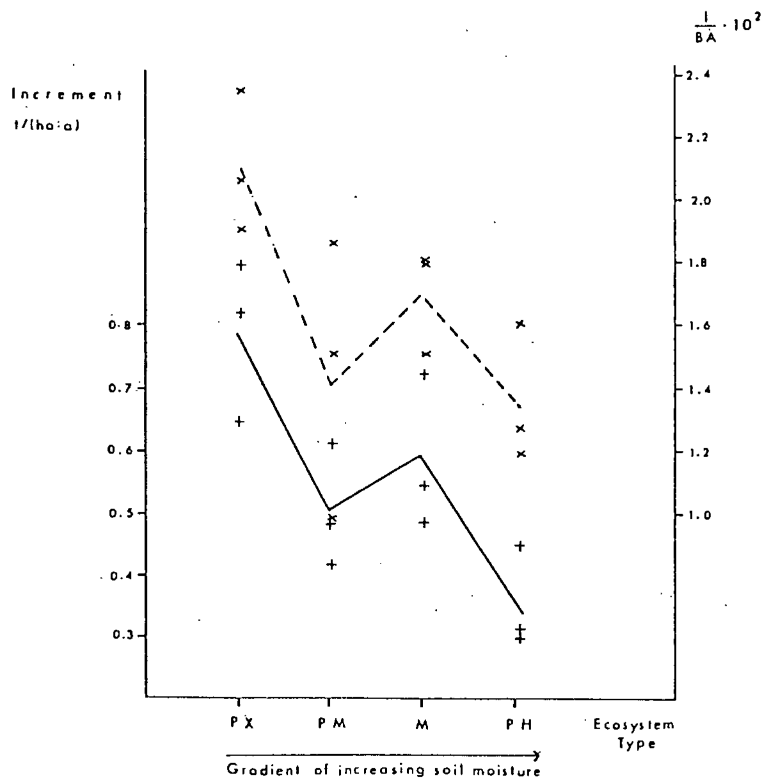


Figure 5.8. Periodic annual wood increment on sample plots (t/(ha·a))--continuous line and the ratio of periodic annual wood increment/BA--dashed line.

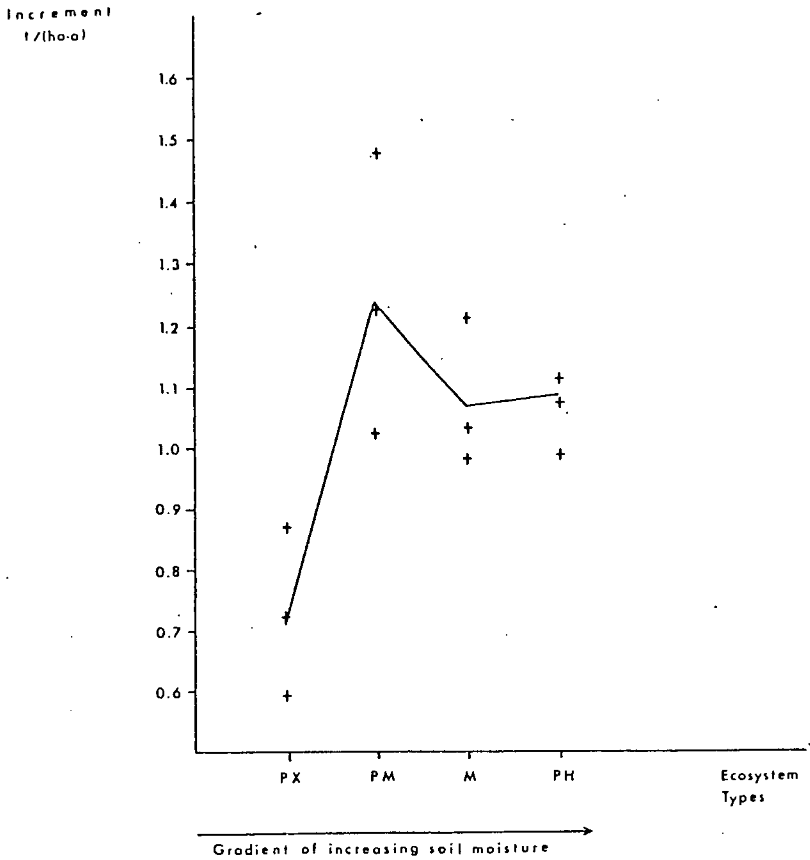


Figure 5.9. Mean annual wood increment on sample plots.

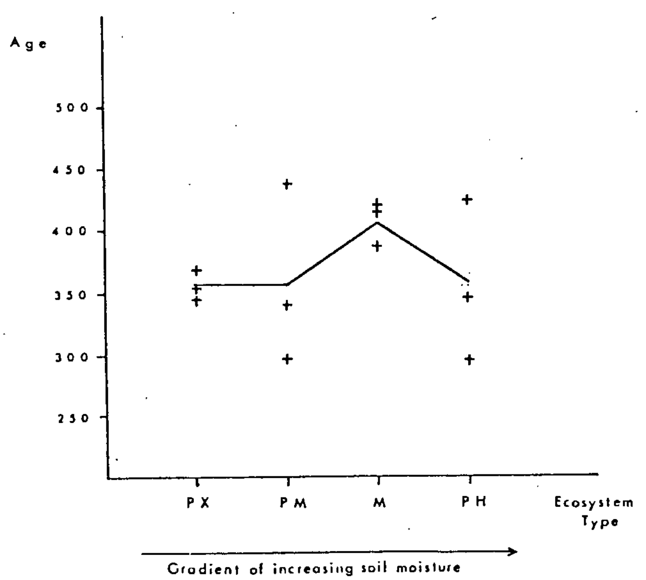


Figure 5.10. Mean stand age of sample plots.

The current annual net primary production (NPP) and the nutrient uptake by NPP are summarized in Table 5.2. The NPP in tonnes per hectare may not be the best expression of productivity since the density of trees on different plots inevitably was not equal. I therefore used the ratio of NPP to basal area (NPP kg/BA m^2). These two expressions of production are compared in Figure 5.11. The NPP on the less densely stocked PH plots is smaller in absolute terms (t/ha) than the other plots, whereas the ratio of NPP/BA is equal on PM, M, and PH plots and decreases on PX plots. It seems to me that the ratio NPP/BA is a more meaningful expression of productivity for the purpose of comparing different sample plots with unequal stocking.

The estimated above-ground NPP in the studied area (1.77-3.35 t/ha) is considerably lower than other published results. According to Rodin and Bazilevich (1967), the annual above-ground net primary production in fully formed ecosystems (30-80 years old) in the coniferous and mixed forest subzone varies between 7 and 20 t/ha. According to Kira and Shidei (1967), most of the coniferous forests in subarctic and subalpine regions have an annual productivity of 10-15 t/ha. They found only a very small number of these forests to have a productivity of less than 5 t/ha.

Kira and Shidei (1967) also discuss the relationship between stand age and gross production, stand respiration and net production. Gross production increases rapidly early in the life of a stand, reaches a peak, and levels off. Respiration increases more steadily and more gradually from youth to old age and approaches the level of gross production only at an advanced age. The difference between gross production and respiration (net production) has the greatest value at intermediate stand ages (40-70 years) at the time when gross production reaches its peak and starts leveling off. From this point on, stand respiration gradually approaches the level of gross production, and net production decreases. The relationship is expressed in Figure 5.12. The advanced age of the studied stands is probably the main reason for the very low annual net primary production.

On the 10-point net productivity classification scale of Rodin and Bazilevich, PX and PH plots can be described as P_2, and PM and M plots as P_3. All sample plots can be described as u_1 according to the mineral uptake by net primary production.

Table 5.2. Current annual net primary production (t/ha), ratio of net primary production to basal area (kg/m^2) and the uptake of macronutrients in N.P.P. (kg/ha).

Plot	NPP (t/ha)	NPP (kg/ha)* / B.A. (m^2/ha) (kg/m^2)	N	P	K	Ca	Mg
			(kg/ha)				
PX1	2.13	26	8.08	1.00	1.83	12.25	1.29
PX2	2.39	26	8.46	1.21	1.77	11.21	1.11
PX3	2.20	21	8.86	0.97	1.76	11.38	0.85
$\overline{PX}$	2.24	24	8.47	1.06	1.79	11.61	1.08
PM1	3.08	26	14.30	1.90	2.59	15.64	1.77
PM2	3.05	37	14.12	1.92	2.72	14.16	1.62
PM3	2.73	31	15.27	1.77	2.35	16.62	1.08
$\overline{PM}$	2.95	31	14.56	1.86	2.55	15.47	1.49
PH1	1.77	27	8.82	0.94	1.25	11.97	0.84
PH2	2.09	30	11.80	1.01	1.64	13.77	0.86
PH3	1.86	28	11.91	1.31	1.49	13.52	0.80
$\overline{PH}$	1.91	28	10.84	1.09	1.46	13.09	0.83
M1	3.35	32	16.77	2.03	2.35	16.52	1.07
M2	2.45	29	14.22	1.76	2.19	12.92	0.92
M3	2.67	33	15.32	1.79	2.28	13.82	0.97
$\overline{M}$	2.82	31	15.44	1.86	2.27	14.42	0.99

* kg of annual net primary production per 1 m^2 of basal area

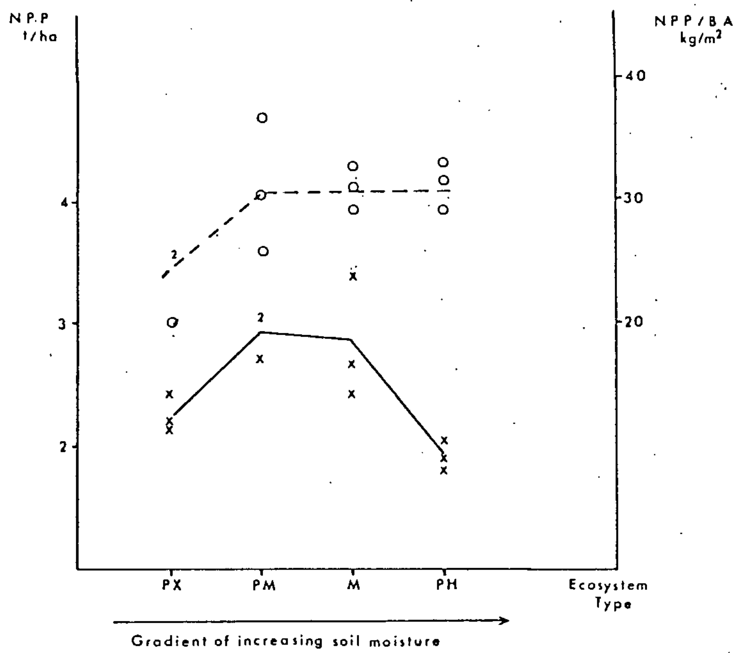


Figure 5.11. Comparison between annual net primary production (t/ha)--continuous line and the ratio net primary production/ basal area (kg/m^2)--dashed line.

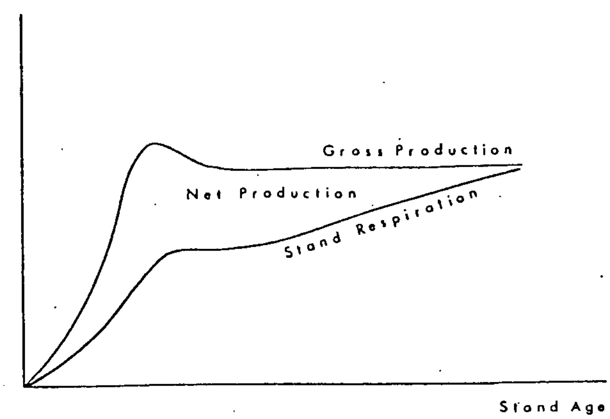


Figure 5.12. Relationship between stand age, gross production, stand respiration, and net production (after Kira and Shidei, 1967).

5.3 Litter production and its nutrient content

5.3.1. The biomass of litterfall

The biomass and macronutrient content of annual litterfall measured on the twelve plots are summarized in Table 5.3, Appendix 7, and Figure 5.13. The largest amount of litterfall occurred on the mesic sites [2.82 t/(ha•a) (PM plots) and 2.44 t/(ha•a) (M plots)] while the xeric and hygric sites (PX and PH plots) both produced a substantially smaller quantity of litterfall [1.67 t/(ha•a)].

The amount of litterfall on the sample plots is comparable to the results in the literature. Rodin and Bazilevich (1967) give a range of 2-7 t/(ha•a) for cool temperate forests. They state (pp.52) that (presumably within broad limits) the amount of litterfall is not dependent on plant biomass; this is not in agreement with my results. Figure 5.14 shows the relationship between above-ground tree biomass and the amount of litterfall on the study plots. The relationship can be expressed by the linear regression equation:

$$y = -31.94 + 4.24x$$

where, y = amount of litterfall in kg/(ha•a)

x = amount of above-ground tree biomass in t/ha

The coefficient of determination is $r^2 = 0.58$ ($r = 0.76$). The discrepancy between my results and Rodin and Bazilevich (1967) may or may not be due to the fact that their data represent a broad spectrum of forest stands while my data are limited to a small geographic area and narrow growth conditions.

Table 5.3. Annual biomass of litterfall and nutrient content of litterfall (in kg/ha)

Element	Litter component	PX	PM	PH	M
			kg/(ha•a)		
N	1*	6.51	11.59	8.65	12.00
	2	1.47	2.76	0.99	2.35
	3	1.32	2.45	1.53	2.59
	4	0.24	0.28	0.37	0.55
	SUM	9.54	17.07	11.54	17.49
P	1	0.79	1.49	0.85	1.43
	2	0.16	0.32	0.11	0.27
	3	0.13	0.27	0.15	0.28
	4	0.02	0.03	0.03	0.05
	SUM	1.10	2.11	1.14	2.04
K	1	1.13	1.94	1.03	1.60
	2	0.26	0.45	0.14	0.39
	3	0.14	0.27	0.18	0.26
	4	0.01	0.02	0.03	0.04
	SUM	1.54	2.68	1.37	2.29
Ca	1	9.71	12.62	10.31	10.51
	2	0.84	1.17	0.61	0.94
	3	1.19	2.12	2.08	2.52
	4	0.21	0.41	0.48	1.01
	SUM	11.95	16.32	13.47	14.99
Mg	1	0.89	1.26	0.66	0.72
	2	0.10	0.17	0.05	0.13
	3	0.07	0.14	0.10	0.14
	4	0.01	0.02	0.02	0.03
	SUM	1.06	1.58	0.83	1.02
Biomass	1	1125	1833	1107	1454
	2	213	373	112	272
	3	285	546	380	594
	4	42	67	71	122
	SUM	1666	2819	1670	2442

* 1-foliage
2-epiphytic lichens
3-twigs and branches
4-other litter

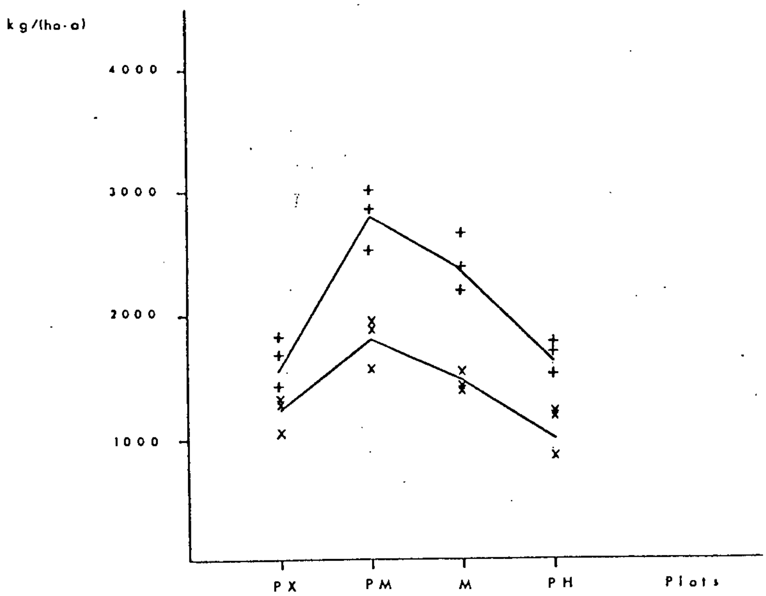


Figure 5.13. Total annual above-ground litterfall (+) and annual leaf litterfall (x) biomass on sample plots.

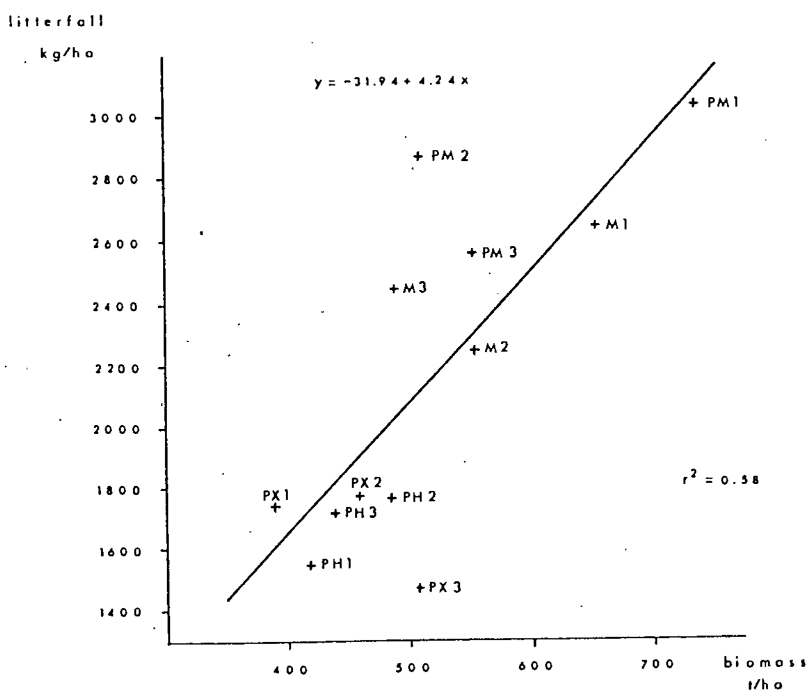


Figure 5.14. Relationship between above-ground tree biomass and litterfall biomass.

According to Bray and Gorham (1964), litterfall of cool temperate forests averages 3.5 t/(ha•a). The litterfall data from the Pacific Northwest, which are summarized in Table 2.2, has a range of 1.05 - 6.92 t/(ha•a). The litterfall on the study plots is well within this range. According to Rodin and Bazilevich's (1967) 10 point scale, the litterfall of the stands would be classified as L_{2-3} (Table 5.10).

5.3.2. Composition of litterfall

Litterfall was sorted into the following litter components: foliage, epiphytic lichens, twigs and branches and other litter. Foliage made up most of the litterfall on all sites: from 57 to 72%. Twigs and branches made up the second largest portion followed by epiphytic lichens, and other litter. Epiphytic lichens constituted a significant proportion of annual litterfall; their litterfall biomass ranged from 71 to 426 kg/(ha•a), representing 5 to 16% of total litterfall biomass. The proportion of various litter components on different plots was similar.

The mean, standard error of the mean, and 95% confidence limits of foliage litterfall biomass and macronutrient content are summarized in Table 5.4. Since foliage litterfall from each collector was analysed separately from litter collections 1 and 2, and was bulked from collections 3, 4, and 5, it was not possible to calculate confidence limits for the whole sampling period of 24 months. The confidence limits were therefore calculated for collections 1 and 2 combined, and 3, 4, and 5 combined. The confidence limits of other litterfall components were not determined because these components were bulked into one sample per plot.

Table 5.4. Statistics of foliage litterfall (mean, standard error of the mean and 5% confidence limits) for collections 1+2 (set 1) and 3+4+5 (set 2). For further explanation see text.

PLOT	SET	Biomass	N	P	K	Ca	Mg
		kg/ha					
PX1	1	943 (93)	4.96 (0.60)	0.60 (0.07)	1.01 (0.11)	9.19 (1.38)	0.95 (0.07)
		733-1152*	3.60-6.32	0.45-0.75	0.76-1.25	6.07-12.31	0.79-1.11
	2	1393 (176)	7.54 (1.03)	0.91 (0.12)	1.51 (0.19)	11.98(1.51)	1.28 (0.16)
		944-1792	5.22-9.86	0.64-1.18	1.07-1.95	8.57-15.40	0.92-1.65
PX2	1	1045 (176)	5.51(0.80)	0.79 (0.12)	0.87 (0.13)	8.76(1.23)	0.88 (0.17)
		648-1443	3.70-7.31	0.51-1.07	0.59-1.15	5.98-11.53	0.50-1.26
	2	1249 (122)	6.95 (0.79)	1.01 (0.10)	1.17 (0.11)	9.79 (0.87)	0.91 (0.09)
		973-1524	5.17-8.73	0.77-1.24	0.92-1.42	7.81-11.87	0.72-1.10
PX3	1	973(289)	6.25 (1.73)	0.64 (0.18)	0.97 (0.29)	9.26 (3.61)	0.65 (0.14)
		319-1627	2.33-10.16	0.24-1.05	0.32-1.62	1.08-17.43	0.32-0.97
	2	1150 (197)	7.87(1.34)	0.81 (0.14)	1.23 (0.22)	9.27 (1.61)	0.68 (0.12)
		704-1596	4.85-10.90	0.50-1.12	0.74-1.71	5.63-12.91	0.42-0.94
PM1	1	1908 (132)	9.90 (0.71)	1.40 (0.08)	1.90 (0.15)	10.50 (1.03)	1.60 (0.16)
		1615-2201	8.27-1.14	1.20-1.57	1.52-2.20	8.26-12.84	1.22-1.95
	2	2064 (109)	12.00(0.68)	1.60 (0.09)	2.20 (0.11)	14.90 (0.76)	1.50 (0.08)
		1822-2307	10.49-13.53	1.41-1.81	1.92-2.41	13.18-16.55	1.32-1.67
PM2	1	1668(130)	9.00 (0.64)	1.30 (0.11)	1.60 (0.14)	9.00 (0.88)	1.30 (0.14)
		1379-1958	7.54-10.40	1.06-1.56	1.32-1.95	7.06-10.98	0.97-1.62
	2	2077 (120)	13.40(0.80)	1.80 (0.10)	2.50 (0.14)	13.90 (0.77)	1.50 (0.09)
		1809-2344	11.60-15.17	1.56-2.03	2.18-2.80	12.14-15.59	1.25-1.65
PM3	1	1439(177)	9.80 (1.14)	1.10 (0.13)	1.40 (0.20)	13.10 (1.74)	0.80 (0.10)
		1043-1834	7.23-12.31	0.79-1.37	0.94-1.79	9.22-16.98	0.54-0.98
	2	1838 (193)	15.60 (1.69)	1.80 (0.19)	2.10 (0.22)	16.30 (1.70)	1.00 (0.10)
		1408-2269	11.79-19.32	1.35-2.21	1.62-2.61	12.54-20.11	0.74-1.18
PH1	1	796(120)	5.98 (0.99)	0.57 (0.10)	0.81 (0.14)	7.27 (1.29)	0.75 (0.32)
		525-1067	3.74- 8.22	0.35-0.80	0.49-1.13	4.34-10.20	0.03-1.47
	2	990 (147)	7.59 (1.26)	0.89 (0.26)	0.95 (0.13)	9.96 (1.49)	0.55 (0.08)
		658-1323	4.75-10.43	0.31-1.48	0.65-1.24	6.59-13.33	0.37-0.72
PH2	1	1121(113)	8.23 (0.79)	0.76(0.07)	0.92 (0.09)	9.54 (0.96)	0.64 (0.09)
		864-1377	6.45-10.01	0.59-0.92	0.72-1.13	7.37-11.71	0.44-0.83
	2	1292 (99)	10.55(0.76)	0.76(0.06)	1.21(0.09)	12.52 (0.93)	0.71 (0.06)
		1069-1515	8.81-12.28	0.63-0.89	1.01-1.41	10.41-14.64	0.58-0.84
PH3	1	1143-(153)	9.08 (1.13)	0.98(0.13)	1.06(0.14)	9.28(1.11)	0.65(0.11)
		798-1489	6.53-11.64	0.67-1.28	0.75-1.36	6.77-11.79	0.41-0.89
	2	1299 (98)	10.5 (0.76)	1.16(0.08)	1.21(0.09)	13.28 (0.98)	0.68 (0.06)
		1077-1521	8.79-12.21	0.97-1.35	1.01-1.42	11.06-15.49	0.56-0.81
MM1	1	1348 (128)	9.80 (0.97)	1.20 (0.11)	1.40 (0.11)	9.90 (1.48)	0.70 (0.05)
		1074-1621	7.58-11.93	0.93-1.42	1.12-1.62	6.59-13.20	0.57-0.81
	2	1700 (230)	16.60(1.96)	2.00(0.23)	1.70(0.22)	14.70 (2.02)	0.80 (0.11)
		1189-2212	12.18-20.94	1.46-2.49	1.24-2.24	10.23-19.24	0.61-1.08
MM2	1	1267 (83)	9.30(0.86)	1.10 (0.09)	1.40(0.09)	8.10 (1.05)	0.60(0.03)
		1082-1452	7.42-11.27	0.94-1.34	1.19-1.60	5.81-10.47	0.56-0.71
	2	1604 (83)	13.40(0.79)	1.70 (0.09)	1.90 (0.10)	12.40 (0.66)	0.80(0.04)
		1418-1789	11.61-15.12	1.45-1.86	1.63-2.10	10.94-13.90	0.71-0.89
MM3	1	1193 (73)	9.50 (0.74)	1.10 (0.08)	1.30 (0.10)	8.10(0.59)	0.60 (0.05)
		1029-1356	7.84-11.13	0.90-1.26	1.06-1.51	6.75-9.36	0.48-0.72
	2	1611(146)	13.50 (1.28)	1.60 (0.15)	2.00 (0.16)	12.90(1.15)	0.80 (0.07)
		1285-1938	10.66-16.38	1.24-1.89	1.58-2.32	10.37-15.51	0.62-0.92

Set 1 - Litter Collection one and two, September 1974 and July 1975.

Set 2 - Litter Collection three, four and five, September 1975 and July and September 1976.

* mean (SE)
95% confidence limit.

Leaf litterfall makes up 53 to 90% of the total litterfall according to Rodin and Bazilevich (1967), or 60-76% according to Bray and Gorham (1964). This compares well with the 57-72% observed on the study plots. The quantity of leaf litterfall of cool temperate forests is reported to average 2.5 t/(ha•a) (Bray and Gorham, 1964) which is appreciably higher than the volumes obtained in this study. The relationship between total litterfall and leaf litterfall on the sample plots can be expressed by the linear regression equation:

$$y = 129.51 + 0.58x$$

where, y = weight of leaf litterfall in kg

x = weight of total litterfall in kg

The coefficient of determination is $r^2 = 0.92$ ($r = 0.96$), indicating a good correlation between the quantity of leaf litterfall and total litterfall.

5.3.3. Nutrient concentrations

The concentrations of macronutrients and ash in summer and winter litterfall are given in Table 5.5. Data for one plot only from each group of plots are presented, since the macronutrient concentrations were very similar within the same plant association. The ash content was determined only for collection one. Foliage litterfall had a considerably higher concentration of nitrogen and phosphorus in winter than in summer, due to the higher proportion of green leaf litterfall in the winter: the result of wind and snowbreak. There is also a possibility that the concentration of N and P in snow buried litter is altered by the invasion of fungi and algae. Potassium exhibited the opposite trend, probably because of

Table 5.5. Concentration of macronutrients and ash in summer and winter litterfall (in per cent).

Collection 1, September 1974.

PLOT	L.C.[1]	N	P	K	Ca[1]	Ca[2]	Mg	Ash
PX1	1	.323(.008)[2]	.053(.002)	.134(.011)	.696(.063)	.970(.057)	.137(.005)	3.407(.144)
	2	.635	.060	.179	.142	.312	.044	2.629
	3	.466	.041	.049	.153	.267	.017	2.288
	4	.368	.030	.047	.438	.602	.023	2.846
PM1	1	.332(.010)	.070(.003)	.119(.003)	.546(.022)	*	.116(.004)	2.756(.079)
	2	.681	.082	.196	.166	*	.044	1.714
	3	.598	.069	.085	.197	*	.033	1.203
	4	.553	.055	.074	.920	*	.033	3.067
PH1	1	.561(.049)	.048(.004)	.146(.015)	.973(.054)	*	.062(.002)	3.417(.150)
	2	.786	.085	.182	.317	*	.040	2.403
	3	-	-	-	-	*	-	-
	4	.392	.050	-	-	*	-	-
M1	1	.488(.026)	.069(.002)	.125(.005)	.603(.033)	*	.072(.001)	4.854(.086)
	2	.626	.091	.274	.142	*	.034	3.284
	3	.340	.030	.039	.306	*	.014	3.172
	4	.450	.041	.094	.347	*	.033	3.668

Collection 2, July 1975

PLOT	L.C.	N	P	K	Ca[1]	Ca[2]	Mg	Ash
PX1	1	.694(.018)	.072(.002)	.083(.003)	.564(.075)	.911(.055)	.075(.003)	3.925(.202)
	2	.835	.074	.113	.272	.588	.052	2.941
	3	.375	.032	.032	.247	.384	.018	1.536
	4	.587	.047	.035	.449	.723	.024	2.739
PM1	1	.631(.017)	.075(.002)	.083(.002)	.565(.028)	.878(.038)	.063(.003)	*
	2	.761	.085	.107	.279	.525	.053	*
	3	.461	.045	.043	.317	.437	.024	*
	4	.633	.048	.033	.454	.596	.021	*
PH1	1	.785(.014)	.076(.003)	.088(.003)	.835(.048)	1.121 (.048)	.053 (.002)	*
	2	.909	.087	.119	.318	.613	.053	*
	3	.311	.026	.033	.427	.504	.025	*
	4	.403	.033	.038	.707	.855	.027	*
M1	1	.791 (.031)	.092 (.003)	.101 (.006)	.630 (.051)	.878 (.049)	.048 (.001)	*
	2	.781	.088	.105	.258	.466	.043	*
	3	.293	.031	.026	.367	.422	.022	*
	4	.397	.036	.025	.898	1.008	.022	*

1 L.C.-litter component 1 - foliage
2 - epiphytic lichens
3 - twigs and branches
4 - other litter

Ca[1] determined by acetylene - air flame
Ca[2] determined by acetylene - nitrous oxide flame

2 mean (SE of the mean) S.E. determined for leaf litterfall only, other components of the litterfall were bulked.

-quantity of sample too small to permit analysis.
*missing data

leaching during the period of snowmelt. Magnesium shows the same pattern as potassium, possibly for the same reason. The concentration of calcium remained similar in both summer and winter litterfall.

The concentration of nitrogen, phosphorus and potassium in epiphytic lichen litterfall was higher than in foliage litterfall throughout the year. Concentrations were higher in the winter than in the summer, but the reason for this is not known. Since epiphytic lichens seem to play a significant role in the nutrient turnover, especially in the turnover of nitrogen, they should be studied in more detail.

The amount of ash in the leaf litterfall was determined for collection one only. Concentrations on different sample plots are compared in Figure 5.15. There was considerable variation among sample plots. The mean ash content in leaf litterfall is almost equal on the M and PH plots. The smallest value was obtained for the PM plots. Rodin and Bazilevich (1967) give a range from 0.5 to 5% for various types of coniferous forests in the northern temperate zone. The data from this study fall into the upper half of this range. The ash concentration can be described as A_{4-5} on the 10 point classification scale of Rodin and Bazilevich (1967).

According to Rodin and Bazilevich (1967) the concentration of nitrogen in leaf litterfall varies within comparatively narrow limits for all types of conifer stands, between 0.4 and 1.3%. The data from this study fall into the lower half of this range, between 0.3 and 0.8%.

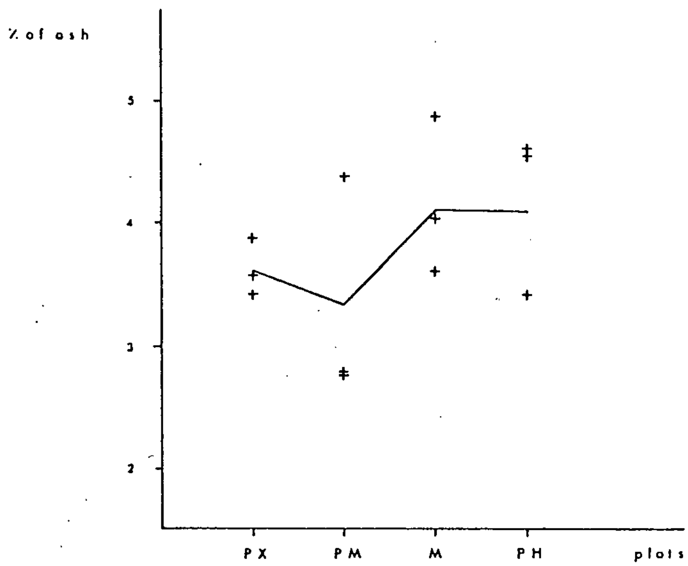


Figure 5.15. Percentage of ash elements in foliage litterfall on sample plots.

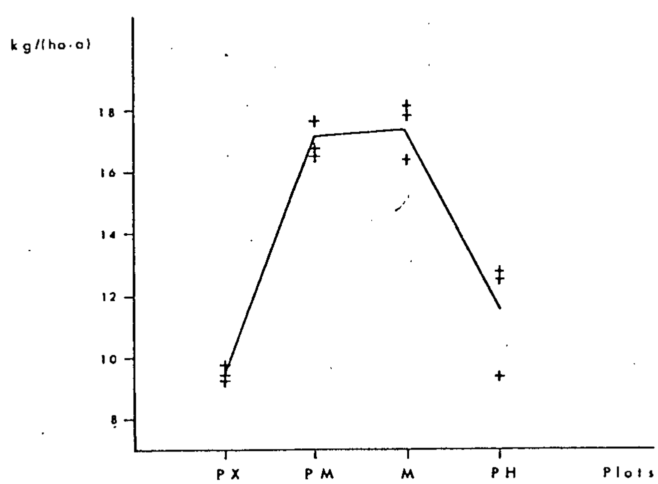


Figure 5.16. Quantity of nitrogen in litterfall on sample plots.

5.3.4 Macronutrient content of litterfall

The quantity of N + P + K + Ca + Mg returned with litterfall ranged from 24 to 41 kg/(ha•a) and was proportional to the litterfall biomass. Calcium was the most abundant element on PX and PH plots, while nitrogen was predominant on PM and M plots (Table 5.3). The quantity of macronutrients in litterfall on investigated sites are compared in Figures 5.16 - 5.20. The quantity of macronutrients returned with litterfall on PX and PH plots was similar: 25 and 28 kg/(ha•a), respectively. The quantity returned on PM and M plots was also similar: 40 and 38 kg/(kg•a), respectively.

Foliage litterfall contained the largest portion of the five macronutrients. Twigs and branches contain the second largest portion of calcium while the second largest portion of the other five macronutrients is either within epiphytic lichens or twigs and branches. Seven to 19% of the nitrogen reaching the forest floor in litterfall is in epiphytic lichens which as noted, also constitute 5 to 16% of the litterfall biomass. The epiphytic lichens represented, on average, 15% of the nitrogen reaching the forest floor in litterfall on the xeric site (PX plots), 16 and 13% on the mesic sites (PM and M plots, respectively), and 9% on the hygric site (PH plots).

Return of mineral elements with litterfall is reported to vary between 40 and 230 kg/(ha•a) (Rodin and Bazilevich, 1967). Data on the amount of mineral elements returned with litterfall in the Pacific Northwest are in Table 2.3 (page 19). Values for the study plots are similar to the lowest value given by Rodin and Bazilevich (1967) and are comparable with some of the lower

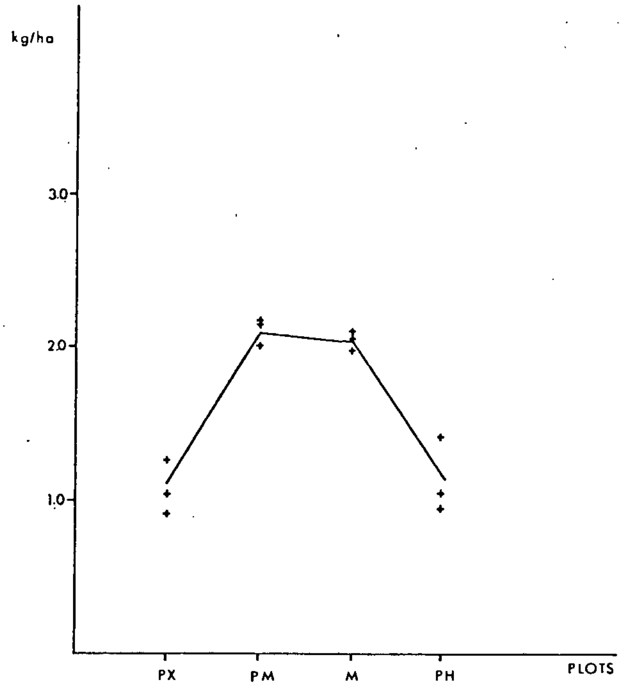


Figure 5.17. Quantity of phosphorus in litterfall on sample plots.

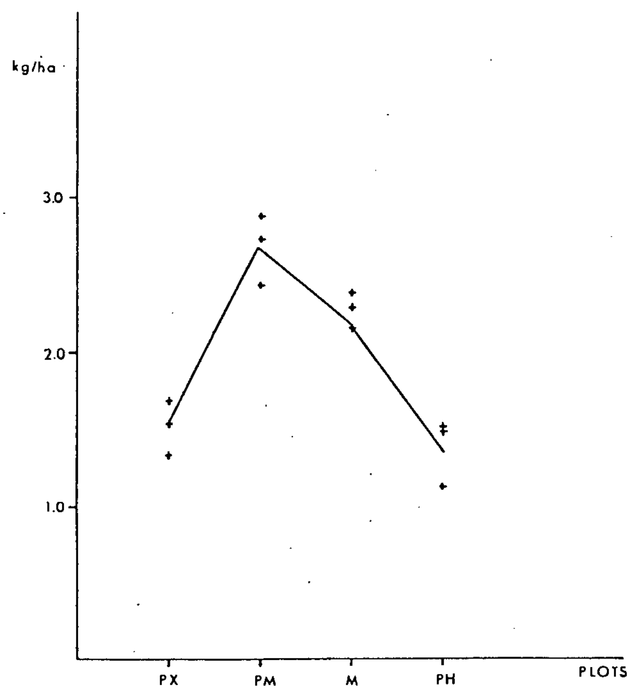


Figure 5.18. Quantity of potassium in litterfall on sample plots.

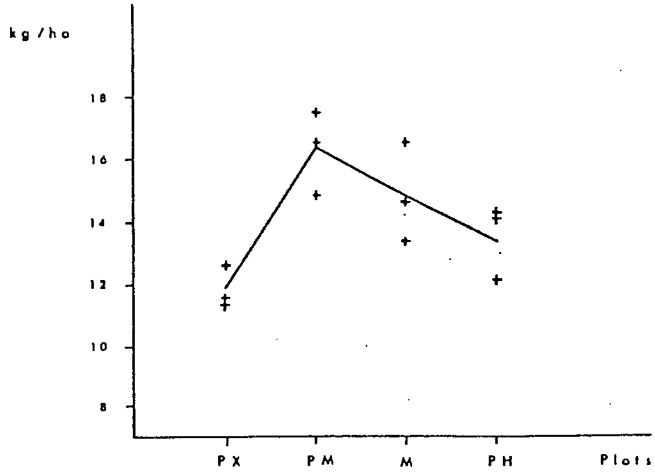


Figure 5.19. Quantity of calcium in litterfall on sample plots.

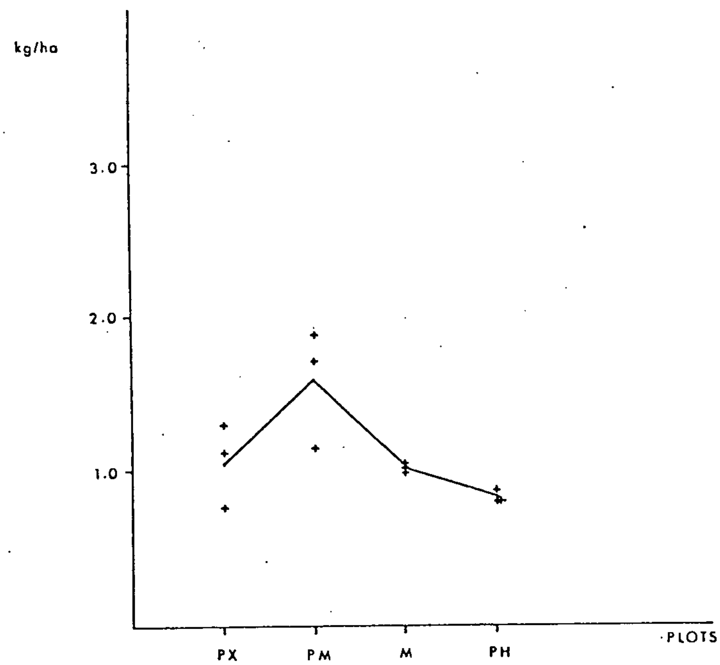


Figure 5.20. Quantity of magnesium in litterfall on sample plots.

values from other sites in the Pacific Northwest. Return of nitrogen in litterfall on the study plots is similar to the lower end of the reported range of 13 to 116 kg/(ha•a) (Rodin and Bazilevich, 1967). On the 10 point classification scale of Rodin and Bazilevich (1967), the amount of mineral elements returned with litterfall can be described as r_1 (Table 5.10).

5.3.5. Comparison of litterfall among plant associations

Quantities of annual litterfall biomass on the study sites are compared in Figure 5.13. The absolute weight of litterfall (in t/ha) is not necessarily the best method for comparing the study plots because of variation in tree densities between plots and because there is a relationship between amount of biomass and litterfall. I therefore used the ratio between litterfall and basal area (Figure 5.21). However, this transformation of litterfall data did not produce any major change in the rating of the plots (compare Figures 5.13 and 5.21).

Bonnevie-Svendsen and Gjems (1957) and Crosby (1961) (from Bray and Gorham, 1964) have shown a distinct correlation between annual litterfall and basal area, with values of 70 to 75 kg/m^2. In this study the litterfall values were 14 to 34 kg/m^2 of basal area, and there is a very weak correlation ($r^2 = 0.28$) between litterfall and basal area, expessed by the linear regression equation:

$$y = 651.88 + 17.29x$$

where, y = weight of the litterfall in kg/ha

x = basal area m^2/ha

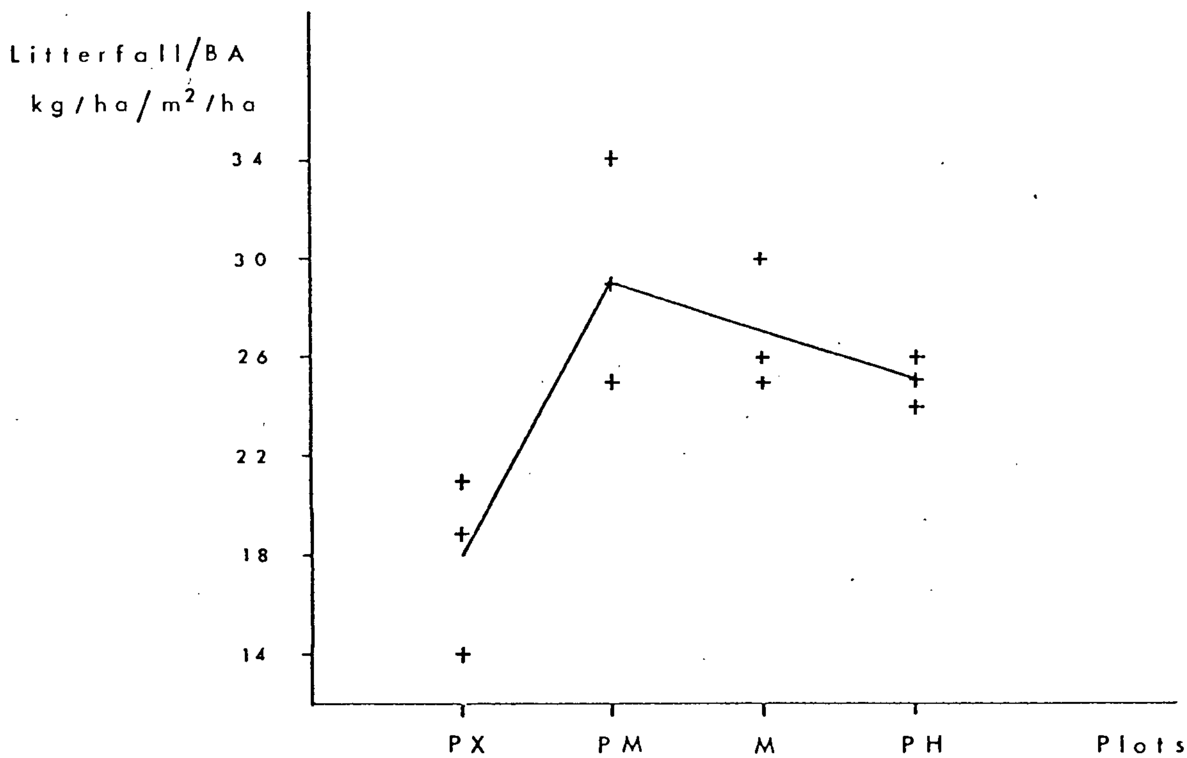


Figure 5.21. The ratio of litterfall biomass/basal area.
Litterfall biomass--kg/ha
Basal area--m^2/ha

One-way analysis of variance and Duncan's multiple range test were used to compare the mean quantity of leaf litterfall and the amount of macronutrients within leaf litterfall and to group plots together into homogeneous groups. Because of different sources of variation in litterfall collections (1 + 2) and (3 + 4 + 5) (see chapter 4.3.4), the statistical analysis had to be run separately for these two groups.

The homogeneity of plots within the same plant association was tested first (Table 5.6). The only heterogeneity in the PM plots throughout the entire period was the amount of magnesium in leaf litterfall which differed in PM3. The other differences among plots of the same plant association occured in only one of the two collection periods. Only in two cases is more than one element nonhomogeneous: calcium and magnesium on PM plots and phosphorus and calcium on PH plots. We can therefore conclude that plots representing each plant association are essentially homogeneous in terms of leaf litterfall biomass and macronutrients returned with leaf litterfall.

Table 5.7 shows ecosystems ordered into homogeneous groups according to their leaf litterfall biomass and its macronutrient content. In terms of biomass, the PX and PH sites are not significantly different, while the M and PM sites are significantly different from each other and from the PX and PH sites. In terms of quantity of nitrogen returned with litterfall, the M and PM sites are not significantly different, while the PX and PH sites are significantly different from each other and from the M and PM sites as well. Similar interpretations can be made for the other elements.

In 12 tested differences among the studied sites in leaf litterfall biomass and amount of macronutrients returned with leaf litterfall, the PX and PH plots were not different 8 times, M and PM plots 5 times, M and PH pltos 4 times, and M and PX plots twice. PX and PM plots and PM and PH plots were always significantly different.

Table 5.6. Homogeneity of leaf litterfall on sample plots from the same plant association. (Duncan's multiple range test).

Leaf Litterfall Parameter	Litterfall Collection: Collection # (1+2) PX	PM	PH	M	Collection # (3+4+5) PX	PM	PH	M
biomass	*[1]	*	*	*	*	*	*	*
N	*	*	*	*	*	*	*	*
P	*	*	(1,2)(2,3)[2]	*	*	*	*	*
K	*	*	*	*	*	*	*	*
Ca	*	(2,1)(3)	(1)(3,2)	(3,2)(1)	*	*	*	*
Mg	*	(3)(2,1)	*	*	(3,2)(1)	(3)(2,1)	*	*

1 * = all plots of the same plant association are homogeneous

2 Plots in parentheses represents homogeneous group .

Table 5.7. Homogeneous sets of leaf litterfall (Duncan's multiple range test) from different plant associations.

Litterfall collection

Leaf Litterfall Parameter	Collection # (1+2)				Collection # (3+4+5)			
biomass	PX	PH	M	PM*	PH	PX	M	PM
N	PX	PH	M	PM	PX	PH	PM	M
P	PX	PH	M	PM	PX	PH	PM	M
K	PH	PX	M	PM	PH	PX	M	PM
Ca	PX	PH	M	PM	PX	PH	M	PM
Mg	M	PH	PX	PM	PH	M	PX	PM

*Plots are ordered according to increasing quantity from left to right
Plots joined by a line are not significantly different at p<0.05: interruption of the line indicates statistically significant difference between plant associations.

5.4. Forest floor biomass

Depth, bulk density, and biomass of the forest floor on the sample plots are summarized in Table 5.8. The forest floor on all sample plots was rather thick, with mean depths varying from 5.5 cm to 12.7 cm. The mean bulk density of the forest floor ranged from 0.13-0.18 g/cm^3, higher than the bulk density usually quoted in literature--0.13 g/cm^3. The higher bulk density is the result of snow compaction, a large proportion of woody material, and the fact that roots smaller than 0.64 cm (1/4 inch) were included as forest floor.

On June 7, 1975 I took 10 snow cores for the purpose of determing snow specific gravity, snow depth, and snow weight. I sampled only on the PX plots and adjacent areas because at lower elevations most of the snow had already melted. The average snow depth was still 144 cm (S.E. 12.5 cm), the snow bulk density was 0.464 g/cm^3 (S.E. 0.017) (range 0.37-0.55 g/cm^3), and the average weight of snow cover was 668 kg/m^2. Early in the spring, when snow cover is considerably deeper (on some places up to 4 m) the snow weight is much greater. The weight of the snow layer makes the forest floor very compacted.

The duration of snow cover, 8-9 months a year in the studied area, is also an important factor determining slow decomposition.

The biomass of forest floor is considerably higher than other data in the literature: 88-190 t/ha. Rodin and Bazilevich (1967) give an average weight of forest floor for coniferous forests of 10-50 t/ha. Turner and Singer (1975) found the biomass of the forest floor under a 175-year-old Pacific silver fir-mountain hemlock stand at an elevation of 1200 m in Washington state to be 53.5 t/ha.

It is not known whether forest floor biomass in the studied area is in a steady state or whether it is still increasing. If we assume that the forest floor biomass is in a steady state, then we can calculate the decay rate as a proportion between litterfall and forest floor biomass. The estimated decay rate* for the plots ranges from 31 to 123 years (Table 5.10), indicating an extremely slow rate of litter decomposition. It has to be realized, however, that we consider only tree litterfall, not the understory litterfall, and therefore the decay rate is overestimated. Yarie (1978) found the relative contribution of understory litter to the total litterfall during the growing season to be 28%, 11%, and 26% on hygric, mesic and xeric sites respectively. The decay rate overestimation is therefore smaller on mesic sites with less understory vegetation and larger on hygric and xeric sites with heavy understory vegetation. The root litter was not considered either, its consideration would further reduce presented decay rates.

The quantity of organic matter of the forest floor functions as a sink for nutrients and immobilizes great quantities of nutritional elements for a long period of time.

According to Rodin and Bazilevich's (1967) 10 point scale, the forest floor biomass of these sites would be classified as F_{9-10} (Table 5.10).

* decay rate is a ratio between forest floor biomass and litter biomass.

Table 5.8. Forest floor biomass on 12 sample plots. *1

PLOT	n	LFH depths in cm mean (S.E.)	LFH bulk density g/cm^3, mean (S.E.)	LFH biomass t/ha
PX1	13	8.98 (1.96)	0.17 (0.01)	153*2
PX2	8	8.00 (0.96)	0.15 (0.01)	120
PX3	6	7.12 (0.70)	0.16 (0.01)	114
PM1	14	8.94 (1.04)	0.18 (0.01)	161
PM2	12	5.51 (0.73)	0.16 (0.01)	88
PM3	9	8.31 (1.29)	0.16 (0.01)	133
PH1	7	12.66 (1.69)	0.15 (0.01)	190
PH2	10	10.73 (2.00)	0.14 (0.01)	150
PH3	10	11.16 (1.53)	0.13 (0.01)	145
M-plots*3	30	9.09 (1.15)	0.18 (0.01)	164

n number of samples per plot

SE standard error of the mean

*1 data on forest floor depth and forest floor bulk density were provided by Dr. J.P. Kimmins.

*2 includes small roots up to diameter of 0.64 cm (1/4 inch)

*3 M-plots were sampled together as a group

5.5 Throughfall and atmospheric precipitation

As already mentioned in Chapter 4, sections 1.4 and 1.5, throughfall and atmospheric precipitation were sampled only during the late summer of 1974 and during the summers of 1975 and 1976. The data for atmospheric precipitation from 1974 are of doubtful value since only two collectors were used, and the data from all three open sampling sites varied excessively.

The mean quantities of throughfall and atmospheric precipitation and the associated nutrient content are presented in Figure 5.22 and 5.23. Quantities for individual plots are summarized in Appendix 8.

Comparison of the data for incident precipitation and throughfall does not indicate that a great amount of water is intercepted in tree crowns. On some plots the throughfall collected under trees exceeded the precipitation collected in the open. Schlesinger and Reiners (1974) found that a conventional open rain collector received only 1/5 of the amount that collected when simulated tree foliage was placed above the collector (see Chapter 2, section 2.2). Their data suggest that in areas of high wind and frequent exposure to clouds or fog, as in the montane areas of New England, measurements of total precipitation and elemental deposition require an evaluation of interception. The same may hold true on the study plots. The simple funnel type collectors in the open may grossly underestimate the amount of atmospheric precipitation. They do not collect fog, which impacts on tree foliage and drips into the collectors under the tree canopy. The rain is also often accompanied by wind, which may also result in an underestimation

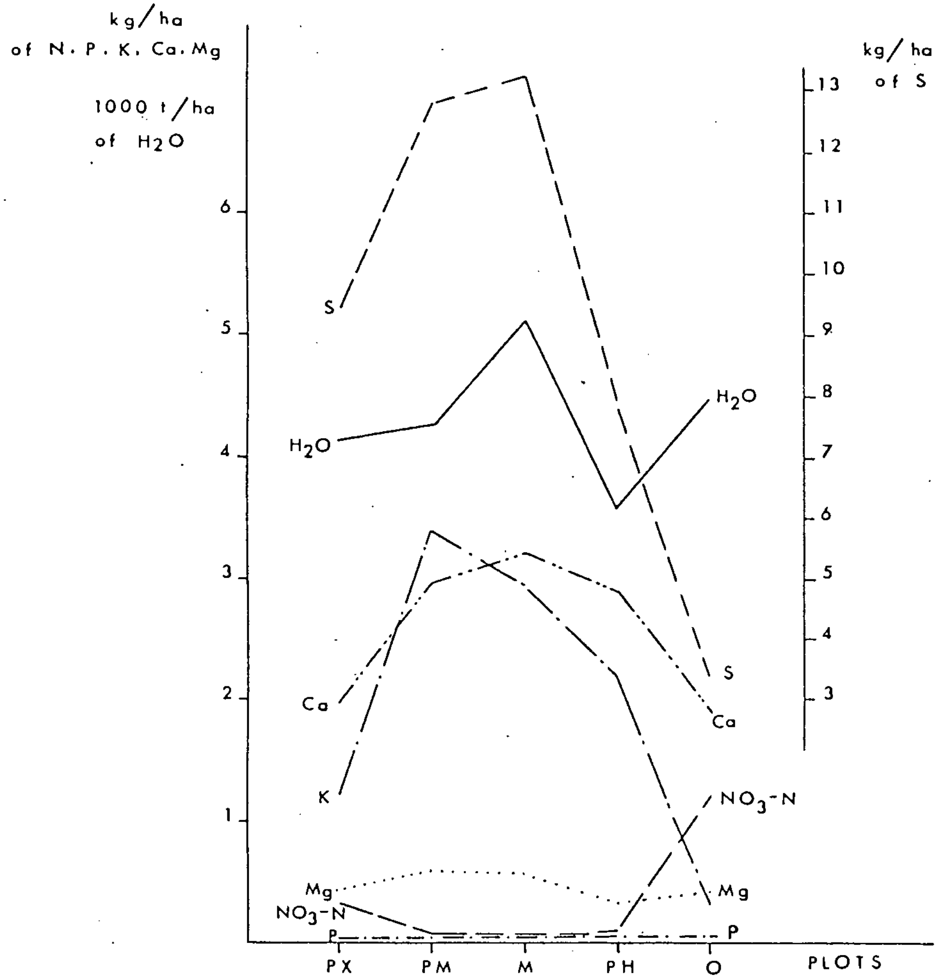


Figure 5.22. Quantity of throughfall and nutrients in throughfall during the summer of 1975. (13 weeks sampling period).

O plots - collectors in open area

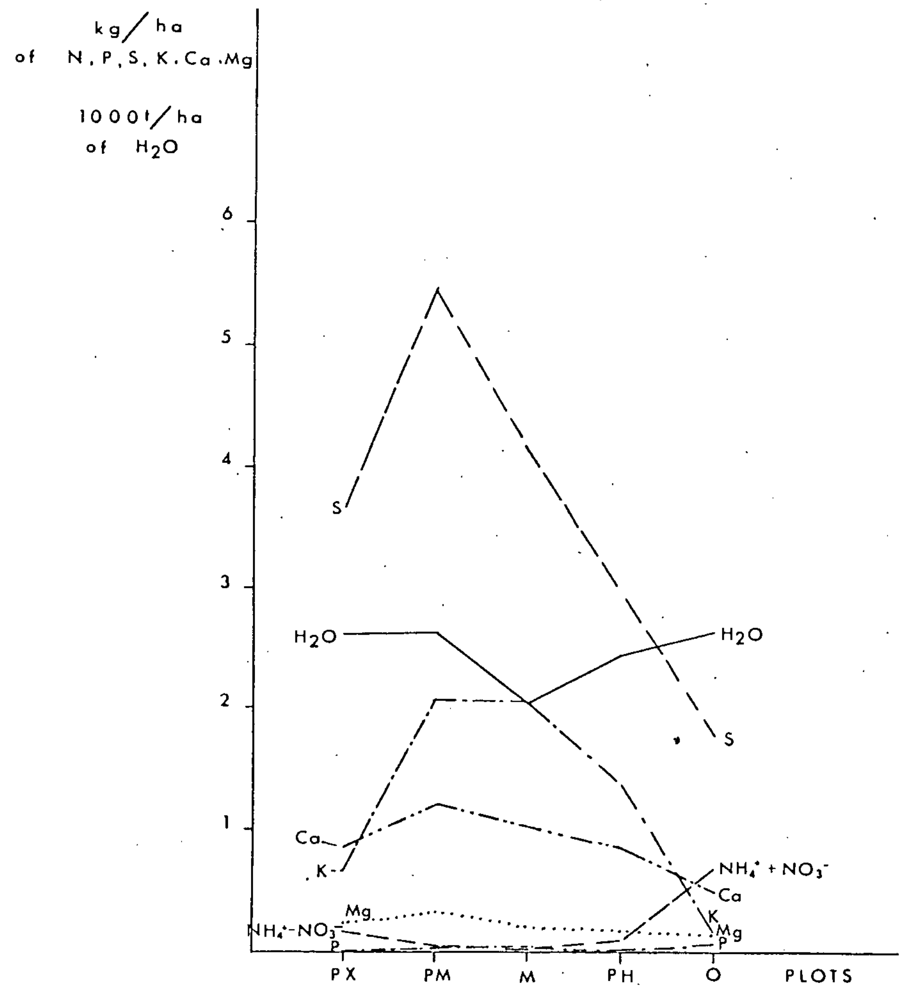


Figure 5.23. Quantity of throughfall and nutrients in throughfall during the summer of 1976. (8 weeks sampling period).

O plots - collectors in open area

by the open collector. The sampling method does not permit one to draw conclusions about the difference in the amount of water collected in the open under the tree canopy.

The relative amount of nutrients in the throughfall and rainwater on different plots and in the open is very similar during the summers of 1975 and 1976 (Figures 5.22 and 5.23). The amount of nitrogen is highest in the open, with much smaller quantity of N (both NO_3^- and NH_4^+) in throughfall. This reflects the ability of tree canopies to extract nitrogen from rainwater as reported by Carlisle et al. (1967) for an oak woodland in England. My data indicate that there may be over 1 kg/ha of nitrate nitrogen extracted from the rainwater by the tree canopy on some of the sample plots during the 13-week sampling period of summer 1975: a considerable amount in terms of tree nutrition. However, this study does not indicate whether the nitrogen uptake occurs from precipitation whenever it falls as rain or only during the summer. The data do not indicate the relative importance of foliage and epiphytes. I feel these questions should be answered in future studies, since nitrogen is thought to be the most critical nutrient element in determining the productivity of these ecosystems.

The quantity of phosphorus in rainwater is very small, and the quantity in throughfall seems to be even smaller, indicating a possible extraction of P by the tree canopy. However, the evidence is not conclusive because the concentration of P in many samples was below the detection limit of the analytical equipment. The only conclusion that can be drawn safely is that the quantity of phosphorus in atmospheric precipitation and in throughfall is normally negligible in the study area.

The quantity of potassium and calcium in throughfall is much greater than in rainwater, indicating strong leaching of these two elements, particularly potassium. This is in agreement with other studies on nutrient leaching (see Chapter 2, sets 2.2 and 2.3). Potassium is known as one of the two most readily leachable elements (potassium and sodium). Up to 3 kg/ha of K and 1 kg/ha of Ca were leached from the tree canopy during the 13-week sampling period of summer 1975. The amount of K in rainfall was approximatly 0.3 kg/ha, and the amount of Ca was close to 2 kg/ha.

The quantity of magnesium in the throughfall was only slightly higher than in rainfall. The amount of Mg leached from tree crowns was 0.0-0.2 kg/ha during the summer of 1975. According to Tukey (1970), Mg is an element leached in moderate quantities (1-10% of leaf nutrient content). However, in this study Mg did not seem to be very readily leached. The amount of Mg supplied by rainwater was approximately 0.4 kg/ha during summer 1975.

The quantity of sulphur was almost 3 kg/ha in rainwater and up to 13 kg/ha in throughfall during the 13-week sampling period of summer 1975. Eriksson (1952) gives values of S input in rainwater as low as 2.7 kg/(ha•a) in rural Russia (Smolensk) and as high as 234 kg/(ha•a) in Chicago, USA. His data indicate a close correlation between the amount of S in atmospheric precipitation and the amount of industry in the area. I suspect that most of the sulphur input to the plots originates from a pulpmill located just south of Squamish, B.C.

Not necessarily all sulphur in throughfall is leached from foliage and other components of tree crowns. A great proportion of this S may originate from crown wash. Particles of dust containing sulphur may adhere to crowns and be washed off by rain. The same may be true for other elements, for example K and Ca, the origin of which may be dust from logging roads. However, the data obtained in this study do not provide an adequate basis for an estimate of the proportions of elements that originate from leaching and crown washing. Future studies must answer this question.

It is very difficult to make a more extensive comparison between the data obtained in this study and data of other researchers. Reliable data obtained in this study are for 13-week and 8-week periods of summers 1975 and 1976, respectively. The majority of publications give data for the whole year.

As far as comparison of different ecosystems goes, the data obtained indicate that the PM and M plots have the greatest quantity of K, Ca, and S in throughfall and are more efficient in absorption of N from rainwater than the other plots during the period for which data are available.

5.6 Comparison of the biogeochemical character of the four sites

The various biogeochemical parameters discussed above for the study plots and the plant associations they represent were ranked according to the ten-point biogeochemical classification scale of Rodin and Bazilevich (1967) (Table 5.9). The scale values are summarized in Table 5.10. It is important to remember that only the above-ground tree biomass and its nutrient dynamics were studied and that data presented in Table 5.10 do not adequately describe the entire biogeochemical characteristics of either the tree component or the entire plant community.

Rodin and Bazilevich (1967) selected five relationships as a basis for characterizing major patterns of ecosystem function. There were:

1. Predominant mineral element in litterfall
2. Standing crop biomass of the vegetation
3. Quantity of annual litter production
4. Litter decay rate
5. Ash content of litterfall

These five characteristics were used as the basis for their proposed classification of world vegetation, which involves 14 vegetation types, 12 type groups and 9 type classes.

The accumulation of above-ground tree biomass was very high on the investigated sites. PM plots, M plots (with exception of M3) and plot PX3 qualify for the highest class (over 500 t/ha) of the classification system--B_{10}. With the exception of PX1 which is B_8 (301-400 t/ha), the rest of the sample plots can be

Table 5.9. Ten-point scale of numerical indices of biogeochemical parameters of ecosystems. (Rodin and Bazilevich, 1967).

Scale number	Biomass (cntr/ha)* B	Net primary production (cntr/ha) P		Organic part: Litter-fall (cntr/ha) L	Organic part: True increment (cntr/ha) I	Forest Floor (cntr/ha) F	Decay rate D	
1	<25	<10	Very poorly productive	<10	<0.5	<1	>50	Stagnant
2	26-50	11-25		11-25	0.6-1	1-5	21-50	
3	51-125	26-40	Poorly productive	26-35	2-10	6-25	16-20	Very retarded
4	126-250	41-60		36-45	11-15	26-75	11-15	
5	251-500	61-80	Medium productive	46-75	16-25	76-125	6-10	
6	501-1500	81-100		76-100	26-35	126-250	1.6-5	Retarded
7	1501-3000	101-150		101-125	36-50	251-400	0.8-1.5	Intensive
8	3001-4000	151-300	Highly productive	125-225	51-65	401-600	0.3-0.7	
9	4001-5000	301-500		226-400	66-80	601-1000	0.1-0.2	Very intensive
10	5000 and above	>500	Very highly productive	>400	>80	>1000	<0.1	

* cntr = metric centner = 100 kg

Table 5.9. (con't). Ten-point scale of numerical indices of biogeochemical parameters of ecosystems. (Rodin and Bazilevich, 1967).

Scale number	Mineral elements: Accumulation in plant biomass (kg/ha) b	Uptake by n.p.p. (kg/ha) u	Returned with litter fall (kg/ha) r	Retained by true increment (kg/ha) x	Contained in forest floor (kg/ha) f	Mean ash content of litterfall (%) A	
1	<50	<50	<50	<1	<50	>1.5	Low
2	50-100	51-100	51-100	1.1-5	50-100	1.6-2.0	
3	101-150	101-150	101-150	6-25	101-200	2.1-2.5	
4	201-500	151-250	151-225	26-45	201-300	2.6-3.5	Medium
5	501-1000	251-350	226-300	46-80	301-750	3.6-5.0	
6	1001-2000	351-500	301-500	81-125	751-2000	5.1-6.5	Elevated
7	2001-3000	501-800	501-700	126-200	2001-5000	6.6-8.0	
8	3001-5000	801-1500	701-1300	201-300	5001-10000	8.1-9.5	High
9	5001-10000	1501-5000	1301-3600	301-600	10001-25000	9.6-12.0	
10	>10000	>5000	>3600	>600	>25000	>12.0	Very high

Table 5.10. Classification of the study ecosystem types according to the 10 point-scale classification system of Rodin and Bazilevich (1967)

Plot	Above-ground Tree Biomass B	t/ha	NPP P	t/ha	Litter-fall L	t/ha	True incr. I	t/ha	Forest Floor F	t/ha	Decay Rate D	years	Mineral elements: Accumulat. in plant biomass b	kg/ha	Uptake by NPP u	kg/ha	Returned with litterfall r	kg/ha	Retained by true increment x	kg/ha	Mean ash content of litterfall A	%	Four main indices of vegetata. type
PX1	B_8	389	P_2	2.13	L_2	1.74	I_3	0.64	F_{10}	153	D_1	88	b_6	1572	u_1	24	r_1	26	x_2	1.36	A_4	3.4	$B_8L_2D_1A_4$
PX2	B_9	458	P_2	2.39	L_2	1.78	I_3	0.90	F_{10}	120	D_1	67	b_6	1845	u_1	24	r_1	25	x_2	1.87	A_5	3.8	$B_9L_2D_1A_5$
PX3	B_{10}	510	P_2	2.20	L_2	1.48	I_3	0.82	F_{10}	114	D_1	77	b_7	2177	u_1	24	r_1	24	x_2	1.71	A_5	3.6	$B_{10}L_2D_1A_5$
PM1	B_{10}	731	P_3	3.08	L_3	3.02	I_3	0.42	F_{10}	161	D_1	53	b_7	2931	u_1	36	r_1	40	x_1	0.87	A_4	2.8	$B_{10}L_3D_1A_4$
PM2	B_{10}	511	P_3	3.05	L_3	2.87	I_3	0.61	F_9	88	D_2	31	b_7	2052	u_1	35	r_1	38	x_2	1.26	A_4	2.8	$B_{10}L_3D_2A_4$
PM3	B_{10}	550	P_3	2.73	L_3	2.57	I_3	0.49	F_{10}	133	D_1	52	b_7	2282	u_1	37	r_1	41	x_2	1.02	A_5	4.4	$B_{10}L_3D_1A_5$
PH1	B_9	419	P_2	1.77	L_2	1.54	I_3	0.31	F_{10}	190	D_1	123	b_6	1759	u_1	24	r_1	24	x_1	0.65	A_4	3.4	$B_9L_2D_1A_4$
PH2	B_9	482	P_2	2.09	L_2	1.77	I_3	0.45	F_{10}	150	D_1	85	b_6	1954	u_1	29	r_1	30	x_1	0.94	A_5	4.5	$B_9L_2D_1A_5$
PH3	B_9	435	P_2	1.86	L_2	1.71	I_3	0.29	F_{10}	145	D_1	85	b_6	1803	u_1	29	r_1	31	x_1	0.61	A_5	4.6	$B_9L_2D_1A_5$
M1	B_{10}	652	P_3	3.35	L_3	2.84	I_3	0.72	F_{10}	164	D_1	58	b_7	2655	u_1	39	r_1	40	x_2	1.52	A_5	4.9	$B_{10}L_3D_1A_5$
M2	B_{10}	556	P_3	2.45	L_2	2.24	I_3	0.48	F_{10}	164	D_1	73	b_7	2286	u_1	32	r_1	35	x_1	1.00	A_5	4.0	$B_{10}L_2D_1A_5$
M3	B_9	486	P_3	2.67	L_2	2.44	I_3	0.55	F_{10}	164	D_1	67	b_6	1989	u_1	34	r_1	38	x_2	1.13	A_5	3.6	$B_9L_2D_1A_5$

Table 5.11. Classification of some other Pacific Northwest forest sites.

Reference	Biomass (B) t/ha	NPP (P) t/ha	Organic part		Forest Floor biomass (F) t/ha	Decay rate (D) years
			Litterfall (L) t/ha	True increment (I) t/ha		
Turner and Singer 1975[1]	464.8 (B_9)	-	3.0 (L_3)	-	53.5 (F_8)	17.8 (D_3)
Grier and Logan[2]	718.0 (B_{10})	8.0 (P_5)	4.3 (L_4)	-3.7	51.2 (F_8) 241.0 (F_{10})*	11.9 (D_4) 56.0 (D_1)*

Table 5.11. (con't).

Mineral elements					
Accumulation in plant biomass (kg/ha) b	Uptake by n.p.p. (kg/ha) u	Returned with litter fall (kg/ha) r	Retained by true increment (kg/ha) x	Contained in floor (kg/ha) f	Mean ash content of litterfall (%) A
2805 (b_7)	68.5 (u_2)	71.8 (r_2)	-	1494 (f_6)	-
-	-	-	-	-	-

1 175 year old forest
2 450 year old forest
* includes fallen logs

described as B_9 (401-500 t/ha of biomass).

According to the amount of accumulated macronutrients in the above-ground tree standing biomass, the PM and M plots (with exception of M3) and PX3 plot can be described as b_7 (2001-3000 kg/ha), while all other plots qualified for b_6 (1001-2000 kg/ha).

Net primary production of the study plots was not excessively large, probably because of their advanced age. The PM and M plots can be described as P_3 and the PX and PH plots as P_2. The uptake of mineral elements in net primary production belongs to the lowest category of the classification system on all the study plots - u_1.

The biomass of litterfall on the PM plots and plot M1 can be classified as L_3 and as L_2 on all other plots. The amount of macronutrients returned with this litterfall was low on all plots, which qualified as r_1 according to the ten-point scale. Mean ash content of leaf-litterfall was very variable on the sample plots and can be classified as A_{4-5} according to the ten-point classification system.

The true increment of the above-ground tree biomass (increment of tree-bole wood in the case of this study) on all plots was classified as I_3 according to the ten-point classification scale. The quantity of macronutrients retained by this increment was low: the first or second class of the ten-point classification system, x_{1-2}.

The biomass of forest floor on all plots was very large and all plots except PM2 qualify for the highest of the ten classes, F_{10}. PM2 belongs to F_9. The decay rate can be described as stagnant and on all plots but PM2 it is classified as D_1 on the ten-point scale; PM2 is classified as D_2. However, some other plots may be transferred to D_2 or higher class when understory above-ground litter and root litter is considered.

The classes as proposed by Rodin and Bazilevich (1967) in the ten-point scale classification system of world vegetation are too broad to reflect differences among plant associations on the elevation transect located in one biogeoclimatic zone (sensu Krajina 1965). Some differences between the 3 plant associations are reflected in classification of biomass B_{9-10}, net primary productivity P_{2-3}, litterfall biomass L_{2-3}, immobilization of macronutrients in plant biomass b_{6-7} and mean ash content of leaf litterfall A_{4-5}. However, this variation is too small to support the suggestion that this classification can be used for local purposes in its present stage of development.

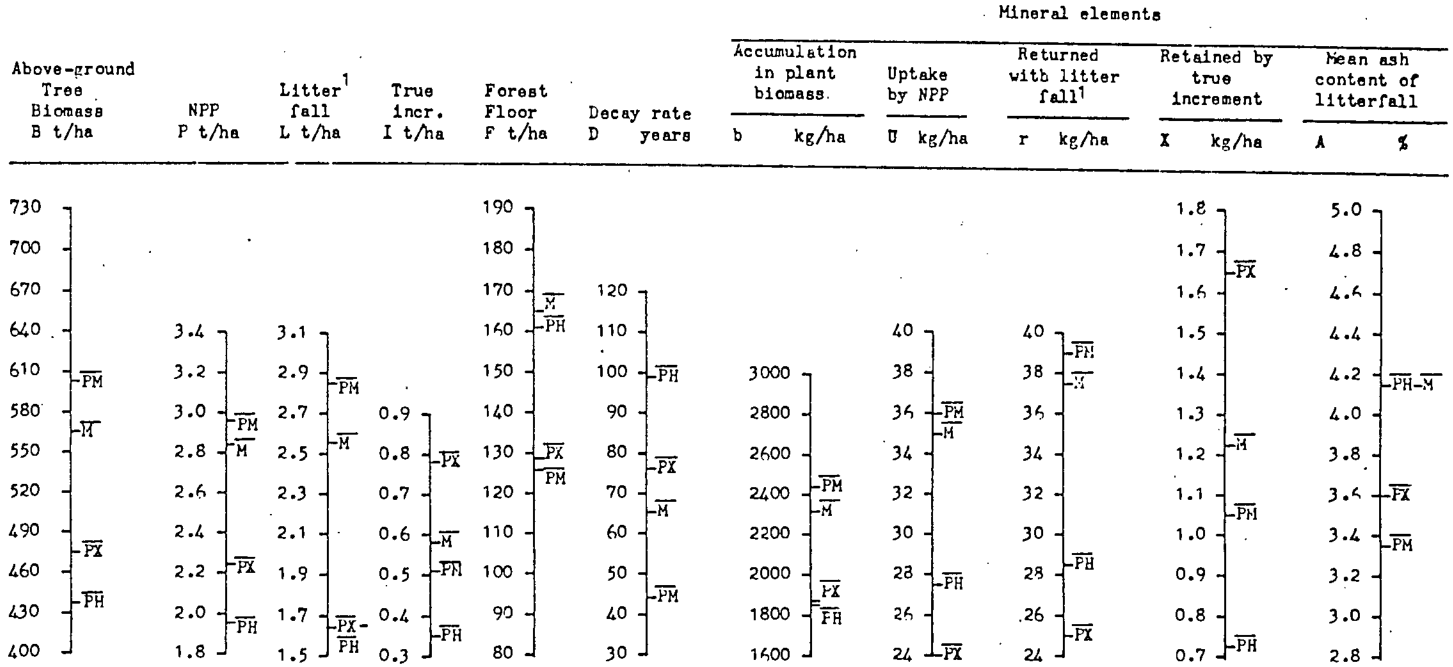
The plant associations of the Subalpine Mountain Hemlock Zone (Krajina 1965) can be described according to Rodin and Bazilevich (1967) as follows:

PM and M sites as calcic-nitric (nitrogen predominates in litterfall).

PX and PH sites as nitric-calcic (calcium predominates in litterfall).

All four investigated sites have: high accumulation of biomass, comparable to biomass of tropical rain forest as described in Rodin and Bazilevich's (1967) system; poor production of litterfall, comparable to the production of tundra and taiga (poor spruce forest) in Rodin and Bazilevich's (1967) system;

Figure 5.24. Relationship among xeric, mesic and hygric sites: a local classification scale.



[1] Total above ground litterfall, includes epiphytes

very slow decomposition of litter (stagnant decay rate), comparable to the decay rate of tundra in Rodin and Bazilevich's (1967) system; medium amount of ash in litterfall, comparable to ash content of birch forest in taiga zone in Rodin and Bazilevich's (1967) system.

These forest sites do not compare well with any single vegetation type proposed by Rodin and Bazilevich (1967). It may therefore be appropriate to propose the addition of another vegetation type to the Rodin and Bazilevich (1967) classification: the subalpine coniferous forest with almost equal amount of N and Ca in the litterfall, medium ash (A_{4-5}), high accumulation of biomass (B_{8-10}), poor litter production (L_{2-3}), and stagnant decay rate (D_1). Results from other forest sites from the Pacific Northwest are in Table 5.11. Unfortunately the amount of information available on this type of forest is very limited.

The tree sites along the elevation transect show statistically different tree dbh, tree height, litter production and amount of macronutrients recycled in litterfall. There is also considerable difference in periodic annual wood increment and in mean annual wood increment but these differences were not tested statistically. The fourth site, which in plant species composition is similar to the middle site on the elevation transect, is also most similar to the latter in a majority of the ecosystem parameters examined (Figure 5.24). Figure 5.24 also indicates that PX and PH sites bear certain similarities to each other.

The subalpine forest sites that were investigated can be separated according to their patterns of ecosystem function. If the classes used by Rodin and Bazilevich (1967) are narrowed, a hypothetical classification based on the data obtained in this study can be proposed to distinguish mesic ecosystems from xeric and hygric.

The mesic ecosystems in this study are calcic-nitric (nitrogen predominates in litterfall), with above-ground tree standing biomass 490-730 t/ha, above-ground tree litter production 2.2 - 3.1 t/(ha•a), N, P, K, Ca, Mg accumulation in above-ground tree biomass 2 000 - 2 700 kg/ha, and N, P, K, Ca, Mg returned with above-ground tree litterfall 32 - 41 kg/(ha•a). The litter decay rate, based on the above-ground tree litterfall is 30 - 70 years.

The xeric and hygric sites in this study are nitric-calcic (calcium predominates in litterfall), with above-ground tree standing biomass 390 - 500 t/ha, above-ground tree litter production 1.5 - 1.8 t/(ha•a), N, P, K, Ca, Mg accumulation in above-ground tree biomass 1 600 - 2 200 kg/ha, and N, P, K, Ca, Mg returned with above-ground tree litterfall 24 - 29 kg/(ha•a). The litter decay rate (based on the above-ground tree litterfall) is 65 - 90 years on xeric sites and 85 - 120 years on hygric sites.

The ash content of tree litterfall is too broad (2.8 - 4.4% on mesic sites, 3.4 - 4.6% on hygric sites) to be effectively used for distinguishing sites.

The true increment (PAI) and amount of N, P, K, Ca, and Mg immobilized in it clearly separates the xeric and hygric sites. The question whether some similarity between xeric and hygric sites is real or merely the result of the parameters that were measured deserves the attention of future research studies. A greater amount of data is needed to run statistical analyses (e.g. principal component analysis) to answer this question. Figure 5.24 is not advanced as a proposed new classification of the subalpine forest ecosystems in British Columbia. Insufficient data are available on the regional variation in biogeochemical parameters within this ecological zone to permit such a proposal at this time. However, Figure 5.24 could form the basis for such a classification in the future when the type of study reported in this thesis had been replicated elsewhere in the Subalpine Mountain Hemlock Zone.

5.7. Discussion

Many subalpine forest ecosystems have a large amount of standing timber, often of high quality. The forest industry is highly interested in utilizing this resource, yet very little is known about the function of these ecosystems. It was a goal of this study to provide information on some important parameters of ecosystem function, particularly on above-ground tree litterfall, the amount of major macronutrients (N, P, K, Ca, Mg) recycled in this litterfall and amount of major macronutrients recycled in throughfall.

Two hypotheses were tested:

1. differences in plant species composition among three sites located on a topographic sequence along a short elevation transect are accompanied by sufficiently large differences in patterns of ecosystem function to distinguish these sites on a functional basis.

2. the same plant association occurring on two different parent materials cannot be distinguished by different patterns of ecosystem function.

The results of this study show that the difference in species composition among sites located on a short elevation transect (the same climatic climax tree species are present, in different proportion and with different understory species composition) is accompanied by sufficiently large changes in patterns of ecosystem function to distinguish these sites. The differences were varified by statistical analyses.

The two mesic sites belong to the same plant association but are located on two kinds of soil parent material (quartz diorite and dacite). They were very similar to each other in a majority of investigated parameters. However, statistical tests revealed statistically significant differences between these two sites in dbh, tree height, weight of annual above-ground litterfall and amount of some macronutrients (K, Mg, and Ca during part of the sampling period) recycled in above-ground litterfall. This difference was much smaller than the difference between mesic and xeric and mesic and hygric sites. It can therefore be concluded that there were some statistically detectable differences in biochemical cycles between one plant association growing on two different types of parent material, but that these differences were of lesser magnitude than differences between two plant associations. The possibility that the differences between the two mesic sites reflect factors other than or in addition to differences in soil parent material cannot be discarded.

The xeric and hygric sites exhibit similar patterns of function (e.g. standing tree biomass, amount of above-ground tree litterfall), but they differ in parameters such as true increment (PAI) and the amount of nutrients immobilized in it. Future research should answer the question of whether this similarity is significant or merely coincidental.

The results indicate that a plant association (Klinka, 1976) is not a completely homogeneous unit in terms of ecosystem function. Soil properties and parent material have to be considered in distinguishing functionally homogeneous units, ecosystem type or biogeocoenose (Klinka, 1976).

The question was posed earlier as to whether the biogeochemical classification of world ecosystems proposed by Rodin and Bazilevich (1967) could be applied to the differentiation of the study sites. The classification was found to be too broad to discriminate among the different sites. However, as shown above it is possible to produce a classification scale (based on the same principles as the scale of Rodin and Bazilevich, 1967, but with narrower classes) to classify the subalpine sites according to their pattern of function. Such a classification will become increasingly useful as the gap between world demand for and world supply of forest products continues to widen and as intensive forest management is extended into subalpine forest areas.

CHAPTER 6

THE CHARACTER OF NUTRIENT CYCLING IN COASTAL SUBALPINE FOREST AS REPRESENTED IN THE STUDY AREA

An attempt is made in this chapter to explain the unique combination of biogeochemical characteristics observed on the study sites, including high tree standing biomass, low ltterfall biomass, low uptake of nutrients by NPP and low reurn of nutrients with litterfall. The explanation advanced is consistent with the results obtained in this study but is not derived entirely from the data reported herein. General field observations and the results and observations of other investigators who have worked in the study area are also incorporated in the explanation. It should be noted that the suggested explanation is speculative in nature. It is presented more as a source of testable hypothesis for future research than as a well documented axiom.

The climate in the study area is mild and wet as a result of the proximity of the Pacific Ocean to the west of the study area and the general westerly flow of weather systems. Before the onset of winter the soil becomes thoroughly moistened by the heavy autumn rains. This recharging of soil moisture is augmented by the characteristic fluctuating autumnal temperatures which result in the melting of the first few snowfalls. The ground is subsequently covered by snow usually as early as mid-October. This is prior to the onset of uninterrupted freezing temperatures which do not begin before mid-December to January, by which time the soil is covered by about one meter of snow. The accumulating snow-pack insulates the soil sufficiently to prevent freezing throughout the winter. Snow-packs of up to 5m are not uncommon, and the snowpack generally keeps increasing in depth until late March. Snowmelt starts in April, but is gradual so that snow cover under the canopy of the forest usually lasts until mid-July.

As a result of these climatic conditions tree roots experience unfrozen and generally moist soil throughout the year. Except for a brief period in July or August on areas with rapidly drained soils the trees are not thought to experience sufficient moisture stress to significantly affect their growth. Thus, the roots are in a reasonably favorable environment as far as water is concerned for much of the year.

The young soil which originates from glacial parent material usually contains a sufficient amount of mineral nutrients for tree growth. However, root metabolism and the ability of roots to absorb nutrients may be significantly limited by low soil temperature which under snow cover is just above freezing point. Because the soil is unfrozen, slow but significant decomposition activity takes place throughout much of the 8 - 9 snowy months. Slow decomposition results in slow release of nitrogen. In the study area nitrogen is probably the most limiting macronutrient element.

Thick, wet, acid, and year round unfrozen forest floor is an excellent growth medium for fungi. There is a heavy mat of fungal hyphae in the LFH layer with numerous attachments to fine roots and it appears that these fungi are active beneath the snow in winter. It is thought that these mycorrhizal fungi play a vital role in tree nutrition, particularly in nitrogen uptake.

Daytime air temperatures are above freezing point for approximately six months of the year: from mid-April until mid-October. Photosynthesis will be active throughout this period because of the lack of moisture stress and it will also occur during the frequent warm spells that occur regularly throughout the winter. During the first half of this time period (until mid-July), the trees are growing in soil which is very wet, but cold (around 0°C), because the water is derived from melting snow. It is thought that nutrient availability is limited during this period because of slow decomposition in the cold, excessively wet forest floor.

How have the trees in the study area adapted to these conditions? Foliage is retained for an average of 15-20 years, and some green, apparently functional needles of 31 years of age have been found (Kimmins, personal communication). Only a small portion of foliage is shed and replaced annually. By dividing foliage into a large number of age classes, only a small biomass is changed each year and only a small biomass of new foliage must be created. Internal cycling of nutrients such as nitrogen and phosphorus from old to young foliage prior to abcision further reduces the loss of nutrients from trees via litterfall. The large biomass that is characteristic of these forests retains a large pool of nutrients which are then available for internal recycling within foliage and probably also within stem, branches and root system.

The combination of long needle retention and efficient internal cycling enables the trees in the study area to operate with low uptake of nutrients from the soil. Thus, a large tree biomass retaining a considerable amount of nutrients, long foliage retention, internal nutrient redistribution within foliage and probably also within the bark and wood, low loss of nutrients in litterfall and the apparent ability of tree crowns to extract nitrogen from rain-water permit the tree to achieve its NPP with a small uptake of nutrients from the soil. This uptake occurs in what might be considered a soil environment that is not conducive to nutrient uptake: it occurs because of the large amount of mycorrhizal fungi that are apparently able to decompose organic matter in the forest floor albeit slowly, throughout most of the year.

The central part of the elevation transect, the mesic plots, have the most favorable growth conditions. The snow duration is slightly shorter there than on the PX plots, and approximately the same as on the PH plots. The soil is moderately well drained, but the thick forest floor and relatively flat terrain retains enough moisture that trees do not suffer from moisture stress during the short summer dry period. Tree biomass and litterfall are higher on this site than on the xeric or hygric sites. Since soil moisture and soil aeration are balanced, trees are capable of utilizing solar energy more efficiently than on PX or PH plots and thus have a faster nutrient cycle.

At the top of the elevation transect, the PX plots are located on small ridges. The snow duration in this area is so long that trees are able to establish themselves only on elevated terrain which becomes free of snow earlier than the lower depressions. The soil is rapidly drained and trees may suffer some moisture stress during short dry summer periods. As a result, tree biomass on these sites is smaller than on either of the other two sites and this is accompanied by a small amount of litterfall and slow tree growth. The deep and prolonged snow cover has an adverse effect on young trees that are not yet as tall as the maximum depth of snowpack. It is not unusual in this area to find a tree 100 to 150 years old and only 2-3m high. Once the trees get their crowns above the snowpack, their growth rate increases considerably. This may be a partial explanation of the almost equal mean annual increment and periodic annual increment in trees as old as 350 years.

At the bottom of the elevation transect, the PH plots are located at the foot of a steep slope. Seepage water from rain and melting snow keeps the forest floor and mineral soil saturated throughout most of the year. The trees are growing mainly on minor topographic emniences where conditions are more favorable for root growth. The tree density is generally low and individual tree size is very variable. Tree size is larger than on the PM and PX plots. Because tree density is smaller, total tree biomass per hectare is smaller than on the mesic plots; it is very similar to the biomass of the xeric sites where trees are small but present in large numbers. Litterfall biomass follows the same trend. Decay of the forest floor on the PH plots is very slow because of the excessive wetness and as a result the forest floor is deeper here than on the other sites.

The similarity between the PX and PH plots in tree biomass, biomass of litterfall and litterfall macronutrient content does not indicate an ecological similarity between these sites. It merely reflects the reciprocal relationship between tree size and number of trees per unit of area.

CHAPTER 7

THE USEFULNESS OF NUTRIENT CYCLING STUDIES IN FOREST MANAGEMENT

There are several possible applications of the knowledge of nutrient cycling in forest management. Such knowledge can be used in the classification of forest ecosystems, in the evaluation of forest productivity and in the prediction of the response of ecosystems to forest management. Recently a number of publications have appeared which deal with the relationship between ecosystem stability and nutrient cycling characteristics. Knowledge of forest biogeochemistry may prove to be useful in evaluating ecosystem stability. This chapter presents a very brief review of the literature on these topics and an evaluation of the impact that logging may have on the investigated sites and their potential ability to recover.

"The chemical elements of which plants are composed are involved in intermeshing and mutually dependent cycles of uptake and return to the environment. Knowledge of these cycles is important not only to the scientific understanding of the factors which determine the character of vegetation but also to the effective use of forest, pasture and wilderness which is becoming an increasing practical necessity under present conditions" (Rodin and Bazilevich,1967).

Sukachev (1944) outlined the importance of biological, biochemical and geochemical cycles of elements in genetic classifications of forest ecosystems. Recently Rodin and Bazilevich (1967) proposed a classification of biological cycles of elements. They evaluated the importance of knowledge of nutrient cycles and their classification by the following statement: "Once the types of biological cycles have been classified in detail for all steps in the hierarchical ladder, we shall have the most important of criteria for understanding the biogeocoensis as a cybernetic system and we shall be able to see how a biogeocoenosis might be manipulated so as to yield maximum productivity of organic matter."

"A recurrent theme in ecological literature is that ecosystem stability is related to nutrient-cycling characteristics. Odum (1969) suggested that the closing of nutrient cycles through ecosystem development contributes to increased stability. Pomeroy (1970) related the stability of several ecosystem types to elemental standing crops and turnover times, biomass and productivity. Jordan _et al_. (1972) examined ecosystem stability in relation to models of forest nutrient cycles." (Webster _et al_. 1975). They concluded that in forest ecosystems where mineral recycling rates are high relative to input and output rates, the systems have a low relative stability. If the rate of element input into a forest system is higher than the recycling rate, the stability of that system will be high.

Webster _et al_. (1975) investigated relations between observable characteristics of nutrient cycles and the system-level concept of stability. Their results indicate that resistance, the ability of an ecosystem to resist displacement, is related to large storage, long turnover times and large amounts of recycling. Resilience, the ability of an ecosystem to return (at a certain rate) to a reference state once displaced, is related to rapid turnover and recycling rates.

The four sites investigated in the Subalpine Mountain Hemlock Zone exhibit large biomass storage and slow turnover. This indicates that they most probably have high resistance and low resilience. In practice, this means that these ecosystems can successfully resist the perturbative forces of their environment. The advanced age of these stands and lack of charcoal in the forest floor supports this hypothesis. When tree biomass is removed by logging and the forest floor is partially or completely destroyed by the combined action of yarding, slashburning and erosion, the large biomass and nutrient storage is to a greater or lesser extent lost. The high resistance of the ecosystem is destroyed. In practice this is often accompanied by excessive loss of nutrients by leaching, soil erosion and on some steep slopes by soil mass wasting. The slow turnover and recycling rates indicate low resilience. The very slow regeneration observed on a clearcut adjacent to M plots is consistent with this hypothesis; these sites would need a longer time to return to their previous stage, a "climax" forest, than the low elevation forest.

To provide more specific answers on the impact of logging on the nutrient cycling of the investigated sites, data on biochemcial, biogeochemical and geochemical cycles (Switzer and Nelson 1972, Duvigneaud and Denaeyer-De Smet 1975) of disturbed, maturing and mature ecosystems are needed. This study was concerned predominantly with certain aspects of the biogeochemical cycle of overmature ecosystems and does not provide sufficient data with which to predict the consequences of forest management. A simulation model of nutrient cycling calibrated and validated with a far larger body of information than is presently available would be necessary to provide specific answers on the impact of management practices. The topic of ecosystem analyses is beyond the scope of this study, but it is hoped that the data provided here will be incorporated in such future analyses of subalpine forest ecosystems.

The brief literature review presented above indicates three major areas where nutrient cycling studies may contribute significantly to forest management:

1. The development of a functional forest ecosystem classification which together with biogeoclimatic ecosystem classification would enable forest managers to make improved site specific treatment decisions;

2. The provision of basic data for ecosystem analyses directed toward the increase of forest productivity by ensuring optimal supply of essential plant nutrients required for tree growth;

3. The provision of information for analysis of forest ecosystem stability in relation to nutrient cycling characteristics. Better understanding of stability would enable forest managers to predict more accurately the behaviour of the system after major disturbance such as logging or fire.

I would like to conclude this chapter with the statement of Duvigneaud and Denaeyer-De Smet (1975): "Mineral cycling appears to be one of the best and easiest ways to characterize the general metabolism and functioning of ecosystems, but many years are still required (several IBP or SCOPE programs) to obtain sufficient data to make valuable models and predictions."

CHAPTER 8

SUMMARY OF RESULTS

1. The range of litterfall biomass on 12 study plots was found to be from 1.48 to 3.02 t/(ha•a). The production of litter on mesic sites was considerably higher than on xeric or hygric sites.

2. Leaf litterfall was from 57 to 72% of the total litterfall; epiphytic lichen litterfall was from 5 to 16% of the total litterfall.

3. The biomass of epiphytic lichen litterfall was from 71 to 426 kg/(ha•a) containing a quantity of nitrogen of between 0.64 and 2.87 kg/(ha•a). This amount represents 7 to 19% of nitrogen reaching the forest floor in the form of litterfall. The amount of nitrogen returned to the forest floor in epiphytic lichen litterfall is equivalent to the amount of nitrogen returned in twigs and branches litterfall; it is the second largest amount of N after leaf litterfall.

4. The concentration of N, P and K in epiphytic lichen litterfall was higher than in foliage litterfall throughout the year.

5. The quantity of macronutrients returned to the forest floor in litterfall was 24 to 41 kg/(ha•a). The largest quantities of nutrients were returned on mesic sites, with smaller quantities on the xeric and hygric sites.

6. Concentrations of N and P were highest in winter litterfall; concentrations of K and Mg were highest in summer litterfall. Concentration of Ca was fairly similar in summer and winter litterfall.

7. Throughfall and atmospheric precipitation were sampled only during summer. The winter collections were unsuccessful, therefore no winter data were collected.

8. The quantity of nitrogen was higher in atmospheric precipitation than in throughfall. This indicates a removal of nitrogen from rain water by some component of the tree canopy. On some sample plots over 1 kg/ha of N was removed from rain water during the 13 week summer sampling period. Mesic sites seem to be more efficient in absorbing nitrogen from rain water than xeric and hygric sites.

9. The results indicate that on mesic sites larger quantities of K, Ca and S are cycled in throughfall than on xeric or hygric sites.

10. Potassium was found to be the most readily leachable element. The second most readily leachable element was calcium.

11. The mean depth of the forest floor on the study plots ranged from 5.5 to 12.7 cm. The weight of forest floor organic matter ranged from 88 to 190 t/ha. The great amount of accumulated organic matter indicates very slow decomposition and slow release of nutrients.

12. The amount of above-ground tree standing biomass on the sample plots ranged from 389 to 731 t/ha. The values were larger on mesic sites than on xeric or hygric sites, even though tree ages were comparable.

13. Foliage, twigs and branches accounted for relatively small proportions of biomass, yet they accounted for considerable proportions of macronutrients, particularly nitrogen.

14. The range of mean annual net increment of above-ground tree stem wood was estimated to be from 1.46 $m^3/(ha \cdot a)$ to 3.74 $m^3/(ha \cdot a)$. The range of periodic annual net increment (based on last 20 years) of above-ground tree stem wood was estimated to be from 0.8 $m^3/(ha \cdot a)$ to 2.2 $m^3/(ha \cdot a)$.

15. Periodic annual increment was smaller than mean annual increment on all sites but xeric. Trees on the xeric site, at the age of 350 years, still have a periodic annual increment equal to or larger than the mean annual increment. This indicates that the largest timber production on xeric sites is attained at a higher age than on mesic and hygric sites.

16. The annual net primary production was estimated to be from 1.77 to 3.35 t/ha. This is rather low in comparison to the production of other subalpine forests. The advanced age of the study forests is most probably the main reason for the low production.

CHAPTER 9

CONCLUSIONS

1. The difference in species composition among three plant associations located on a short elevation transect was accompanied by sufficiently large changes in productivity and nutrient cycling to separate these sites. This implies that by identifying forest sites according to their phytosociological characteristics, one can identify sites with different patterns of nutrient uptake and cycling.

2. One plant association growing on two different parent materials showed statistically different patterns of biomass production and nutrient cycling. This suggests that the plant association is not a functionally homogeneous unit. Soil properties and parent material have to be included when distinguishing between functionally homogeneous units - ecosystem types or biogeocoenoses.

3. The classificaiton scale of world ecosystems proposed by Rodin and Bazilevich (1967) was found to be insufficiently sensitive to separate plant associations of one biogeoclimatic zone. It would be possible to separate these plant associations if the scale were redesigned to have narrower classes.

4. The investigated forest sites do not compare well with any single vegetation type proposed by Rodin and Bazilevich (1967). It may therefore be appropriate to propose the addition of another vegetation type to the Rodin and Bazilevich (1967) classification: the subalpine coniferous forest with almost equal amounts of N and Ca in the litterfall, medium ash content,

high accumulation of biomass, poor litter production, and stagnant decay rate.

5. Trees on xeric sites appear to be still in the period of maximum growth at the age of about 350 years, while mesic and hygric sites are well past their period of maximum growth. Xeric sites seem to mature more slowly than other plots; their growth curve is less steep and their net growth more prolonged. This is an interesting finding that deserves the attention of fuuture research.

6. The results of this study indicate the existence of correlation between above-ground tree standing biomass and litterfall biomass. This is contradictory to results of some other publications, such as Rodin and Bazilevich (1967).

7. Epiphytic lichens are an important component of litterfall since they contain a large proportion of the macronutrients reaching the forest floor in the form of litter. The role of epiphytic lichens in tree nutrition should be further studied.

8. The tree canopy was found to have an ability to remove nitrogen from precipitation. It is not known whether this phenomenon occurs only during summer or during wet winter months as well. The mechanism of nitrogen absorption is not understood either. Since N is considered to be the most limiting nutrient to tree growth in the investigated area, the phenomenon of N absorption from rain water by the tree canopy should be an object of future research studies.

9. The high biomass storage and slow nutrient turnover of the investigated forest ecosystems is considered in the light of

some recent publications to be an indicator of high resistance and low resilience. This theory is in agreement with the great age of the trees, the lack of charcoal and slow regeneration of logged stands in the vicinity of the investigated area.

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APPENDIX 1

Plant Species List

Nomenclature of the vascular plants follows Hitchcock *et al.* (1969), Schofield (1969 a and b) for mosses and Otto and Ahti (1967) for lichens.

TREES

Abies amabilis (Dougl.) Forbes   Pacific silver fir

Chamaecyparis nootkatensis (D. Don) Spach   yellow cedar

Thuja plicata D. Don   red cedar

Tsuga heterophylla (Raf.) Sarg.   western hemlock

Tsuga mertensiana (Bong.) Carr.   mountain hemlock

SHRUBS

Oplopanax horridum (J.E. Smith) Miq.   devils club

Rhododendron albiflorum Hook.   white rhododendron

Ribes bracteosum Dougl.   stink currant

Sambucus pubens Michx.   red-berry Elder

Sorbus sitchensis Roemer   sitka mountain-ash

Vaccinium alaskaense Howell   Alaska blueberry

V. *deliciosum* Piper   Cascade bilberry

V. *membranaceum* Dougl. ex Hook   mountain bilberry

V. *ovalifolium* Smith   oval-leaved blueberry

V. *parvifolium* Smith   red huckleberry

HERBS, SMALL SHRUBS, AND FERNS

Athyrium filix-femina (L.) Roth.   lady-fern

Blechnum spicant (L.) With.   deer-fern

Caltha leptosepala DC.   white marsh marigold

Cassiope mertensiana (Bong.) G. Don.   white heather

Clintonia uniflora (Schult.) Kunth.   queen's cup

Cinna latifolia (Trevir.) Griseb.

Dryopteris austriaca (Jacq.) Woynar ex Schinz & Thell. spiny wood-fern

Gymnocarpium dryopteris (L.) Newm. oak fern

Listera cordata (L.) R. Br.

Luzula parviflora (Ehrh.) Desv.

Osmorhiza chilensis H. & A.

Phyllodoce empetriformis (Sm.) D. Don red heather

Pyrola secunda L. wintergreen

Rubus pedatus J.E. Smith trailing rubus

R. spectabilis Pursh salmonberry

Streptopus amplexifolius (L.) DC. twisted stalk

S. roseus Michx.

S. streptopoides (Ledeb.) F. & R.

Tiarella unifoliata Hook. foam flower

Valeriana sitchensis Bong. mountain valerian

Veratrum viride Ait. indian hellebore

Viola glabella Nutt. yellow violet

BRYOPHYTES

Bazzania denudata (Torr) Trev.

Brachythecium spp.

Dicranum fuscescens Turn.

D. scoparium Hedw.

Hypnum spp.

Lepidozia reptans (L.) Dumort.

Lophozia spp.

Mnium spp.

Plagiothecium denticulatum (Hedw.) B.S.G.

P. undulatum (Hedw.) B.S.G.

Pleurozium schreberi (Brid.) Mitt.

Pohlia nutans (Hedw.) Lindb.

Ptilidium californicum (Aust) Underv. & Cook

Rhizomnium magnifolium (Horik.) Kop.

R. nudum (Britt. & Williams) Koponen

Rhytidiadelphus loreus (Hedw.) Warnst.

R. squarrosus (Hedw.) Warnst.

Rhytidiopsis robusta (Hook.) Broth.

LICHENS

Alectoria spp.

Cladonia bellidiflora (Ach.) Schaer.

Hypogymnia spp.

Usnea spp.

APPENDIX 2

Rock Specimens From Sample Plots

Examination of rocks from Paul Ridge near Squamish

MM-1: Weathered foliated quartz diorite; one specimen of finer grained dark diorite.

MM-2: Weathered foliaged quartz diorite.

MM-3: Weathered quartz diorite and hornblende diorite.

PH-1: 7 specimens of hard green micaceous foliated quartz diorite
1 hard feldspar porphyry possibly of Garibaldi volcanic rock origin
1 green schist; 5 Garibaldi volcanics (Dacite).

PH-2: 4 hard foliated quartz diorite; one greenschist, remainder Garibaldi volcanic rocks (Dacite).

PH-3: 1 quartz diorite, 3 dense porphyritic rocks which may be Garibaldi volcanic rocks.

PM-1: 4 hard quartz diorite foliated and micaceous; one greenschist; remainder pink and blue grey Garibaldi dacite, some with weathered rinds indicating they are from older flows.

PM-2: 1 green schist; one quartz diorite, remainder Garibaldi volcanic rocks (Dacite).

PM-3: Mostly Garibaldi volcanic rocks pink and grey dacites; 2 feldspar porphyrys one greenish and one black.

PX-1: 13 hard quartz diorite; 1 porphyry, remainder pink and blue grey dacite.

PX-2: 2 hard quartz diorite, 2 green porphyry, remainder Garibaldi volcanic rocks (Dacite).

PX-3: 2 Hornblende quartz diorite, remainder Garibaldi volcanic rocks (Dacite).

DISCUSSION: The rock appear to belong to at least four groups: Most are Garibaldi volcanic flow rocks which are mostly dacite. They are pink and blue grey in colour and usually quite angular and relatively easy to break.

Next in abundance are rounded coarse grained hornblende-quartz diorites. These are foliated and partly micaceous. They are hard and often difficult to break. Some are fine grained and much darker in colour than the coarse grained varieties. They are probably older Mesozoic in age.

Next are a few dense and heavy porphyritic rocks which may be parts of dense Garibaldi flows. They are fresh but very hard.

Lastly are a few dark green schistose rocks which may represent metamorphosed older volcanic rocks into which the older diorites were intruded.

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APPENDIX 3

Diameter, Height and Timber Volume of Trees on Sample Plots

Appendix 3. Diameter, height and timber volume of trees on 12 sample plots

Plot	SP	D (cm)	H (m)	VOL (m^3)
PX1	H 85/50	37.8 (1.5) 13.7 - 74.7	15.5 (0.6) 3 - 24.5	0.851 (0.078) 0.026 - 3.325
	PF 75/45	16.9 (1.0) 5.6 - 45.2	7.7 (0.5) 2.0 - 20.5	0.138 (0.022) 0.003 - 0.857
	YC 9/5	29.2 (3.4) 7.6 - 41.9	13.5 (1.4) 4.0 - 17.5	0.469 (0.096) 0.010 - 0.928
	Plot 169	28.1 (1.2) 5.6 - 74.7 25.7 30.4	11.9 (0.5) 2.0 - 24.5 11.0 12.9	0.314 (0.049) 0.003 - 3.325 0.418 0.610
PX2	H 74/64	30.7 (1.5) 8.9 - 70.9	14.1 (0.6) 3.0 - 23.0	0.562 (0.063) 0.008 - 2.854
	PF 38/33	22.6 (1.6) 7.6 - 45.5	11.1 (0.9) 2.0 - 23.5	0.315 (0.056) 0.004 - 1.595
	YC 4/3	27.0 (4.3) 14.2 - 32.5	15.4 (3.0) 7.0 - 21.0	0.458 (0.144) 0.054 - 0.735
	Plot 116	27.9 (1.1) 7.6 - 70.9 25.7 30.2	13.2 (0.5) 2.0 - 23.5 12.1 14.2	0.478 (0.046) 0.004 - 2.854 0.387 0.568
PX3	H 19/36	60.5 (5.3) 19.8 - 99.1	20.5 (1.4) 7.5 - 31.0	2.528 (0.464) 0.114 - 7.814
	PF 33/64	33.7 (3.6) 7.9 - 82.0	15.0 (1.4) 3.0 - 27.0	1.047 (0.214) 0.009 - 4.462
	Plot 52	43.5 (3.5) 7.9 - 99.1 36.6 50.5	17.0 (1.1) 3.0 - 31.0 14.8 19.2	1.588 (0.237) 0.009 - 7.814 1.113 2.063
PX	Plots 337	30.4 (0.9) 5.6 - 99.1 28.6 32.3	13.1 (0.4) 2.0 - 31.0 12.4 13.9	0.667 (0.051) 0.003 - 7.814 0.566 0.768
M1	H 44/69	45.2 (2.4) 17.8 - 70.9	24.1 (1.2) 6.0 - 34.0	1.845 (0.198) 0.063 - 4.612
	PF 20/31	44.3 (3.5) 15.0 - 76.5	24.5 (1.6) 6.5 - 35.0	1.983 (0.329) 0.053 - 5.470
	Plot 64	44.9 (1.9) 15.0 - 76.5 41.0 48.8	24.3 (1.0) 6.0 - 35.0 22.3 26.2	1.888 (0.169) 0.053 - 5.470 1.550 2.227
PM2	H 29/60	45.0 (2.7) 18.3 - 75.9	24.9 (1.3) 10.5 - 32.5	1.811 (0.231) 0.133 - 5.041
	PF 19/40	47.4 (3.4) 18.0 - 69.6	26.6 (1.6) 10.0 - 34.5	2.375 (0.350) 0.119 - 4.957
	Plot 48	45.9 (2.1) 18.0 - 75.9 41.7 50.2	25.6 (1.0) 10.0 - 34.5 23.5 27.6	2.034 (0.199) 0.119 - 5.041 1.634 4.812
PM3	H 4/12	67.4 (16.9) 17.0 - 88.4	29.5 (8.1) 6.0 - 43.0	5.472 (1.948) 0.054 - 9.201
	PF 29/88	54.3 (3.6) 15.2 - 80.8	29.6 (2.0) 7.5 - 42.5	3.654 (0.453) 0.064 - 7.878
	Plot 33	55.9 (3.7) 15.2 - 88.4 48.3 63.5	29.6 (2.0) 6.0 - 43.0 25.6 33.6	3.875 (0.460) 0.054 - 9.201 2.937 4.812
PM	Plots 145	47.8 (1.4) 15.0 - 88.4 44.9 50.6	25.9 (0.7) 6.0 - 43.0 24.5 27.3	2.389 (0.158) 0.053 - 9.201 2.076 2.702
PH1	H 13/29	43.1 (6.7) 13.2 - 90.9	22.2 (3.1) 5.5 - 40.0	2.158 (0.792) 0.031 - 8.675
	PF 32/71	47.0 (3.7) 14.5 - 96.0	28.1 (2.3) 5.5 - 52.0	3.036 (0.519) 0.042 -10.980
	Plot 45	45.9 (3.3) 13.2 - 96.0 39.3 52.4	26.4 (1.9) 5.5 - 52.0 22.6 30.2	2.782 (0.433) 0.031 -10.980 1.909 3.656
PH2	H 6/24	78.2 (11.4) 39.4 -110.0	35.7 (5.7) 17.5 - 49.0	7.393 (2.281) 0.794 -15.727
	PF 19/76	62.3 (5.4) 23.9 -101.6	36.3 (3.4) 9.0 - 53.5	6.130 (1.116) 0.232 -16.588
	Plot 25	66.1 (5.0) 23.9 -110.0 55.8 76.4	36.2 (2.8) 9.0 - 53.5 30.3 42.0	6.433 (0.991) 0.232 -16.588 4.387 8.479
PH3	H 10/29	68.4 (7.7) 29.7 -114.3	29.8 (2.7) 17.0 - 42.0	4.275 (0.842) 0.466 - 8.962
	PF 24/71	60.3 (4.1) 15.5 - 94.5	34.8 (2.2) 6.0 - 48.0	5.020 (0.741) 0.052 -12.930
	Plot 34	62.7 (3.7) 15.5 -114.3 55.1 70.2	33.3 (1.8) 6.0 - 48.0 29.7 37.0	4.801 (0.575) 0.052 -12.930 3.630 5.971
PH	Plots 104	56.2 (2.4) 13.2 -114.3 51.5 60.9	31.0 (1.3) 5.5 - 53.5 28.5 33.5	4.320 (0.381) 0.031 -16.588 3.563 5.076
MM1	H 8/28	85.9 (13.2) 41.9 -141.0	32.4 (1.9) 26.0 - 40.0	7.795 (2.277) 1.384 -19.507
	PF 21/72	59.8 (4.6) 24.5 - 99.6	30.3 (2.0) 13.5 - 44.0	4.317 (0.739) 0.290 -12.572
	Plot 29	67.0 (5.3) 24.6 -141.0 56.2 77.8	30.9 (1.5) 13.5 - 44.0 27.8 33.9	5.276 (0.852) 0.290 -19.507 3.530 7.022
MM2	H 13/46	54.8 (5.6) 25.4 - 75.4	27.1 (3.3) 11.0 - 42.0	3.175 (0.687) 0.238 - 6.755
	PF 15/54	68.5 (5.6) 33.3 -109.5	33.6 (2.3) 15.5 - 44.5	5.814 (0.954) 0.578 -12.050
	Plot 28	62.2 (4.1) 25.4 -109.5 53.8 70.6	30.6 (2.0) 11.0 - 44.5 26.4 34.8	4.589 (0.644) 0.238 -12.050 3.268 5.909
MM3	H 4/16	88.5 (18.9) 38.6 -119.9	28.7 (3.7) 19.5 - 35.0	6.894 (2.311) 0.866 -11.642
	PF 21/84	60.7 (4.1) 35.6 -105.9	30.5 (2.0) 15.0 - 45.0	4.281 (0.704) 0.627 -12.247
	Plot 25	65.2 (4.8) 35.6 -119.9 55.3 75.1	30.2 (1.7) 15.0 - 45.0 26.7 33.8	4.699 (0.701) 0.627 -12.247 3.251 6.146
MM	Plots 82	64.8 (2.7) 24.6 -141.0 59.4 70.2	30.6 (1.0) 11.0 - 45.0 28.6 32.6	4.865 (0.426) 0.238 -19.507 4.018 5.213

mean (SE)
n/% min - max
95% conf. limit

APPENDIX 4

Nutrient Concentration in Foliage

Appendix 4. Nutrient concentration in foliage

As mentioned in Chapter 4, Section 1.6, foliage was sampled from the lowest living branch only. Foliage was sampled three times during the summer of 1975 to determine the changes during the growing period. Samples of foliage obtained in September 1976 were separated as follows in order to obtain information on change of nutrient concentration with age of foliage. Foliage of mountain hemlock was separated into two categories, current foliage and one or more years old. Foliage of Pacific silver fir was separated into three categories, current foliage, one year old (last year), and two or more years old.

The decrease of foliar concentration of N, P, and K and the increase of concentration of Ca with age of foliage is in agreement with the literature (Morrison 1974). The concentration decrease indicated an internal redistribution of N and P from older to younger foliage. Due to the difficulties of obtaining foliage samples (large size of standing trees and the restriction on cutting trees down in the Provincial park where most of the study was conducted) the data obtained are too limited to draw more specific conclusions. More detailed studies of this type are being conducted by other researchers involved in the subalpine forest research project. The data appended were used in this thesis to ensure that biomass concentration obtained in a previous study from the M plots could legitimately be used to apply to the P plots.

Appendix 4: Nutrient gradient in foliage PX-plots

Plot	SP	N	P	K	Ca	Mg	Ash	Age of foliage Year[1]	Date D M Y
		%							
PX1	M.h.	0.88	0.16	0.48	0.75	0.13	2.74	C	31 07 75
		0.91	0.17	0.42	1.06	0.21	3.62	C	01 09 75
		0.95	0.17	0.55	0.92	0.16	3.50	C	20 10 75
		0.80	0.15	0.35	0.97	0.16	3.19	C	02 09 76
PX1	P.s.f.	1.37	0.23	-	-	-	- *	C	31 07 75
		1.01	0.16	0.77	0.60	0.09	2.85	C	01 09 75
		0.94	0.15	0.88	0.46	0.09	2.84	C	20 10 75
		0.97	0.19	0.93	0.38	0.07	2.58	C	02 09 76
		0.75	0.08	0.44	1.03	0.08	3.50	1	02 09 76
		0.72	0.08	0.31	1.10	0.08	3.06	2+	02 09 76
PX2	M.h.	0.79	0.17	0.77	0.28	0.06	2.19	C	31 07 75
		0.80	0.18	0.55	0.59	0.10	2.95	C	01 09 75
		0.91	0.20	0.56	0.51	0.13	2.85	C	20 10 75
		0.99	0.18	0.77	0.21	0.06	2.08	C	02 09 76
		0.70	0.14	0.44	0.61	0.06	2.51	1+	02 09 76
PX2	P.s.f.	1.45	0.26	0.94	0.53	0.12	3.07	C	31 07 75
		0.91	0.18	0.66	0.43	0.13	2.41	C	01 09 75
		0.93	0.18	0.85	0.53	0.13	2.85	C	20 10 75
		1.06	0.20	0.68	0.43	0.09	2.30	C	02 09 76
		0.98	0.13	0.42	0.96	0.14	3.19	1	02 09 76
		0.80	0.10	0.36	1.07	0.13	3.27	2+	02 09 76
PX3	M.h.	1.17	0.20	0.61	0.32	0.08	2.18	C	31 07 75
		0.84	0.12	0.41	0.62	0.09	2.62	C	01 09 75
		0.95	0.15	0.53	0.51	0.09	2.19	C	20 10 75
		1.09	0.20	0.66	0.21	0.06	1.77	C	02 09 76
		0.78	0.10	0.35	0.58	0.07	2.08	1+	02 09 76
PX3	P.s.f.	1.50	0.22	0.94	0.42	0.08	2.74	C	31 07 75
		1.01	0.15	0.66	0.46	0.08	2.20	C	01 09 75
		1.04	0.18	0.88	0.49	0.09	2.96	C	20 10 75
		1.16	0.21	0.88	0.20	0.06	1.97	C	02 09 76
		0.82	0.12	0.70	0.43	0.07	2.30	1	02 09 76
		0.77	0.08	0.42	0.71	0.05	2.41	2+	02 09 76

[1] C = current foliage
1 = one year old
2+ = two years old and older

* insufficient quantity of sample to perform all analyses.

Appendix 4. (cont'd) Nutrient gradient in foliage PM-plots

Plot	SP	N	P	K (%)	Ca	Mg	Ash	Age of foliage Year[1]	Date
PM1	M.h.	1.13	0.20	0.88	0.25	0.07	2.41	C	31 07 75
		0.83	0.14	0.66	0.48	0.09	2.63	C	01 09 75
		0.82	0.15	0.74	0.49	0.09	2.73	C	24 10 75
		0.95	0.19	0.77	0.20	0.05	1.98	C	02 09 76
		0.79	0.11	0.42	0.61	0.09	2.52	1+	02 09 76
	P.s.f.*								
PM2	M.h.	1.35	0.22	0.87	0.38	0.10	2.62	C	31 07 75
		1.08	0.18	0.61	0.77	0.16	3.39	C	01 09 75
		1.00	0.17	0.72	0.44	0.11	2.19	C	24 10 75
		1.17	0.21	0.89	0.24	0.08	4.69	C	02 09 76
		1.01	0.17	0.55	0.73	0.14	3.29	1+	02 09 76
PM2	P.s.f.	1.73	0.28	1.31	0.35	0.09	3.18	C	31 07 75
		1.08	0.19	1.05	0.40	0.09	2.73	C	01 09 75
		1.02	0.21	1.18	0.41	0.08	3.29	C	24 10 75
		1.08	0.21	0.83	0.28	0.07	1.65	C	02 09 76
		0.96	0.13	0.57	0.63	0.07	2.65	1	02 09 76
		0.89	0.11	0.35	0.79	0.07	3.18	2+	02 09 76
PM3	P.s.f.	1.75	0.29	1.14	0.36	0.09	2.95	C	31 07 75
		1.09	0.21	0.92	0.39	0.08	2.73	C	01 09 75
		1.10	0.23	0.88	0.41	0.08	2.51	C	24 10 75
		1.30	0.23	0.89	0.27	0.07	2.41	C	02 09 76
		1.02	0.15	0.46	0.55	0.07	2.40	1	02 09 76
		0.89	0.14	0.46	0.57	0.06	2.63	2+	02 09 76
	M.h.*								

[1] C = current foliage
1 = one year old
2+ = two years old and older

* no suitable tree for sampling was available on the plot.

Appendix 4. (cont'd) Nutrient gradient in foliage PH-plots

Plot	SP	N	P	K	Ca	Mg	Ash	Age of foliage Year[1]	Date
				%					
PH1	M.h.	1.22	0.17	0.83	0.25	0.07	2.30	C	31 07 75
		1.08	0.11	0.50	0.63	0.07	2.51	C	01 09 75
		1.24	0.19	0.79	0.16	0.06	1.97	C	02 09 76
		0.90	0.10	0.44	0.41	0.09	1.96	1+	02 09 76
PH1	P.s.f.	1.10	0.21	0.90	0.41	0.08	2.52	C	01 09 75
		1.02	0.20	1.03	0.36	0.08	2.85	C	20 10 75
		1.25	0.25	1.10	0.24	0.07	2.63	C	02 09 76
		0.80	0.15	0.42	0.27	0.05	2.19	1	02 09 76
		0.81	0.12	0.44	0.79	0.07	2.63	2+	02 09 76
PH2	M.h.	1.41	0.13	0.53	0.55	0.10	2.52	C	31 07 75
		1.25	0.12	0.46	0.60	0.10	2.62	C	01 09 75
		1.28	0.12	0.54	0.75	0.10	2.73	C	20 10 75
		1.54	0.22	0.88	0.34	0.09	2.52	C	02 09 76
		1.23	0.11	0.43	0.59	0.08	2.19	1+	02 09 76
PH2	P.s.f.	1.74	0.25	1.17	0.44	0.10	3.28	C	31 07 75
		0.96	0.16	1.10	0.36	0.09	2.96	C	01 09 75
		1.11	0.19	1.07	0.41	0.10	2.95	C	20 10 75
		1.28	0.23	1.14	0.25	0.07	2.73	C	02 09 76
		1.00	0.13	0.74	0.42	0.07	2.17	1	02 09 76
		0.91	0.11	0.48	0.79	0.08	2.63	2+	02 09 76
PH3	M.h.	1.28	0.19	0.66	0.44	0.09	2.30	C	31 07 75
		1.22	0.17	0.61	0.53	0.11	2.94	C	01 09 75
		1.29	0.18	0.68	0.56	0.10	2.74	C	20 10 75
		1.40	0.25	0.87	0.24	0.10	3.05	C	02 09 76
		1.06	0.18	0.56	0.52	0.13	2.30	1+	02 09 76
PH3	P.s.f.	1.85	0.31	1.42	0.49	0.10	3.83	C	31 07 75
		1.22	0.21	1.05	0.48	0.08	3.06	C	01 09 75
		1.07	0.22	1.18	0.49	0.08	3.17	C	20 10 75
		1.47	0.25	1.01	0.34	0.07	2.52	C	02 09 76
		1.02	0.15	0.59	0.65	0.07	2.18	1	02 09 76
		0.94	0.14	0.48	0.82	0.07	2.40	2+	02 09 76

[1] C = current foliage
1 = one year old
2+ = two years old and older

APPENDIX 5

Distribution of Biomass and Macronutrients in the Above-ground Tree Components on the Sample Plots

Abbreviations used in Appendix 5:

SP	-	tree species
PLOT	-	sample plot
WOOD	-	tree bole wood
BARK	-	tree bole bark
BRAN 1	-	branches of diameter over 1 inch (2.54 cm)
BRAN 2	-	branches of diameter 1/4 - 1 inch (0.64 - 2.54 cm)
TWIG	-	twigs, diameter smaller than 1/4 inch (0.64 cm)
FOLI	-	foliage, needles
TWFO	-	twigs and foliage together
TRUNK	-	tree trunk, bole wood and bark
CROWN	-	tree crown, branches, twigs and foliage
TREE	-	above ground part of a tree
M.h.	-	mountain hemlock
P.s.f.	-	Pacific silver fir

Appendix 5. Distribution of biomass by component and species on the sample plots (in t/ha).

SP/PLOT	WOOD	BARK	BRAN 1	BRAN 2	TWFO	TWIG	FOLI	TRUNK	CROWN	TREE
M.h.	224.46	78.51	23.81	9.04	17.47	4.11	10.40	302.97	50.32	353.29
P.s.f.	20.29	4.07	3.80	3.42	4.14	-	-	24.36	11.36	35.72
PX1	244.75	82.58	27.61	12.46	21.61	-	-	327.33	61.68	389.01
M.h.	252.63	83.02	23.33	14.34	16.34	4.07	9.46	335.66	52.02	387.66
P.s.f.	42.12	8.53	6.65	5.25	7.44	-	-	50.65	19.34	70.00
PX2	294.75	91.55	29.98	19.59	23.78	-	-	386.31	71.36	457.66
M.h.	199.80	77.46	36.84	3.36	16.84	4.86	9.91	277.26	57.04	334.30
P.s.f.	112.28	23.19	17.62	8.04	14.86	-	-	135.47	40.52	175.98
PX3	312.08	100.65	54.46	11.40	31.70	-	-	412.73	97.56	510.28
M.h.	361.57	100.67	34.80	8.18	33.67	8.43	20.36	462.25	76.65	538.89
P.s.f.	130.51	27.04	15.91	6.61	12.47	-	-	157.55	34.99	192.54
PM1	492.08	127.71	50.71	14.79	46.14	-	-	619.80	111.64	731.43
M.h.	213.44	58.37	19.73	4.88	19.66	3.81	11.88	271.81	44.27	316.08
P.s.f.	133.65	27.74	15.61	6.15	11.76	-	-	161.39	33.49	194.90
PM2	347.09	86.11	35.34	11.03	31.42	-	-	433.20	77.76	510.98
M.h.	68.78	20.08	10.63	0.67	3.83	2.14	2.00	88.87	15.13	104.00
P.s.f.	309.91	64.78	34.64	11.75	24.92	-	-	374.69	71.33	446.02
PM3	378.69	84.86	45.27	12.42	28.75	-	-	463.56	86.46	550.02
M.h.	75.62	21.25	9.00	1.63	4.95	2.50	2.77	96.87	15.56	112.43
P.s.f.	211.23	44.15	22.44	9.09	19.50	-	-	255.38	51.02	306.40
PH1	286.85	65.40	31.44	10.72	24.45	-	-	352.25	66.58	418.83
M.h.	83.31	21.98	12.59	0.63	2.53	5.09	1.24	105.29	15.76	121.04
P.s.f.	255.30	53.83	24.73	7.81	18.80	-	-	309.13	51.33	360.46
PH2	338.61	75.81	37.32	8.44	21.33	-	-	414.42	67.09	481.50
M.h.	87.44	28.65	15.18	0.99	6.30	3.11	3.56	116.08	22.47	138.56
P.s.f.	206.85	43.44	21.55	7.35	17.13	-	-	250.29	46.03	296.32
PH3	294.29	72.09	36.73	8.34	23.43	-	-	366.37	68.50	434.88
M.h.	176.07	61.15	42.93	1.25	5.65	7.04	2.94	237.22	49.83	287.04
P.s.f.	251.73	52.79	29.76	9.37	20.99	-	-	304.52	60.12	364.65
MM1	427.80	113.94	72.69	10.62	26.64	-	-	541.74	109.95	651.69
M.h.	136.30	37.90	15.82	2.05	11.00	5.10	6.31	174.21	28.87	203.07
P.s.f.	244.92	51.54	28.98	8.27	19.57	-	-	296.46	56.83	353.29
MM2	381.22	89.44	44.80	10.32	30.57	-	-	470.67	85.70	556.36
M.h.	80.28	30.84	21.07	0.61	2.95	1.48	1.45	111.12	24.63	135.75
P.s.f.	243.19	50.97	28.96	8.60	18.49	-	-	294.16	56.05	350.21
MM3	323.47	81.81	50.03	9.21	21.44	-	-	405.28	80.68	485.96

Appendix 5. Distribution of nitrogen by component and species on the sample plots (in kg/ha).

SP/PLOT	WOOD	BARK	BRAN 1	BRAN 2	TWFO	TWIG	FOLI	TRUNK	CROWN	TREE
M.h.	112.23	141.32	28.57	15.37	104.02	15.62	88.40	253.55	147.96	401.51
P.s.f.	10.15	9.77	5.70	7.52	30.64	-	-	19.92	43.86	63.78
PX1	122.38	151.09	34.27	22.89	134.66	-	-	273.47	191.82	465.29
M.h.	126.32	149.44	28.00	24.38	95.88	15.47	80.41	275.76	148.26	424.02
P.s.f.	21.06	20.47	9.98	11.55	55.06	-	-	41.56	76.59	118.12
PX2	147.38	169.91	37.98	35.93	150.94	-	-	317.29	224.85	542.14
M.h.	99.90	139.43	44.21	5.71	102.71	18.47	84.24	239.33	152.63	391.96
P.s.f.	56.14	55.66	26.43	17.69	109.96	-	-	111.80	154.08	265.88
PX3	156.04	195.09	70.64	23.40	212.67	-	-	351.13	306.71	657.84
M.h.	180.79	181.21	41.76	13.91	205.09	32.03	173.06	362.00	260.76	622.76
P.s.f.	65.26	64.90	23.87	14.54	92.28	-	-	130.16	130.69	260.85
PM1	246.05	246.11	65.63	28.45	297.37	-	-	492.16	391.45	883.61
M.h.	106.72	105.07	23.68	8.30	115.46	14.48	100.98	211.79	147.44	359.23
P.s.f.	66.83	66.58	23.42	13.53	87.02	-	-	133.41	123.97	257.38
PM2	173.55	171.65	47.10	21.83	202.48	-	-	345.20	271.41	616.61
M.h.	34.39	36.14	12.76	1.14	25.13	8.13	17.00	70.53	39.03	109.56
P.s.f.	154.96	155.47	51.96	25.85	184.41	-	-	310.43	262.22	572.65
PM3	189.35	191.61	64.72	26.99	209.54	-	-	380.96	301.25	682.21
M.h.	37.81	38.25	10.80	2.77	33.05	9.50	23.55	76.06	46.62	122.68
P.s.f.	105.62	105.96	33.66	20.00	144.30	-	-	211.58	197.96	409.54
PH1	143.43	144.21	44.46	22.77	177.35	-	-	287.64	244.58	532.22
M.h.	41.66	39.56	15.11	1.07	29.88	19.34	10.54	81.22	46.06	127.28
P.s.f.	127.65	129.19	37.10	17.18	139.12	-	-	256.84	193.40	450.24
PH2	169.31	168.75	52.21	18.25	169.00	-	-	338.06	239.46	577.52
M.h.	43.72	51.57	18.22	1.68	42.08	11.82	30.26	95.29	61.98	157.27
P.s.f.	103.43	104.26	32.33	16.17	126.76	-	-	207.69	175.26	382.95
PH3	147.15	155.83	50.55	17.85	168.84	-	-	302.98	237.24	540.22
M.h.	88.04	110.07	51.52	2.13	51.74	26.75	24.99	198.11	105.39	303.50
P.s.f.	125.87	126.70	44.64	20.61	155.33	-	-	252.57	220.58	473.15
MM1	213.91	236.77	96.16	22.74	207.07	-	-	450.68	325.97	776.65
M.h.	68.15	68.22	18.98	3.49	73.02	19.38	53.64	136.37	95.49	231.86
P.s.f.	122.46	123.70	43.47	18.19	144.82	-	-	246.16	206.48	452.64
MM2	190.61	191.92	62.45	21.68	217.84	-	-	382.53	301.97	684.50
M.h.	40.14	55.51	25.28	1.04	17.95	5.62	12.33	95.65	44.27	139.92
P.s.f.	121.60	122.33	43.44	18.92	136.83	-	-	243.93	199.19	443.12
MM3	161.74	177.84	68.72	19.96	154.78	-	-	339.58	243.46	583.04

Appendix 5. Distribution of phosphorus by component and species on the sample plots (in kg/ha).

SP/PLOT	WOOD	BARK	BRAN 1	BRAN 2	TWFO	TWIG	FOLI	TRUNK	CROWN	TREE
M.h.	44.89	47.11	7.14	3.62	13.91	2.47	11.44	92.00	24.67	116.67
P.s.f.	2.03	1.63	0.76	1.03	4.14	-	-	3.66	5.93	9.59
PX1	46.92	48.74	7.90	4.65	18.05	-	-	95.66	30.60	126.26
M.h.	50.53	49.81	7.00	5.74	12.85	2.44	10.41	100.34	25.59	125.93
P.s.f.	4.21	3.41	1.33	1.57	7.44	-	-	7.62	10.34	17.96
PX2	54.74	53.22	8.33	7.31	20.29	-	-	107.96	35.93	143.89
M.h.	39.96	46.48	11.05	1.34	13.82	2.92	10.90	86.44	26.21	112.65
P.s.f.	11.23	9.28	3.52	2.41	14.86	-	-	20.51	20.79	41.30
PX3	51.19	55.76	14.57	3.75	28.68	-	-	106.95	47.00	153.95
M.h.	72.31	60.40	10.44	3.27	27.46	5.06	22.40	132.71	41.17	173.88
P.s.f.	13.05	10.82	3.18	1.98	12.47	-	-	23.87	17.63	41.50
PM1	85.36	71.22	13.62	5.25	39.93	-	-	156.58	58.80	215.38
M.h.	42.69	35.02	5.92	1.95	15.36	2.29	13.07	77.71	23.23	100.94
P.s.f.	13.36	11.10	3.12	1.84	11.76	-	-	24.46	16.72	41.18
PM2	56.05	46.12	9.04	3.79	27.12	-	-	102.17	39.95	142.12
M.h.	13.76	12.05	3.19	0.27	3.48	1.28	2.20	25.81	6.94	32.75
P.s.f.	30.99	25.91	6.93	3.52	24.92	-	-	56.90	35.37	92.27
PM3	44.75	37.96	10.12	3.79	28.40	-	-	82.71	42.31	125.02
M.h.	15.12	12.75	2.70	0.65	4.55	1.50	3.05	27.87	7.90	35.77
P.s.f.	21.12	17.66	4.49	2.73	19.50	-	-	38.78	26.72	65.50
PH1	36.24	30.41	7.19	3.38	24.05	-	-	66.65	34.62	101.27
M.h.	16.66	13.19	3.78	0.25	4.41	3.05	1.36	29.85	8.44	38.29
P.s.f.	25.53	21.53	4.95	2.34	18.80	-	-	47.06	26.09	73.15
PH2	42.19	34.72	8.73	2.59	23.21	-	-	76.91	34.53	111.44
M.h.	17.49	17.19	4.55	0.40	5.79	1.87	3.92	34.68	10.74	45.42
P.s.f.	20.68	17.38	4.31	2.20	17.13	-	-	38.06	23.64	61.70
PH3	38.17	34.57	8.86	2.60	22.92	-	-	72.74	34.38	107.12
M.h.	35.21	36.69	12.88	0.50	7.45	4.22	3.23	71.90	20.83	92.73
P.s.f.	25.17	21.12	5.95	2.81	20.99	-	-	46.29	29.75	76.04
MM1	60.38	57.81	18.83	3.31	28.44	-	-	118.19	50.58	168.77
M.h.	27.26	22.74	4.75	0.82	10.00	3.06	6.94	50.00	15.57	65.57
P.s.f.	24.49	20.62	5.80	2.48	19.57	-	-	45.11	27.85	72.96
MM2	51.75	43.36	10.55	3.30	29.57	-	-	95.11	43.42	138.53
M.h.	16.06	18.50	6.32	0.24	2.48	0.89	1.59	34.56	9.04	43.60
P.s.f.	24.32	20.39	5.79	2.58	18.49	-	-	44.71	26.86	71.57
MM3	40.38	38.89	12.11	2.82	20.97	-	-	79.27	35.90	115.17

Appendix 5. Distribution of potassium by component and species on the sample plots (in kg/ha).

SP/PLOT	WOOD	BARK	BRAN 1	BRAN 2	TWFO	TWIG	FOLI	TRUNK	CROWN	TREE
M.h.	157.12	70.66	16.67	8.14	37.78	6.58	31.20	227.78	62.59	290.37
P.s.f.	12.17	5.29	3.42	4.10	13.66	-	-	17.46	21.18	38.64
PX1	169.29	75.95	20.09	12.24	51.44	-	-	245.24	83.77	329.01
M.h.	176.84	74.72	16.33	12.91	34.89	6.51	28.38	251.56	64.13	315.69
P.s.f.	25.27	11.09	5.98	6.30	24.55	-	-	36.36	36.83	73.19
PX2	202.11	85.81	22.31	19.21	59.44	-	-	287.92	100.96	388.88
M.h.	139.86	69.71	25.79	3.02	37.51	7.78	29.73	209.57	66.32	275.89
P.s.f.	67.37	30.15	15.86	9.65	49.04	-	-	97.52	74.55	172.07
PX3	207.23	99.86	41.65	12.67	86.55	-	-	307.09	140.87	447.96
M.h.	253.10	90.60	24.36	7.36	74.57	13.49	61.08	343.70	106.29	449.99
P.s.f.	78.31	35.15	14.32	7.93	41.15	-	-	113.46	63.40	176.86
PM1	331.41	125.75	38.68	15.29	115.72	-	-	457.16	169.69	626.85
M.h.	149.41	52.53	13.81	4.39	41.74	6.10	35.64	201.94	59.94	261.88
P.s.f.	80.19	36.06	14.05	7.38	38.81	-	-	116.25	60.24	176.49
PM2	229.60	88.59	27.86	11.77	80.55	-	-	318.19	120.18	438.37
M.h.	48.15	18.07	7.44	0.60	9.42	3.42	6.00	66.22	17.46	83.68
P.s.f.	185.95	84.21	31.18	14.10	82.24	-	-	270.16	127.52	397.68
PM3	234.10	102.28	38.62	14.70	91.66	-	-	336.38	144.98	481.36
M.h.	52.93	19.12	6.30	1.47	12.31	4.00	8.31	72.05	20.08	92.13
P.s.f.	126.74	57.39	20.20	10.91	64.35	-	-	184.13	95.46	279.59
PH1	179.67	76.51	26.50	12.38	76.66	-	-	256.18	115.54	371.72
M.h.	58.32	19.78	8.81	0.57	11.86	8.14	3.72	78.10	21.24	99.34
P.s.f.	153.18	69.98	22.26	9.37	62.04	-	-	223.16	93.67	316.83
PH2	211.50	89.76	31.07	9.94	73.90	-	-	301.26	114.91	416.17
M.h.	61.21	25.78	10.63	0.89	15.66	4.98	10.68	86.99	27.18	114.17
P.s.f.	124.11	56.47	19.39	8.82	56.53	-	-	180.58	84.74	265.32
PH3	185.32	82.25	30.02	9.71	72.19	-	-	267.57	111.92	379.49
M.h.	123.25	55.03	30.05	1.12	20.08	11.26	8.82	178.28	51.25	229.53
P.s.f.	151.04	68.63	26.78	11.24	69.27	-	-	219.67	107.29	326.96
MM1	274.29	123.66	56.83	12.36	89.35	-	-	397.95	158.54	556.49
M.h.	95.41	34.11	11.07	1.84	27.09	8.16	18.93	129.52	40.00	169.52
P.s.f.	146.95	67.00	26.08	9.92	64.58	-	-	213.95	100.58	314.53
MM2	242.36	101.11	37.15	11.76	91.67	-	-	343.47	140.58	484.05
M.h.	56.20	27.76	14.75	0.55	6.72	2.37	4.35	83.96	22.02	105.98
P.s.f.	145.91	66.26	26.06	10.32	61.02	-	-	212.17	97.40	309.57
MM3	202.11	94.02	40.81	10.87	67.74	-	-	296.13	119.42	415.55

Appendix 5. Distribution of calcium by component and species on the sample plots (in kg/ha).

SP/PLOT	WOOD	BARK	BRAN 1	BRAN 2	TWFO	TWIG	FOLI	TRUNK	CROWN	TREE
M.h.	157.12	243.38	38.01	16.27	39.64	7.40	32.24	400.50	93.92	494.42
P.s.f.	12.17	19.94	11.78	9.92	18.22	-	-	32.11	39.92	72.03
PX1	169.29	263.32	49.79	26.19	57.86	-	-	432.61	133.84	566.45
M.h.	176.84	257.36	37.33	25.81	36.66	7.33	29.33	434.20	99.80	534.00
P.s.f.	25.27	41.80	20.61	15.22	32.74	-	-	67.07	68.57	135.64
PX2	202.11	299.16	57.94	41.03	69.40	-	-	501.27	168.37	669.64
M.h.	139.86	240.13	58.94	6.05	39.47	8.75	30.72	379.99	104.46	484.45
P.s.f.	67.37	113.63	54.62	23.32	65.38	-	-	181.00	143.32	324.32
PX3	207.23	353.76	113.56	29.37	104.85	-	-	560.99	247.78	808.77
M.h.	253.10	312.08	55.68	14.72	78.29	15.17	63.12	565.18	148.69	713.87
P.s.f.	78.31	132.50	49.32	19.17	54.87	-	-	210.81	123.36	334.17
PM1	331.41	444.58	105.00	33.89	133.16	-	-	775.99	272.05	1048.04
M.h.	149.41	180.95	31.57	8.78	43.69	6.86	36.83	330.36	84.04	414.40
P.s.f.	80.19	135.93	48.39	17.83	51.74	-	-	216.12	117.96	334.08
PM2	229.60	316.88	79.96	26.61	95.43	-	-	546.48	202.00	748.48
M.h.	48.15	62.25	17.01	1.21	10.05	3.85	6.20	110.40	28.27	138.67
P.s.f.	185.95	317.42	107.38	34.07	109.65	-	-	503.37	251.10	754.47
PM3	234.10	379.67	124.39	35.28	119.70	-	-	613.77	279.37	893.14
M.h.	52.93	65.87	14.40	2.93	13.09	4.50	8.59	118.80	30.42	149.22
P.s.f.	126.74	216.33	69.56	26.36	85.80	-	-	343.07	181.72	524.79
PH1	179.67	282.20	83.96	29.29	98.89	-	-	461.87	212.14	674.01
M.h.	58.32	68.14	20.14	1.13	13.00	9.16	3.84	126.46	34.27	160.73
P.s.f.	153.18	263.77	76.66	22.65	82.72	-	-	416.95	182.03	598.98
PH2	211.50	331.91	96.80	23.78	95.72	-	-	543.41	216.30	759.71
M.h.	61.21	88.81	24.29	1.78	16.64	5.60	11.04	150.02	42.71	192.73
P.s.f.	124.11	212.86	66.80	21.31	75.37	-	-	336.97	163.48	500.45
PH3	185.32	301.67	91.09	23.09	92.01	-	-	486.99	206.19	693.18
M.h.	123.25	189.56	68.69	2.25	21.78	12.67	9.11	312.81	92.72	405.53
P.s.f.	151.04	258.67	92.26	27.17	92.36	-	-	409.71	211.79	621.50
MM1	274.29	448.23	160.95	29.42	114.14	-	-	722.52	304.51	1027.03
M.h.	95.41	117.49	25.31	3.69	28.74	9.18	19.56	212.90	57.74	270.64
P.s.f.	146.95	252.55	89.84	23.98	86.11	-	-	399.50	199.93	599.43
MM2	242.36	370.04	115.15	27.67	114.85	-	-	612.40	257.67	870.07
M.h.	56.20	95.60	33.71	1.10	7.15	2.66	4.49	151.80	41.96	193.76
P.s.f.	145.91	249.75	89.78	24.94	81.36	-	-	395.66	196.08	591.74
MM3	202.11	345.35	123.49	26.04	88.51	-	-	547.46	238.04	785.50

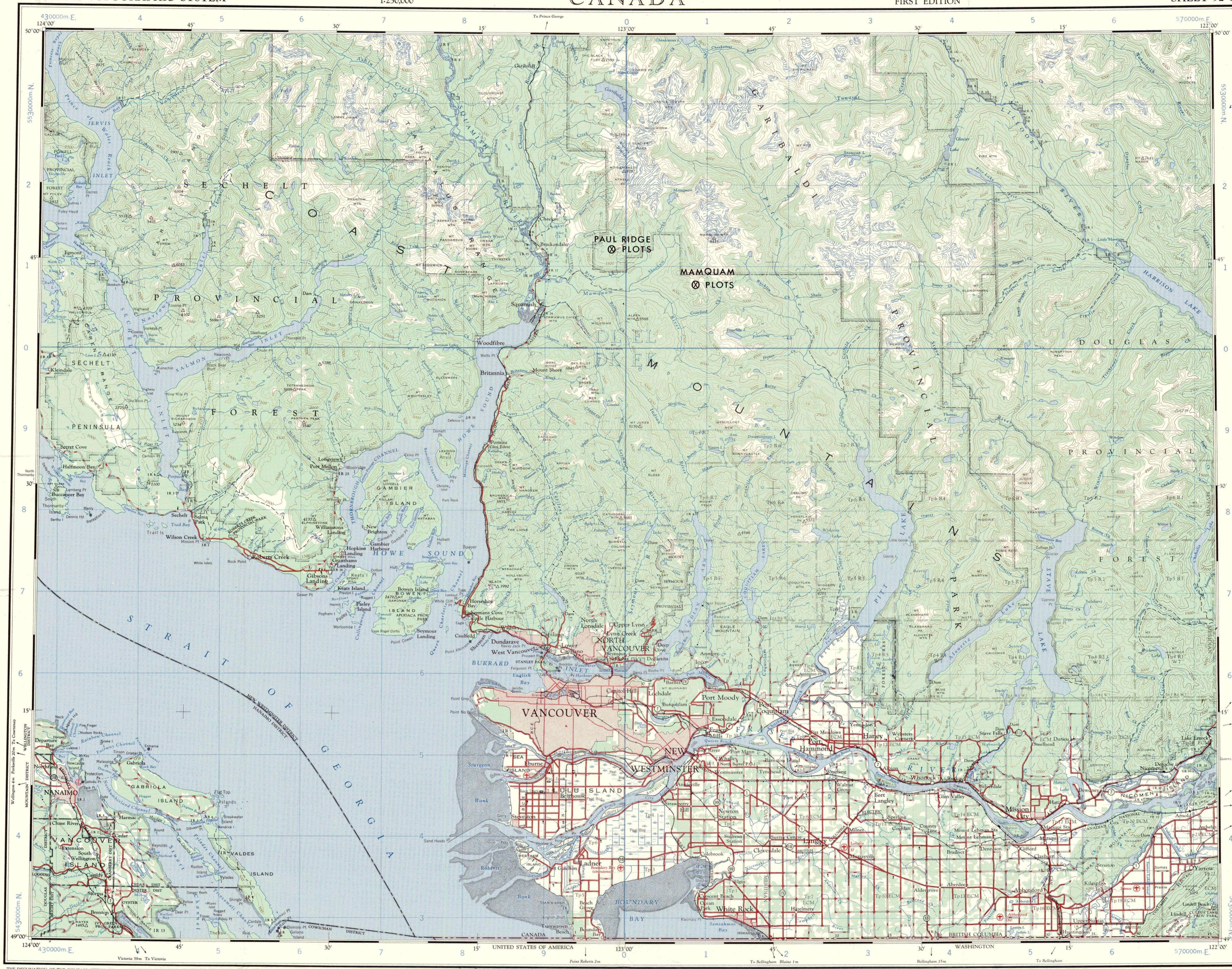
Appendix 5. Distribution of magnesium by components and species on the sample plots (in kg/ha).

SP/PLOT	WOOD	BARK	BRAN 1	BRAN 2	TWFO	TWIG	FOLI	TRUNK	CROWN	TREE
M.h.	44.89	15.70	4.76	2.71	9.96	1.64	8.32	60.59	17.43	78.02
P.s.f.	2.03	1.22	0.76	1.03	2.90	-	-	3.25	4.69	7.94
PX1	46.92	16.92	5.52	3.74	12.86	-	-	63.84	22.12	85.96
M.h.	50.53	16.60	4.67	4.30	9.20	1.63	7.57	67.13	18.17	85.30
P.s.f.	4.21	2.56	1.33	1.57	5.21	-	-	6.77	8.11	14.88
PX2	54.74	19.16	6.00	5.87	14.41	-	-	73.90	26.28	100.18
M.h.	39.96	15.49	7.37	1.01	9.87	1.94	7.93	55.45	18.25	73.70
P.s.f.	11.23	6.96	3.52	2.41	10.40	-	-	18.19	16.33	34.52
PX3	51.19	22.45	10.89	3.42	20.27	-	-	73.64	34.58	108.22
M.h.	72.31	20.13	6.96	2.45	19.66	3.37	16.29	92.44	29.07	121.51
P.s.f.	13.05	8.11	3.18	1.98	8.73	-	-	21.16	13.89	35.05
PM1	85.36	28.24	10.14	4.43	28.39	-	-	113.60	42.96	156.56
M.h.	42.69	11.67	3.95	1.46	11.02	1.52	9.50	54.36	16.43	70.79
P.s.f.	13.36	8.32	3.12	1.84	8.23	-	-	21.68	13.19	34.87
PM2	56.05	19.99	7.07	3.30	19.25	-	-	76.04	29.62	105.66
M.h.	13.76	4.02	2.13	0.20	2.46	0.86	1.60	17.78	4.79	22.57
P.s.f.	30.99	19.43	6.93	3.52	17.44	-	-	50.42	27.89	78.31
PM3	44.75	23.45	9.06	3.72	19.90	-	-	68.20	32.68	100.88
M.h.	15.12	4.25	1.80	0.49	3.22	1.00	2.22	19.37	5.51	24.88
P.s.f.	21.12	13.24	4.49	2.73	13.65	-	-	34.36	20.87	55.23
PH1	36.24	17.49	6.29	3.22	16.87	-	-	53.73	26.38	80.11
M.h.	16.66	4.40	2.52	0.19	3.03	2.04	0.99	21.06	5.74	26.80
P.s.f.	25.53	16.15	4.95	2.34	13.16	-	-	41.68	20.45	62.13
PH2	42.19	20.55	7.47	2.53	16.19	-	-	62.74	26.19	88.93
M.h.	17.49	5.73	3.04	0.30	4.09	1.24	2.85	23.22	7.43	30.65
P.s.f.	20.68	13.03	4.31	2.20	11.99	-	-	33.71	18.50	52.21
PH3	38.17	18.76	7.35	2.50	16.08	-	-	56.93	25.93	82.86
M.h.	35.21	12.23	8.59	0.37	5.17	2.82	2.35	47.44	14.13	61.57
P.s.f.	25.17	15.84	5.95	2.81	14.69	-	-	41.01	23.45	64.46
MM1	60.38	28.07	14.54	3.18	19.86	-	-	88.45	37.58	126.03
M.h.	27.26	7.58	3.16	0.61	7.09	2.04	5.05	34.84	10.86	45.70
P.s.f.	24.49	15.46	5.80	2.48	13.70	-	-	39.95	21.98	61.93
MM2	51.75	23.04	8.96	3.09	20.79	-	-	74.79	32.84	107.63
M.h.	16.06	6.17	4.21	0.18	1.75	0.59	1.16	22.23	6.14	28.37
P.s.f.	24.32	15.29	5.79	2.58	12.94	-	-	39.61	21.31	60.92
MM3	40.38	21.46	10.00	2.76	14.69	-	-	61.84	27.45	89.29

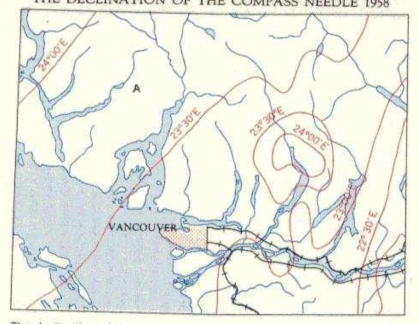
Appendix 5. Distribution of biomass and N, P, K, Ca, and Mg between mountain hemlock and Pacific silver fir on investigated sites (in percent)

Lot	Species	Biomass	N	P	K	Ca	Mg
PX1	M.h.	90.8	86.3	92.4	88.3	87.3	90.8
	P.s.f.	9.2	13.7	7.6	11.7	12.7	9.2
PX2	M.h.	84.7	78.2	87.5	81.2	79.7	85.1
	P.s.f.	15.3	21.8	12.5	18.8	20.3	14.8
PX3	M.h.	65.5	59.6	73.2	61.6	59.9	68.1
	P.s.f.	34.5	40.4	26.8	38.4	40.1	31.9
$\overline{PX}$	M.h.	79.2	73.1	83.8	75.6	74.0	80.5
	P.s.f.	20.8	26.9	16.2	24.4	26.0	19.5
PM1	M.h.	73.7	70.5	80.7	71.8	68.1	77.6
	P.s.f.	26.3	29.5	19.3	28.2	31.9	22.4
PM2	M.h.	61.9	58.3	71.0	59.7	55.4	67.0
	P.s.f.	38.1	41.7	29.0	40.3	44.6	33.0
PM3	M.h.	18.9	16.1	26.2	17.4	15.5	22.4
	P.s.f.	81.1	83.9	73.8	82.6	84.5	77.6
$\overline{PM}$	M.h.	53.5	50.0	63.7	51.4	47.1	59.2
	P.s.f.	46.5	50.0	36.3	48.6	52.9	40.8
M1	M.h.	44.0	39.1	54.9	41.2	39.5	48.9
	P.s.f.	56.0	60.9	45.1	58.8	60.5	51.1
M2	M.h.	36.5	33.9	47.3	35.0	31.1	42.5
	P.s.f.	63.5	66.1	52.7	65.0	68.9	57.5
M3	M.h.	27.9	24.0	37.9	25.5	24.7	31.8
	P.s.f.	72.1	76.0	62.1	74.5	75.3	68.2
$\overline{M}$	M.h.	36.9	33.0	47.8	34.7	32.4	42.0
	P.s.f.	63.1	67.0	52.2	65.3	67.6	58.0
PH1	M.h.	26.8	23.1	35.3	24.8	22.1	31.1
	P.s.f.	73.2	76.9	64.7	75.2	77.9	68.9
PH2	M.h.	25.1	22.0	34.4	23.9	21.2	30.1
	P.s.f.	74.9	78.0	65.6	76.1	78.8	69.9
PH3	M.h.	31.9	29.1	42.4	30.1	27.8	37.0
	P.s.f.	68.1	70.9	57.6	69.9	72.2	63.0
$\overline{PH}$	M.h.	27.9	24.7	37.4	26.2	23.6	32.7
	P.s.f.	72.1	75.3	62.6	73.8	76.4	67.3

Refer to this map as: 92 G EDITION 1 ASE SERIES A 502



THE DECLINATION OF THE COMPASS NEEDLE 1958



The declination of the compass needle at any place along a red line is the declination given on that red line. At other places the declination is between those given on the neighbouring red lines; thus at the place marked A, the declination is between 23°30′ E and 24°00′ E. The declination of the compass needle is decreasing 2.8 minutes annually.

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Transverse Mercator Projection

VANCOUVER
BRITISH COLUMBIA

Contour interval 500 Feet
Elevations in Feet above Mean Sea Level
North American Datum 1927

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REFERENCE

Roads:
- hard surface, all weather: more than 2 lanes; 2 lanes; less than 2 lanes
- loose surface, all weather: 2 lanes or more; less than 2 lanes; dry weather
- wagon; cart track
- Trail or portage

Railway: normal gauge: multiple track; station; single track; flagstop; abandoned

Boundaries:
- international
- county or district
- Indian reserve, park, etc
- township, surveyed
- township, unsurveyed
- Section line

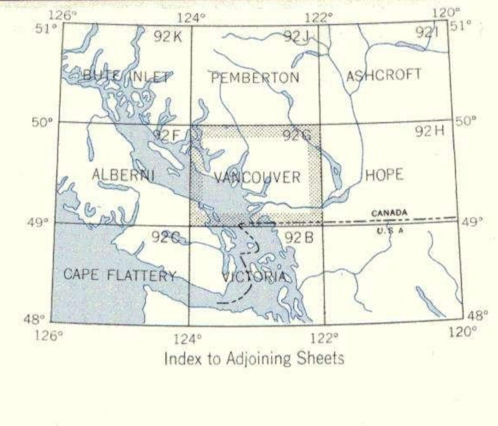
Contours:
- elevation 3000
- depression 2500
- approximate 2000

Spot elevation (in feet) .1885
Power transmission line
Dyke

Scale 1:250,000
1 Inch to 4 Miles Approximately
Miles 5 0 5 10 15 20 Miles
Kilometres 5 0 5 10 15 20 25 30 Kilometres

REFERENCE

- City or large town
- Town
- Village or settlement
- Post office P
- School
- Church
- Boundary monument
- Lighthouse
- Horizontal control point
- Streams: intermittent or dry; indefinite
- Irrigation canal or ditch
- Rapids; falls R F
- Intermittent lake
- Glacier or snowfield
- Marsh or swamp
- Sand, gravel or mud
- Ferry Fy
- Forest
- Airport
- Airfield
- Seaplane base
- Seaplane anchorage



Index to Adjoining Sheets

GRID ZONE DESIGNATION	100,000 M. SQUARE IDENTIFICATION
10 U	DL EL / DK EK; 550; 50

TO GIVE A REFERENCE TO NEAREST 1000 METRES

EXAMPLE: LIGHTHOUSE

SQUARE: Read letters of 100,000 m. square — DK

EASTING: Read number on grid line immediately to left of point — 8. Estimate tenths of a square from this line eastward to point — 1. — 81

NORTHING: Read number on grid line immediately below point — 7. Estimate tenths of a square from this line northward to point — 4. — 74

MILITARY GRID REFERENCE (to nearest 1,000 metres) DK8174

If reporting beyond 18° in any direction, prefix Grid Zone Designation as: 10UDK8174

TEN THOUSAND METRE
UNIVERSAL TRANSVERSE MERCATOR GRID
ZONE 10

VANCOUVER
92G
EDITION 1

APPENDIX 6

Age and Wood Volume Increment of Sampled Trees

Appendix 6. Age and wood volume increment of sampled trees (based on 92 trees).

Plot	n*	Age (years) Mean (SE)		Timber volume increment per sampled tree Mean (SE) $m^3/(tree \cdot 20\ years)$		N**	Timber volume increment: $m^3/(ha \cdot 20\ years)$ Mean (SE) 95% conf. limits	
PX1	5	358	(46)	0.0309	(0.0143)	1018	31.46 0 -	(14.56) 68.89
PX2	8	344	(43)	0.0344	(0.0133)	1275	43.86 4.75 -	(16.96) 82.97
PX3	10	367	(53)	0.0812	(0.0197)	520	42.22 19.41 -	(10.24) 65.03
$\overline{PX}$	23	356		0.0488		938	39.18	
PM1	8	340	(36)	0.0315	(0.0125)	673	21.20 1.81 -	(8.41) 40.59
PM2	7	294	(22)	0.0678	(0.0206)	457	30.98 8.73 -	(9.41) 53.23
PM3	9	434	(44)	0.0849	(0.0421)	311	26.40 0 -	(13.09) 56.01
$\overline{PM}$	24	356		0.0614		480	26.19	
PH1	12	295	(36)	0.0516	(0.0130)	319	16.46 7.42 -	(4.15) 25.50
PH2	7	424	(77)	0.1254	(0.0442)	180	22.57 3.74 -	(7.96) 41.40
PH3	7	346	(57)	0.0817	(0.0273)	190	15.52 3.25 -	(5.19) 27.79
$\overline{PH}$	26	355		0.0862		230	18.18	
M1	8	422	(28)	0.1481	(0.0307)	257	38.06 19.87 -	(7.89) 56.25
M2	7	417	(17)	0.1027	(0.0360)	250	25.67 4.39 -	(9.00) 46.96
M3	4	385	(19)	0.1350	(0.0623)	216	29.16 0 -	(13.46) 66.52
$\overline{M}$	19	408		0.1286		241	30.96	

* n - no. of sampled trees per plot
**N - no. of trees per hectare on the plot

APPENDIX 7

Annual Biomass of Litterfall and Nutrient Content of Litterfall

Appendix 7. Annual biomass of litterfall and nutrient content of litterfall (in kg/ha) - PX-plots.

Element	L.C.*	PX1	PX2	PX3	Ø PX plots
		kg/(ha.a)			
N	1	6.25	6.23	7.06	6.51
	2	1.67	1.84	0.89	1.47
	3	1.33	1.66	0.96	1.32
	4	0.19	0.11	0.43	0.24
	SUM	9.43	9.84	9.34	9.54
P	1	0.76	0.90	0.73	0.79
	2	0.17	0.22	0.08	0.16
	3	0.12	0.17	0.09	0.13
	4	0.02	0.01	0.04	0.02
	SUM	1.06	1.29	0.93	1.10
K	1	1.26	1.02	1.10	1.13
	2	0.29	0.36	0.13	0.26
	3	0.14	0.16	0.11	0.14
	4	0.02	0.01	0.02	0.01
	SUM	1.70	1.55	1.35	1.54
Ca	1	10.59	9.27	9.26	9.71
	2	0.95	1.03	0.56	0.84
	3	1.04	1.24	1.29	1.19
	4	0.21	0.12	0.29	0.21
	SUM	12.78	11.65	11.40	11.95
Mg	1	1.12	0.90	0.66	0.89
	2	0.11	0.13	0.05	0.10
	3	0.06	0.08	0.06	0.07
	4	0.01	0.01	0.01	0.01
	SUM	1.29	1.12	0.78	1.06
Biomass	1	1168	1147	1062	1125
	2	249	289	102	213
	3	280	326	250	285
	4	39	20	67	42
	SUM	1737	1781	1480	1666

*L.C.-litter component

1 - foliage
2 - epiphytic lichens
3 - twigs and branches
4 - other litter

Appendix 7 (con't.). Annual biomass of litterfall and nutrient content of litterfall (in kg/ha)-PM-plots

Element	L.C.*	PM1	PM2	PM3	Ø PM plots
		kg/(ha.a)			
N	1	10.93	11.18	12.66	11.59
	2	2.76	2.77	2.74	2.76
	3	2.85	2.35	2.14	2.45
	4	0.30	0.30	0.22	0.28
	SUM	16.85	16.59	17.77	17.07
P	1	1.50	1.55	1.43	1.49
	2	0.31	0.35	0.31	0.32
	3	0.31	0.25	0.25	0.27
	4	0.03	0.03	0.02	0.03
	SUM	2.15	2.18	2.01	2.11
K	1	2.01	2.06	1.74	1.94
	2	0.42	0.54	0.40	0.45
	3	0.29	0.25	0.27	0.27
	4	0.02	0.02	0.02	0.02
	SUM	2.74	2.87	2.43	2.68
Ca	1	12.82	11.42	13.60	12.62
	2	1.16	1.14	1.21	1.17
	3	2.23	1.75	2.39	2.12
	4	0.32	0.60	0.31	0.41
	SUM	16.53	14.91	17.51	16.32
Mg	1	1.54	1.37	0.86	1.26
	2	0.17	0.18	0.15	0.17
	3	0.16	0.13	0.13	0.14
	4	0.01	0.02	0.01	0.02
	SUM	1.88	1.71	1.16	1.58
Biomass	1	1986	1873	1638	1833
	2	357	426	335	373
	3	624	492	523	546
	4	50	75	77	67
	SUM	3017	2866	2572	2819

*L.C.-litter components

1 - foliage
2 - epiphytic lichens
3 - twigs and branches
4 - other litter

Appendix 7 (con't.). Annual biomass of litterfall and nutrient content of litterfall (in kg/ha)

Element	L.C.*	M1	M2	M3	Ø M plots
		kg/(ha.a)			
N	1	13.16	11.36	11.50	12.00
	2	1.74	2.42	2.87	2.35
	3	2.51	2.31	2.95	2.59
	4	0.75	0.31	0.59	0.55
	SUM	18.15	16.40	17.92	17.49
P	1	1.58	1.40	1.32	1.43
	2	0.19	0.28	0.34	0.27
	3	0.26	0.26	0.33	0.28
	4	0.07	0.03	0.06	0.05
	SUM	2.11	1.97	2.05	2.04
K	1	1.56	1.63	1.62	1.60
	2	0.28	0.43	0.46	0.39
	3	0.26	0.23	0.29	0.26
	4	0.06	0.02	0.04	0.04
	SUM	2.16	2.31	2.39	2.29
Ca	1	11.65	9.93	9.96	10.51
	2	0.72	0.89	1.23	0.94
	3	2.92	2.13	2.52	2.52
	4	1.48	0.56	0.99	1.01
	SUM	16.77	13.50	14.70	14.99
Mg	1	0.77	0.72	0.69	0.72
	2	0.09	0.14	0.15	0.13
	3	0.15	0.11	0.16	0.14
	4	0.04	0.02	0.02	0.03
	SUM	1.05	0.99	1.02	1.02
Biomass	1	1524	1435	1402	1454
	2	217	278	320	272
	3	703	458	621	594
	4	198	69	98	122
	SUM	2642	2240	2441	2442

*L.C.-litter components

1 - foliage
2 - epiphytic lichens
3 - twigs and branches
4 - other litter

Appendix 7 (con't.). Annual biomass of litterfall and nutrient content of litterfall (in kg/ha) - PH - plots.

Element	L.C.*	PH1	PH2	PH3	Ø PH plots
		kg/(ha.a)			
N	1	6.78	9.39	9.79	8.65
	2	0.64	1.19	1.14	0.99
	3	1.63	1.83	1.12	1.53
	4	0.26	0.13	0.71	0.37
	SUM	9.31	12.54	12.76	11.54
P	1	0.73	0.76	1.07	0.85
	2	0.06	0.12	0.15	0.11
	3	0.14	0.17	0.13	0.15
	4	0.02	0.01	0.07	0.03
	SUM	0.95	1.06	1.41	1.14
K	1	0.88	1.07	1.14	1.03
	2	0.09	0.14	0.20	0.14
	3	0.15	0.27	0.12	0.18
	4	0.02	0.01	0.04	0.03
	SUM	1.14	1.49	1.50	1.37
Ca	1	8.61	11.03	11.28	10.31
	2	0.42	0.67	0.74	0.61
	3	2.70	2.23	1.30	2.08
	4	0.46	0.22	0.75	0.48
	SUM	12.19	14.15	14.07	13.47
Mg	1	0.65	0.67	0.67	0.66
	2	0.04	0.06	0.06	0.05
	3	0.12	0.11	0.06	0.10
	4	0.02	0.01	0.03	0.02
	SUM	0.82	0.85	0.82	0.83
Biomass	1	893	1207	1221	1107
	2	71	124	141	112
	3	520	405	214	380
	4	51	33	129	71
	SUM	1535	1768	1706	1670

* L.C.-litter components

1 - foliage
2 - epiphytic lichens
3 - twigs and branches
4 - other litter

APPENDIX 8

Quantity of Chemical Elements in Throughfall and Incident Precipitation

Appendix 8. Quantity of throughfall and nutrients in throughfall.

PLOT	SET	NH_4-N	NO_3^--N	Total inorganic N	PO_4-P	SO_4-S	K	Ca	Mg	H_2O**
					kg/ha					t/ha, mm
PX1	1	0.01	0.07	0.08	0.01	2.19	0.55	0.69	0.21	813
	2	-	0.32	-	0.01	8.64	1.13	1.82	0.44	3841
	3	0.02	0.01	0.04	0.00*	3.94	0.56	0.89	0.28	2300
PX2	1	0.22	0.16	0.38	0.14	3.11	1.42	0.68	0.18	909
	2	-	0.29	-	0.03	9.78	0.99	2.05	0.47	3988
	3	0.03	0.17	0.20	0.00	3.25	0.53	0.84	0.25	2476
PX3	1	0.03	0.11	0.14	0.02	2.50	0.70	0.56	0.14	1057
	2	-	0.22	-	0.01	9.89	1.57	1.90	0.33	4640
	3	0.06	0.20	0.26	0.00	3.81	0.92	0.82	0.19	3042
PM1	1	0.07	0.10	0.16	0.06	4.22	1.37	0.88	0.22	1009
	2	-	0.04	-	0.02	11.33	2.88	2.62	0.56	3850
	3	0.00	0.00	0.00	0.02	5.64	2.02	1.19	0.36	2420
PM2	1	0.01	0.06	0.07	0.06	4.88	1.45	1.01	0.23	1212
	2	-	0.03	-	0.05	13.88	3.70	3.31	0.64	4190
	3	0.00	0.00	0.00	0.02	5.98	2.37	1.29	0.33	2663
PM3	1	0.11	0.10	0.21	0.03	3.80	1.44	0.77	0.17	1068
	2	-	0.10	-	0.04	13.16	3.52	2.95	0.52	4720
	3	0.02	0.00	0.02	0.01	4.59	1.94	1.21	0.24	2722
PH1	1	0.01	0.10	0.11	0.03	2.55	0.85	0.58	0.09	1126
	2	-	0.16	-	0.05	7.08	1.74	1.60	0.27	3426
	3	0.07	0.13	0.19	0.00	2.42	1.04	0.78	0.13	2340
PH2	1	0.01	0.12	0.12	0.02	3.32	1.15	0.77	0.15	1249
	2	-	0.06	-	0.04	9.28	2.71	2.22	0.38	4067
	3	0.02	0.06	0.08	0.00	3.45	1.49	0.90	0.20	2471
PH3	1	0.01	0.08	0.09	0.02	2.99	0.84	0.78	0.12	1267
	2	-	0.06	-	0.08	7.48	2.14	1.73	0.30	3280
	3	0.01	0.02	0.03	0.02	2.87	1.58	0.94	0.17	2581
M1	1	0.01	0.07	0.08	0.06	3.82	0.83	1.82	0.16	1654
	2	-	0.07	-	0.06	13.35	3.05	2.82	0.46	5398
	3	0.03	0.04	0.08	0.02	4.09	2.12	1.11	0.21	2080
M2	1	0.03	0.07	0.10	0.05	3.62	0.87	1.98	0.16	1488
	2	-	0.04	-	0.04	13.35	2.97	3.43	0.57	5176
	3	0.01	0.03	0.04	0.02	4.48	2.23	1.06	0.21	2095
M3	1	0.01	0.05	0.07	0.05	3.44	0.83	1.42	0.13	1467
	2	-	0.01	-	0.03	13.02	2.83	3.45	0.55	4874
	3	0.01	0.01	0.01	0.01	3.90	1.77	0.99	0.19	1944

Appendix 8. Quantity of aerial water precipitation and nutrients in precipitation.

PLOT	SET	NH_4-N	NO_3-N	Total inorganic N	PO_4-P	SO_4-S	K	Ca	Mg	H_2O**
					kg/ha					t/ha, mm
PX0	1	0.03	0.23	0.26	0.00	0.75	0.10	0.44	0.14	824
	2	-	1.40	-	0.00	3.76	0.29	2.61	0.62	4478
	3	0.07	0.56	0.63	0.00	1.54	0.14	0.27	0.09	2693
PH0	1	0.04	0.63	0.67	0.00	1.43	0.11	0.88	0.17	2019
	2	-	1.24	-	0.05	2.21	0.40	1.63	0.33	4639
	3	0.21	0.38	0.59	0.05	1.80	0.15	0.78	0.15	2810
M0	1	0.06	0.53	0.58	0.01	1.35	0.43	1.83	0.30	1105
	2	-	1.08	-	0.03	4.24	0.25	1.26	0.27	4360
	3	0.23	0.60	0.84	0.08	1.96	0.23	0.46	0.08	2339

Set 1 - late summer 1974, collection 1-2
11 weeks sampling period.

Set 2 - summer 1975, collections 5-8,
13 weeks sampling period.

Set 3 - summer 1976, collections 10-11,
8 weeks sampling period.

* below detection limit

** 824 t/ha of H_2O = 82.4 mm of precipitation

APPENDIX 9

Location of Sample Plots