NUTRIENT CYCLING IN A DOUGLAS-FIR ECOSYSTEM WITH RESPECT TO AGE AND NUTRIENT STATUS

by

JOHN TURNER

A dissertation submitted in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

UNIVERSITY OF WASHINGTON

1975

Approved by ______________________________
(Chairman of Supervisory Committee)

Department College of Forest Resources
(Departmental Faculty sponsoring candidate)

Date April 1st, 1975

UNIVERSITY OF WASHINGTON

Date: March 13, 1975

We have carefully read the dissertation entitled Nutrient cycling in a Douglas-fir ecosystem with respect to age and nutrient status submitted by John Turner in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

Mr. John Turner has, in this thesis, provided us with a number of important insights into the storage and transfer of nutrients, within forest ecosystems, that have not been previously described in the scientific literature. Specifically, he has been able to demonstrate that the nutrient requirements of Douglas-fir stands reaches a peak at the time of canopy closure and after that decreases. Differences between nutrients were also described in relation to their rates of transfer and patterns of accumulation. He has determined the relative importance of internal cycling of nutrients to a tree as compared to uptake from and return to the soil. He has shown that as the stand reached maturity, a greater part of its nutrient needs are provided by internal redistribution rather than by uptake from the soil. The relative importance of the understory vegetation in the overall cycling of nutrients within a forest ecosystem and how this importance changed with the development and maturity of the forest was also quantified. Further he was able to evaluate the impact of nitrogen stress and nitrogen fertilization on the uptake and redistribution of nutrients by the tree.

To accomplish this detailed examination of the transfer of nutrients and their utilization by Douglas-fir, Mr. Turner had to assess these functions under a wide array of stand ages ranging from 9 to 100 years. In order to assess the stability of cycling associated with the availability of the nitrogen level in the soil, additional plots with carbohydrate and nitrogen fertilizer additions had to be evaluated.

This thesis by Mr. Turner is an original document, defining for the first time the internal and external nutrient cycling patterns of a forest ecosystem as it progresses from a juvenile to a mature state and as it reacts to a change in nutrient availability.

DISSERTATION READING COMMITTEE: Dale W. Cole

Doctoral Dissertation

In presenting this dissertation in partial fulfillment of the requirements for the doctoral degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this dissertation is allowable only for scholarly purposes. Requests for copying or reproduction of this dissertation may be referred to University Microfilms, 300 North Zeeb Road, Ann Arbor, Michegan 48106, to whom the author has granted "the right to reproduce and sell (a) copies of the manuscript in Microform and/or (b) printed copies of the manuscript made from microform."

Signature John Turner

Date April 4th, 1975.

University of Washington

Abstract

NUTRIENT CYCLING IN A DOUGLAS-FIR ECOSYSTEM WITH RESPECT TO AGE AND NUTRIENT STATUS

by John Turner

Chairman of Supervisory Committee: Professor Dale W. Cole
College of Forest Resources

Annual budgets for organic matter, N, P, K, Ca, Mg, and Mn in an age sequence of Douglas-fir (*Pseudotsuga menziessii* (Mirb.) Franco) were determined. The stands were located in and around the A.E. Thompson Research Center in the Cedar River Watershed, Western Washington, an area which has been intensively studied for the past 14 years. The soils are of glacial origin, coarse, gravelly, and classified in the Everett series. The topography is flat to rolling. The most prominent feature of the climate is the summer drought.

Components of the budgets included the tree (foliage, branch, wood, and bark), understory, forest floor, and soil. Transfers of nutrients between these components were also estimated, including tree litter, understory uptake, and tree and understory internal redistribution. The stands involved had ages of 9, 22, 30, 42, 49, 73, and 95 years, and all were selected to be of similar site quality. In the 42-year-old age class, two stands were included, one normally and the other sparsely stocked, to assess the effect of variation in stand density upon nutrient cycling.

These results were then used to determine if steady-state conditions were being approached in the cycling and redistribution of organic matter and nutrients. Foliar biomass levelled out shortly after crown closure at about 9 - 10,000 kg/ha, but the actual time of crown closure was governed by stand density. Nitrogen, P, K, and Mg generally followed the trend of the foliar biomass, but Ca and Mn continued to accumulate in the foliage as the stand increased in age. Components other than the foliage increased with stand age, but these increases were variable.

The humus and total forest floor organic matter (plant litter), accumulated constantly with stand age (the calculated rate of organic matter increase was 540 kg $ha^{-1}yr^{-1}$), as did the N, Ca, and Mn. After 42 years of age, the K, P, and Mg no longer increased significantly in the forest floor. Understory biomass peaked at around 22 years with 7640 kg/ha and thereafter decreased, the lowest biomass (1200 kg/ha) occurring in the 95-year-old stand. The nutrient contents of the understory followed a similar trend to the organic matter, but the rates of change differed because of differential nutrient accumulation by species.

Nutrient and organic matter return to the forest floor became fairly constant, although there was an increase with age in wood content of the litterfall. Typical nutrient returns to the forest floor were 30, 7, 32, 52, 10, and 112 kg $ha^{-1}yr^{-1}$ for N, P, K, Ca, Mg, and Mn respectively. Results were generally higher than previously reported in the literature, because of the inclusion of the understory return in the present study.

Internal redistribution within the trees and understory was assessed in its role of fulfilling nutrient requirements for current growth. In the case of N, the tree was taking almost 100% of requirement in the 9-year-old stand from the soil, whereas the older stand fulfilled 50% of their requirement from internal redistribution. Potassium and P also had part of their growth requirements filled from internal redistribution. Magnesium, Ca, and Mn generally took up much higher quantities than they "required", this excess being accumulated in the older tissue. Further, as the stand increased in age, the amount taken up from the organic matter on the surface of the soil (forest floor) increased, at the expense of that from the mineral soil itself.

Nitrogen fertilizer was applied to alleviate the N deficiency of the stand and application of carbohydrate temporarily aggravated the N deficiency on other plots. The N fertilizer increased N uptake to three times that of the control, and instead of redistribution from, there was accumulation in, the older needles. This reduced leaf litterfall, *i.e.*, caused retention of an extra year's needles. The increased N stress of the carbohydrate treatment caused increased redistribution, *i.e.*, it increased 60% over the control because of reduced uptake from other sources, and thus caused more leaf fall. This was interpreted as indicating the sensitivity of the tree to the supply of nutrients (especially N) from the organic matter on the soil (forest floor), and that the tree has, for some nutrients, an alternative supply, in the form of internal storage, available for use when there is decreased availability in the soil.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I would firstly like to thank the New South Wales Forestry Commission for allowing me this period of time for study, and also for the financial assistance they afforded me. I also thank Dr. S. W. Gentle, of the Forestry Commission, for his initial guidance in this field of work. I also gratefully acknowledge the financial support from the Coniferous Forest Biome (N. S. F. Grant number GB-36810X).

For his guidance in my studies, and for the general insights he provided into the American way of life, I wish to thank the chairman of my supervisory committee, Dr, Dale W. Cole. I also very much appreciate the help and support of the other members of my committee, Drs. S. P. Gessel, D. R. M. Scott, R. B. Walker, and D. McCaughran. I appreciate the association with, and the help received from, my fellow graduate students in my three years of study, especially Jim Long and Dale Johnson.

I wish to thank Anne Hahnel, Carol Smith, Adela Backiel, and Peggy Fahnestock for their assistance in the analysis of my samples, and to Nancy Powell for typing the manuscript.

Most of all, I thank my wife and co-worker, Suzanne, for her assistance, encouragement, and moral support in all stages of this project.

Finally, we both express out thanks to the many people we have met and whose company we have enjoyed during our stay in the United States.

INTRODUCTION

Forest ecosystems are of great importance in the production of organic matter and specific forest products, and in the maintenance of water quantity and quality. They also provide for wildlife habitats and recreational use by man. The primary factors controlling organic matter production and subsequent forest establishment are energy, water, carbon dioxide, and nutrients, but the nutrient supply is the only one of these factors which lends itself to alteration by man on any large scale basis. The supply of nutrient elements to the trees in forests is dependent upon the biological cycling of these nutrients. Thus, an understanding of the utilization of nutrients by forest stands is highly relevant in terms of continued long term intensive management.

This study is concerned with quantifying the cycling of nutrients within the forest stand, the main emphasis being on changes occurring as the stand matures and as nutrient availability alters. The major thrust of this study was to determine the quantities of nutrients within the tree, forest floor, understory, and soil pools, and the transfers between them, in a Douglas-fir ecosystem over the initial 100 years of its development. This was done in order to evaluate the hypotheses that, first, as a Douglas-fir stand develops all the organic matter and nutrient components involved, except stem wood, reach a steady-state level, and secondly, stability is maintained in nutrient accumulation and utilization within the stand after perturbation. Thus, the stand will return to a steady-state situation after it has been subjected to nutrient addition or manipulation, although it may not be the same steady-state level as before.

These studies are limited to a single site quality within the same general area to reduce the influence of natural variability. Within this site class stands were slected covering ages from 9 to 100 years, and data were collected to quantify nutrients in the components and the nutrient transfers. Comparisons were made between stands to determine trends with increasing stand age and assess the data to find whether steady-state existed. Fertilizer was applied to one stand to alter nutrient availability and thus test for stability.

With the increasing public pressure on the use of forests, which require intensive forest management practices, this thesis provides significant information on nutrient utilization by forests during their development.

OBJECTIVES AND DESIGN

The specific objectives of this study were to assess the changes that occur in the accumulation and cycling of nutrients during the development of a Douglas-fir stand of low site quality. The quantity of nutrients contained in the tree, understory, forest floor, and soil components of the ecosystem were measured, together with the amount of nutrients returned from the tree to the forest floor and leached from the forest floor through the soil. The uptake and utilization within the tree were also estimated. This was carried out in stands of various ages representing different stages in the first 100 years in the development of the ecosystem. These data were used to determine whether or not a steady-state condition existed, and thus evaluate the first hypothesis.

To fulfill these objectives, a series of Douglas-fir stands up to 100 years old was selected for study, the main basis of selection being close proximity to each other and similar site quality. Part of the sequence of stands involved a plantation in an effort to reduce natural variability.

In the literature there were considerable data available on forest stand organic matter distribution and changes in this distribution, representing forest stands throughout the world. Nutrient contents were determined in less than 20% of these stands, while even fewer studies estimated organic matter, nutrient distribution, and nutrient transfers other than litterfall, simultaneously. From these few studies it was difficult to make comparisons of ecosystems (e.g., between species or ages) or assess trends, because the studies were carried out on different species, locations, ages, and/or site qualities. Different methods of data collection and presentation further complicated possible comparisons.

In several of the studies the organic matter and nutrient distribution were measured in an age sequence of stands. These indicated that results over a long period of time were predictable and quite consistent so that with care in selection of stands, much variability associated with the results could be removed. The design involved selecting stands between which age was the only variable.

The significant steps in the study are as follows;

A. The age sequence stands.

1. Select and describe stands, (in this case Douglas-fir of low site quality, covering the range of ages from 9 to 100 years, located in the Cedar River Watershed).

2. Estimate quantities of organic matter in these stands, emphasising the trees, understory, and forest floor (i.e., the biological components).

3. Determine the nutrient concentrations of the stand components.

4. From #2 and #3 above, estimate the nutrient content of the stand.

5. Monitor litterfall, throughfall, stemflow, lysimeter plate transfers, and tree growth, together with their relevant nutrient concentrations for at least 1year.

6. From #5 estimate the annual nutrient transfers in the stands.

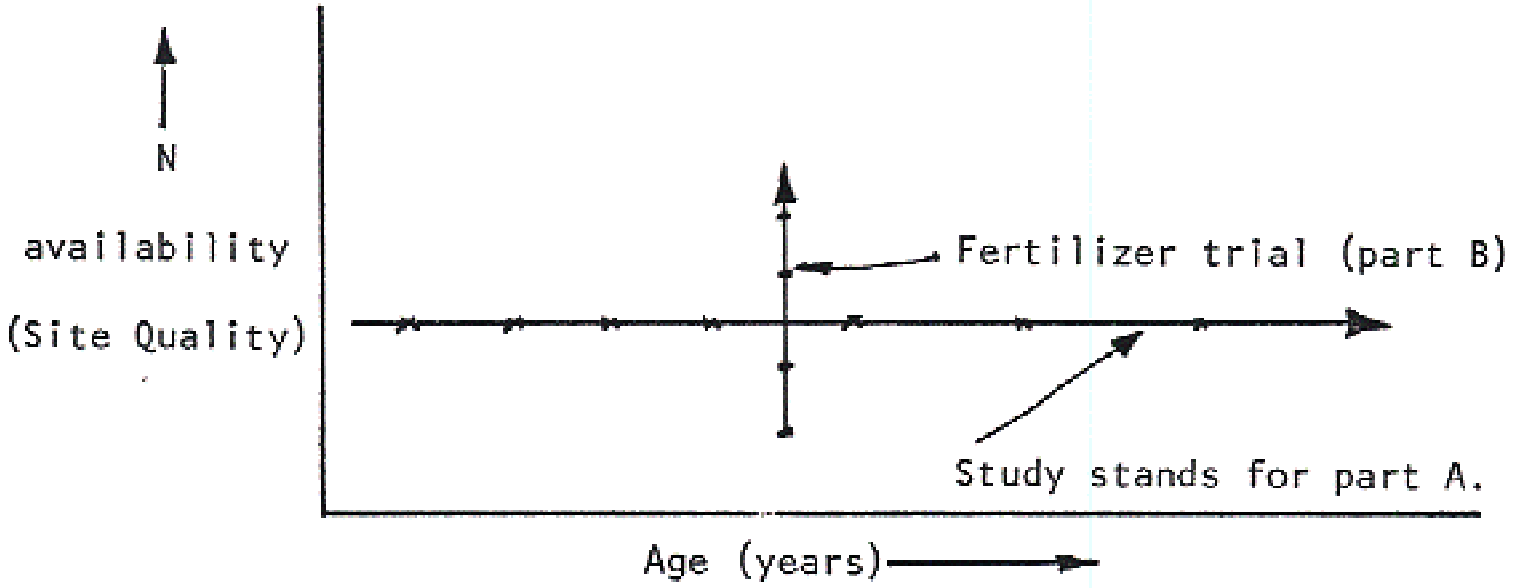
7. Compare stands to determine trends with age and the existence of steady-state in any of the components and/or for any of the nutrients.

B. The fertilizer study.

1. Carry out treatments on the plots in the fertilizer trial and monitor as in section A above.

2. Depending upon the results of #A7 and the treatments applied, draw further conclusions on the stability of the ecosystem in relation to the nutrient supply.

It has been assumed, based on results of past fertilizer experiments, that the low site quality is the result of nitrogen limitation and that fertilizer treatment can alter the N availability. Schematically this could be shown as follows:



LITERATURE REVIEW

1. Historical Background

Trees, in combination with shrubs and non-woody plants, form forest communities which are the most massive and complex in the terrestrial environment. This has led to forest ecologists restricting their research to the features considered of greatest importance, or those that could be most readily studied. Thus, historically, while many of the concepts of nutrient uptake, utlization, and return, and hence the nutrient cycle, were understood, studies were generally limited to measuring individual features as "indicators" of the overall woodland condition (Ovington, 1962). Tansley (1935) introduced the term "ecosystem" to embrace the living organism (and its remains) together with its complex environmental factors in a single unit, but little more was done to quantify forest ecosystems for another two decades. In England, the emphasis was placed on the effects of management upon stand deterioration, so that in the early studies, fundamental understanding arose from practical studies (Wright and Will, 1958). Ecosystem is almost synonymous with the term "biogeocoenose", coined by Sukachev (1944) in Russia. Again, while the concept was present, much of the work was concentrated upon one aspect, that of the soil and soil forming processes (Rodin and Bazilevich, 1967). In Europe and Scandinavia, emphasis was placed upon tree productivity and the organic matter in the system (Burger 1929, 1935, 1945). Thus, while many of the principles of the ecosystem and nutrient cycling were understood, it hasn't been until the last decade that the methods and finances were available for the study of the total system.

2. Definition of Nutrient Cycles

In this study the nutrient cycle was assessed in the form of nutrient budgets. This involved establishing the uptake, utilization, storage, and return of nutrient elements by the plants of the ecosystem (in this case the forest), together with inputs and outputs of the system. The cycle specifically involving the trees and understory has been termed the biological cycle, while the inputs and outputs of the ecosystem constitute the geochemical cycle (Duvigneaud and Denayer-DeSmet, 1970). Much of the large quantity of literature available on the various aspects of nutrient cycling is not directly relatable to other studies, therefore, in the interest of continuity, this review will be of a critical form, selecting only directly applicable studies.

A representation of a nutrient cycle can be presented in various ways depending upon the purpose of, and the detail involved in the study. If the purpose is to define the pools and pathways of the biological cycle, a representation such as that of Curlin (1970) may be used. This representation is shown in Figure 1. This model makes no mention of geochemical inputs and outputs or possible N fixation. The understory compartment was also omitted, but the general trend is obvious. A simplified cycle of Cole *et al.* (1968), showing the gross cycling pattern is drawn in Figure 2a, while 2b shows some current modifications. These modifications indicate patterns of nutrient cycling internal to the plants and distinguishes

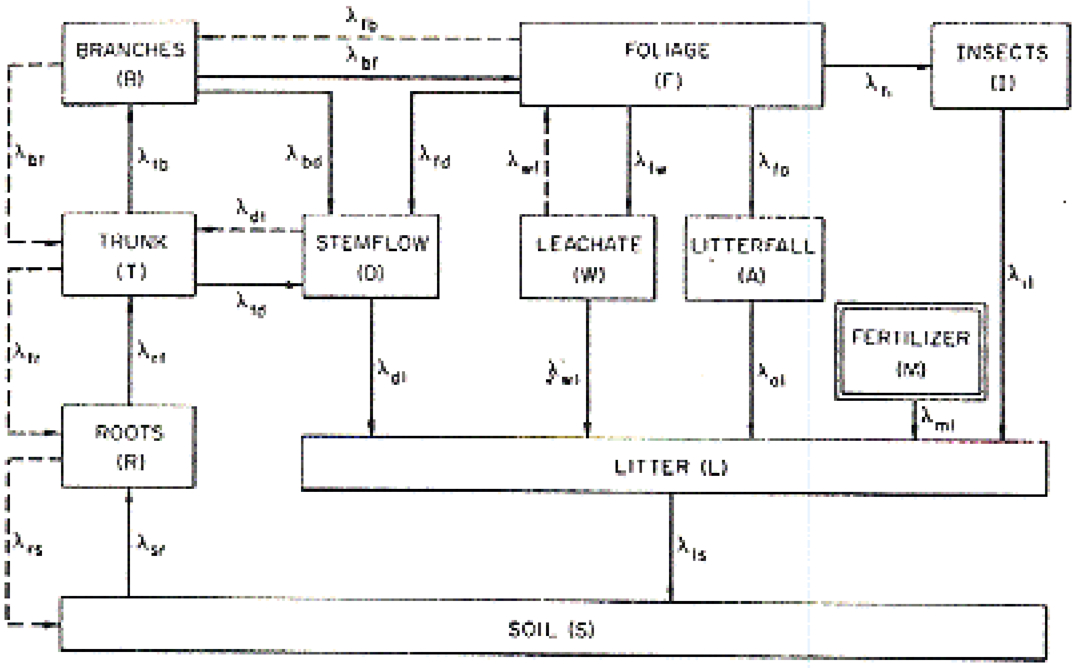


Figure 1. Block diagram of a conceptual model of nutrient cycling in a forest ecosystem: the notation lambda ls, for example, refers to movement from compartment L to compartment S (Curlin, 1966).

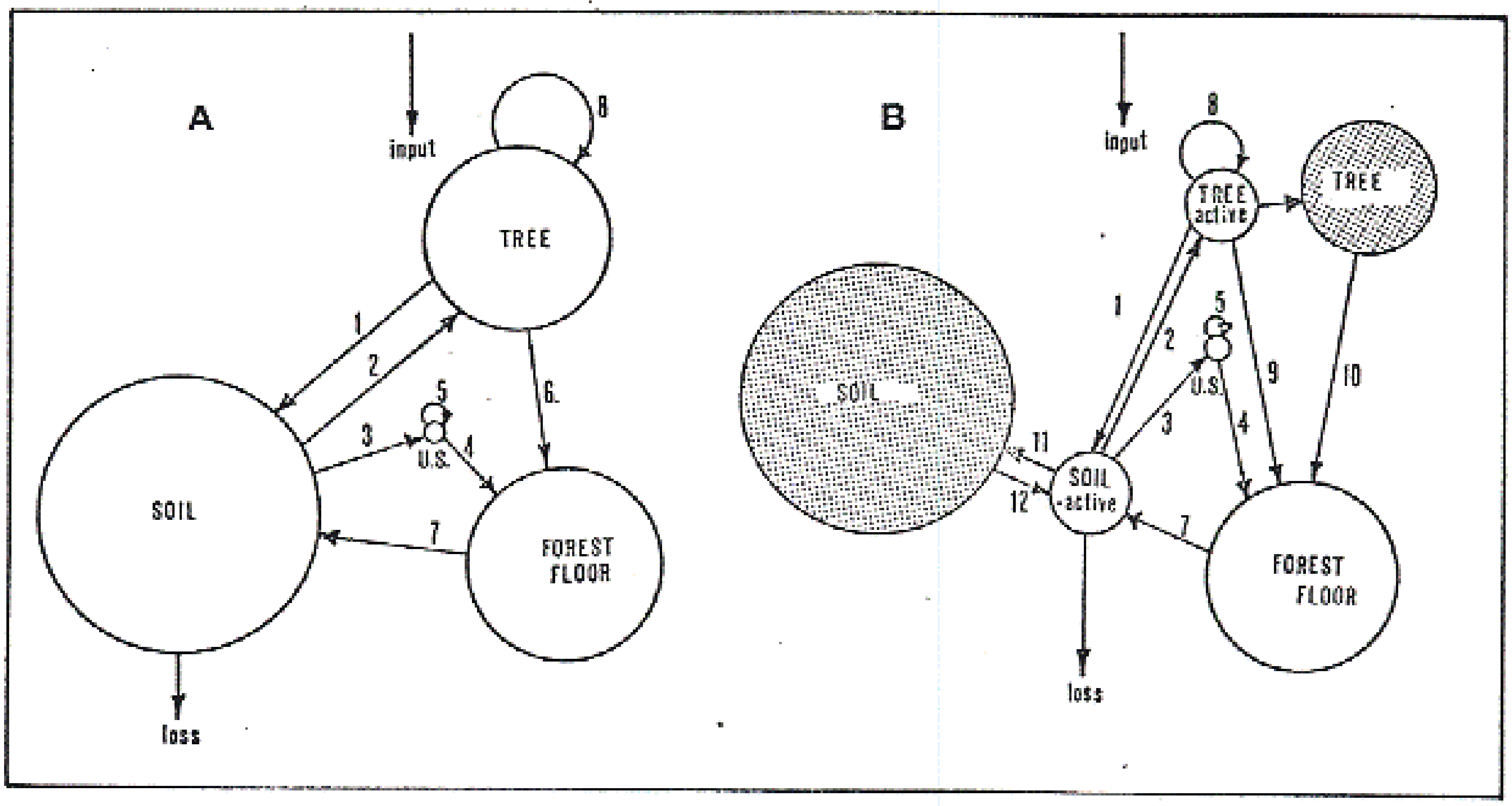


Figure 2. Conceptual models of nutrient cycling in forest ecosystems. A is modified from Cole et al. (1974) and shows total pools and transfers while B subdivides the pools into active (in some time period) and storage (shaded). The transfers are: 1-root loss, 2-tree uptake, 3-understory uptake, 4-understory loss, 5- understory redistribution, 6-return to forest floor (stem, litter, throughfall, stemflow), 7-forest floor loss, 8-tree redistribution, 9-tree return to forest floor (active), 10-tree return to forest floor (storage-mainly stem), 11-soil fixation, 12-soil mineralization.

an active and inactive soil pool. Transfers between active and inactive soil nutrient pools would allow for weathering. Switzer and Nelson's (1972) diagrammatic model places emphasis upon the tree component of the ecosystem, while the representation of Duvigneaud and Denayer-DeSmet (1970) is essentially the same but more artistic.

Cole *et al.* (1973) proposed an alternative approach, shown in Figure 3 which depicts a system centered upon specific processes (in this case the movement of water under gravity). Whereas, in the previous examples the nutrient pools played a dominant role, in this model (Figure 3) the transfers are emphasized. In the first two examples a budget can be established which in turn may be used to estimate pools, transfers, or gross processes which cannot be measured directly. Alternatively, the budget can be used in the comparison of forest ecosystems including the comparisons of pool sizes, the magnitude of transfers, and the effect of some manipulations, *e.g.*, the result of the addition of fertilizer.

In the third case (Figure 3) the objective is to examine the mechanisms involved in nutrient transfer, *e.g.* the process of soil leaching, and the effect on this of management practice (McColl, 1972, 1973 a and b; Cole *et al.*, 1973). In these mechanism studies the time scale is generally small, storm duration as opposed to months or years as is used in the budget studies. By understanding these processes, their application over a wider range of conditions should be possible. The budget and mechanism approach represent two complementary forms of study. Through the budget we can maintain an inventory of the distribution and transfer of material while a study of mechanisms helps explain the direction and amount of transfer and the relative importance of the distribution pattern.

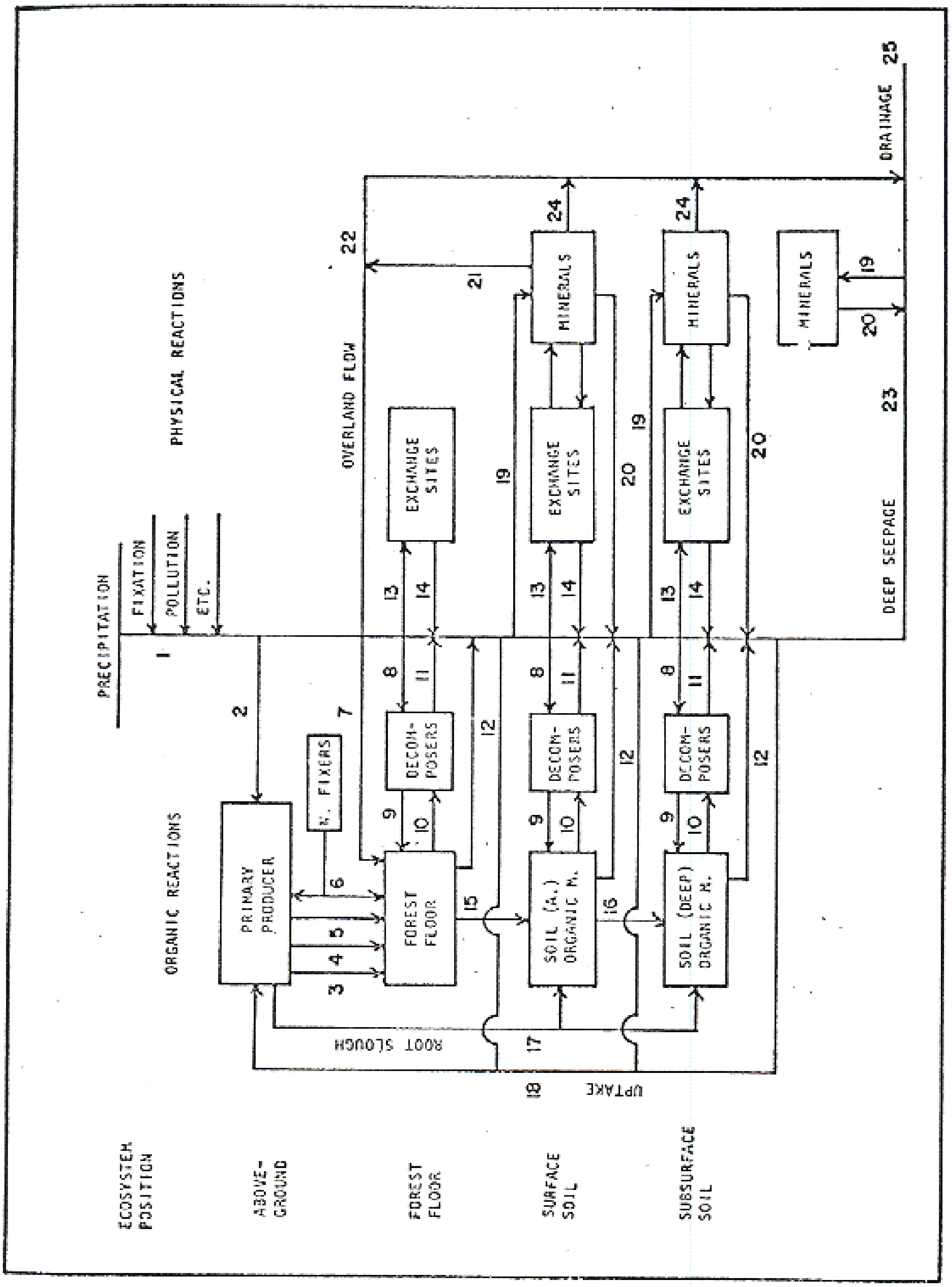


Figure 3. Elemental cycling flow diagram as in Gessel et al. (1973).

Figure 3. Key to the transfers in the elemental cycling flow diagram.

1. Atmospheric inputs, physical (e.g., N-fixation, pollution, fertilization).
2. Ion absorption and/or interception by the aerial portion of the primary producer.
3. Litterfall (dead fall return).
4. Stemflow.
5. Leaf wash.
6. Biological N-fixation.
7. Ion input from the atmosphere.
8. Ion immobilization by decomposers.
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 soil by leaching and organisms.
16. Organic transport within the soil primarily by organic colloidal leaching.
17. Root sloughing.
18. Uptake by primary producer.
19. Ion fixation and precipitation.
20. Mineral weathering.
21. Surface erosion.
22. Overland flow.
23. Deep seepage.
24. Total drainage loss.

The emphasis in this review is on the budget approach to nutrient cycling so reference to Figures 1 and 2 should be of assistance. The specific aim of the review is to show the types of data collected in past studies, what they indicate, and specific deficiencies in the overall data sets. The format will be to discuss the individual nutrient pools, the transfers between these pools, and then their integration into partial or complete cycles. As some of these integrated cycles in the literature (*i.e.*, where most of the pools and transfers have been measured and written up in a comprehensive form) are relevant to this study, they will be briefly mentioned and then detailed in the discussion section. Finally a review of some relevant aspects of forest perturbations, especially fertilizer applications, as a basis for the discussion on ecosystem stability will be given. Methodologies and errors will be discussed where applicable.

3. The Geochemical Cycle

The geochemical cycle, in relation to elemental cycling, involves the nutrient inputs and outputs of a system. This transfer is usually by physical means (*e.g.*, rainfall or leaching) rather than biological. Precipitation and dryfall are usually estimated for inputs and the quantities involved are related to the proximity of the nutrient source. The outputs measured are usually soil erosion and deep leaching. The methods of measurement include the use of a watershed where the outputs are measured in the nutrients contained in the water passing over a weir, closed lysimeters, or open (tension) lysimeters. By comparing the inputs and outputs over some time period, the net loss or accumulation can be estimated.

Table 1. Reported inputs and/or losses of various natural temperate forest ecosystems (kg ha^{-1}yr^{-1}).

Location	N	P	K	Ca	Mg	Na	Reference
New Hampshire, U.S.A., Second growth hardwood							
input	5.7		2.2	2.9	0.9	1.6	Likens *et al.*, 1967
loss	1.8		1.5	6.0	2.2	5.2	Borman *et al.*, 1968
balance	+3.9		+0.7	-3.1	-1.3	-3.6	
New Hampshire, U.S.A., Mature hardwood							
input			1.4	2.6	0.7	1.5	Swank and Elwood, 1971
loss			1.5	10.6	2.5	6.1	
balance			-0.1	-9.0	-1.8	-4.6	
Southeast U.S.A., Second growth hardwood							
input			2.5	3.0	0.7	1.0	Gambell and Fisher, 1966
loss			1.8	8.0	2.6	5.9	
balance			+0.7	-5.0	-1.9	-4.9	
Oak Ridge, U.S.A., Mature hardwood							
input			5.6	41.4	3.8	6.1	Johnson *et al.*, 1969
loss			4.0	100.0	50.5	5.0	
balance			+1.6	-58.6	-46.7	+1.1	
Coweeta, U.S.A.							
Grass							
input			3.0	5.7	1.2	5.1	Johnson and Swank, 1973
loss			6.0	10.4	6.3	10.9	
balance			-3.0	04.7	-5.1	-5.8	
Coppice							
input			3.3	5.8	1.3	5.4	
loss			4.6	5.0	2.7	6.8	
balance			-1.3	+0.8	-1.4	-1.4	
White pine							
input			3.3	6.5	1.3	5.7	
loss			3.6	4.1	1.7	6.1	
balance			-0.3	+2.4	-0.4	-0.4	
Mature hardwood							
input			3.2	6.2	1.3	5.4	
loss			5.2	6.9	3.1	9.7	
balance			-2.0	-0.7	-1.8	-4.3	

Finland, Coniferous				Ca	[illegible]	[illegible]	
input			2.0	2.0	1.0	2.0	Viro, 1953
loss			4.0	12.0	4.0	6.0	
balance			-2.0	-10.0	-3.0	-4.0	
Cedar River, Wa. U.S.A., Coniferous: Douglas-fir							
input	1.1	Tr.	0.8	2.8	0.5		
loss	0.6	Tr.	1.0	4.5	0.9		Cole *et al.*, 1968
balance	+0.5	Tr.	-0.2	-1.7	-0.4		
Andrews Site. Or., U.S.A., Coniferous: Douglas-fir							
input	1.0	0.2	5.0	1.0	1.7		Frederickson, 1972
loss	0:5	1.7	52.0	12.6	29.7		
balance	+0.5	-1.5	-47.0	-11.6	-28.0		
Findley Lake, Wa., U.S.A., Coniferous							
input	1.3	0.4	0.8	0.6	0.1		Turner and Singer, 1974
loss	2.7	0.5	2.1	7.3	1.1		
balance	-1.4	-0.1	-1.3	-6.7	-1.0		
England, Deciduous							
input	8.9	0.3	2.9	7.8	4.8	37.2	Carlisle *et al.*, 1966 Allen *et al.*, 1968
Mediterranean France, Evergreen oak							
input	14.6	0.8	3.8	10.2	1.7	19.1	Rapp, 1971
loss	1.0	0.1	1.3	47.9	5.6	5.1	
balance	+13.6	+0.7	+2.5	-37.7	-3.9	+14.0	
Solling, Germany, hardwood							
input	23.9	0.5	2.0	12.4	1.8		Mayes and Ulrich, 1973
loss	5.8	0.0	2.3	9.5	2.0		
balance	+18.1	+0.5	-0.3	+2.9	-0.2		
New Zealand, Nothofagus							
input			8.0	8.0	11.0	58.0	Miller, 1963
loss			13.0	26.0	13.0	62.0	
balance			-5.0	-18.0	-2.0	-4.0	
New Zealand, Pine							
input		0.3	5.0	3.0		35.6	Will, 1959

In these studies a frequent explicit or implicit assumption, based on their great similarity, is that the outputs and the inputs have some relationship to each other but because of the biological cycle is not adequately considered; this is unfounded. It is doubtful that inputs and outputs are closely related on an annual basis as the physical limitations of movement of nutrients through an ecosystem will cause a lag period. A peak of nutrients in the input, if it does eventually show as a peak on the outputs, may not be noticeable until the following measurement year. Thus there may be apparent deficits one year and accumulations the following year. Further, this may be complicated by the use of an arbitrary twelve month measurement system not relating to the biogeochemical processes of the system.

Table 1 indicates geochemical inputs and outputs for several forest ecosystems. These data indicate that in natural systems the inputs and losses are generally low, and in fact, are insignificant when compared to the magnitude of the total soil pool (Table 2). There are exceptions to this generalization. Inputs are generally low and random except when near some major influence such as the sea supplying large quantities of Na and K (Carlisle *et al.*, 1966; Attiwill, 1966). O'Carroll and McCarthy showed high variation in K input in Ireland dependent upon location in relation to the sea, but over a six year period inputs were consistent for a given location. Ulrich (1973) explains the high input to the Solling research forest (Table 1) as a result of car exhausts. The outputs may be more influenced by the biological system or the geological strata. This effect can be seen in several forest ecosystems which are underlain by bedrock high in Ca (Frederickson, 1972; Johnson *et al.*, 1969; Rapp, 1971).

The effect of the biological system on losses can best be ascertained by manipulative experimentation (e.g., thinning, fertilizer application). Johnson and Swank (1973) studied four different vegetation types (assumed to represent different stages of succession) and concluded that minor differences did exist in nutrient losses (Table 1). Coppenett (1969) compared nutrient losses from cultivated fields and bare ground. He reported losses as 62.2(142), 24.4(46.5), 230(310), and 18(24) kg $ha^{-1}yr^{-1}$ for N, K, Ca, and Mg respectively (bare ground in parentheses), while P remained at 0.7 kg $ha^{-1}yr^{-1}$ for all treatments.

Borman *et al.* (1974) studied losses from a forest ecosystem for three years after vegetation removal and subsequent suppression with biocide. It was not until three years after this drastic treatment that losses became serious indicating high resilience of the ecosystem.

In summary, inputs into the system are generally low and when higher, it is related to some specific source of contamination (such as the ocean, as in the case of N and K). Outputs of forest ecosystems are also generally low except in situations of high natural bedrock weathering. Cultivated land and bare ground have high losses but the recovery period back to vegetative cover and low nutrient losses is usually very short (Johnson and Swank, 1973). The characteristics of a specific nutrient in relation to its additions and losses from a system are important, *e.g.*, P can be immobilized by Fe or Al.

4. The Biological Cycle

(a) Nutrient Storage Compartments

(i) Mineral soil

The soil nutrient content is the "working capital" which will be the major limiting factor in the development of the other nutrient pools. In treating the soil in an ecosystem perspective it must be treated as a dynamic component. To understand it chemical, physical, hydrological, and biological factors must be taken into account. For any of these factors variability will always be of critical importance. This importance is generally accepted, at least implicitly, as most experimentors attempt to account for it in their experimental design.

Variability may occur in the horizontal and/or vertical and/or time dimension. In agriculture Frankland *et al.* (1963) indicated horizontal variability to be of prime importance in sampling for soil nutrient status, whereas Mader (1963) indicated that in forestry the vertical component takes on added importance.

One of the major causes of variability, especially in younger soils, is the parent material variation. Buckman and Brady (1969) state that those soils derived from glacial lake deposits to be one of the most variable. Weathering and biotic activity will tend to obscure parent material differences. Workers such as Hammond *et al.* (1958), Lull and Axley (1958), Aljibury and Evans (1961), and Frankland *et al.* (1963) generally concluded that apparently uniform areas, differences are generally spotted rather than spatial trends (factors such as topographical changes will give definite trends but these are obvious). Metz *et al.* (1966) gave estimates of soil variability for pH, N, P, K, Ca and Mg at three depths. Variability increased with depth, was lowest for pH (C.V.[a] = 2.8), and ranges up to C.V. = P at the lowest depth. Leaf *et al.* (1970) studying a *Pinus resinosa* stand found that although there was great point to point variability, the rooting volume for the trees was sufficient to mask nutrient variability in relation to the trees.

In the Cedar River Watershed, Irby (1967) studied some physical and chemical soil variability in both the Everett and Alderwood series. Point to point variability was high and, using regression analysis, no significant relationship was found between upper and lower horizons for any given variable. The number of samples needed to determine a variable within certain confidence limits were estimated.

Obtaining an estimate of nutrient content in the soil essentially becomes a statistical problem and decisions on sampling have to be made within the context of the study being carried out. Because of the large soil variability involved, methods of examining incremental changes in soil nutrient content by sampling at two different time periods is generally insensitive or impractical because of the potentially large number of samples required.

Soil chemical parameters which are important for nutrient cycling budgets are the nutrient quantities in the soil and the plant available nutrients.

The total soil nutrient quantity is a function of the total soil depth (theoretically to the top of the C-horizon, but in practice to a predetermined depth), its bulk density, and the soil nutrient concentration. More

---

[a] C.V. = coefficient of variation.

important than the total is how much of the nutrient is available to plants, which is a function of the rooting depth, bulk density, unwettable zones, and concentration factors. To decrease sample variability, calculations of nutrient quantities are done as a summation of a series of soil depths. Estimation of rooting depth may be rather arbitrary in that the depth of maximum root concentration is often equated with rooting depth even though roots will penetrate below this level. In addition, rooting depth often varies spacially within a system. Estimates of availability should be relatable to what the plant can obtain from the soil, but in practice an estimate of available cations is made using a solution of pH 7 ammonium acetate. In the long term, plant utilizable nutrients are those which are available plus some contributions from weathering of primary and secondary minerals. Little study has been done on this aspect of nutrient cycling. However, Bowen (1972) in his study of the Cedar River Everett Series A horizon used an acid dissolution technique to determine the release curves and bonding energies of potassium. In general he could relate this to the potassium immediately available, to potassium available in the forseeable future, and to potassium available only over geologic time.

Table 2 lists some soil nutrient quantities (total, hot HCl soluble, and available) in different forest ecosystems (calculated for an area as - area x depth x bulk density x nutrient concentration). It is obvious, when the available nutrient quantities are compared to the total that there is a large proportion, usually greater than 90%, in an unavailable form. This means that there is a potential for a large release from weathering.

Table 2. Nutrient capital of the soil reported for various forest ecosystems of the world (10^3 kg/ha). Figures in parentheses are quantities in available form.

Forest stand and location	Age (yr)	Depth (0- .cm)	N	P	K	Ca	Mg	Reference
Abies amabalis								
Findley Lake, Wa.	175	26, rooting	3.56	1.16	27.98 (0.12)	119.1 (0.08)	50.82 (0.05)	Turner and Singer, 1975
		60, total	15.86	3.21	85.78 (0.24)	180.96 (0.15)	136.84 (0.09)	
Alnus incana, England	22	70, rooting	2.40	(0.19)	(0.12	(8.26)	(0.21)	Ovington, 1962
Betula verrucosa, England	22	70, rooting	1.30	(0.23	(0.13)	(7.11)	(0.16)	Ovington, 1962
Cryptomeria japonica								
Chichibu, Jepan	55	50, rooting[a]	11.16	1.72	16.07			Harada *et al.*, 1972
Amagi, Japan	38	50, rooting[a]	12.40	1.95 (0.01)	2.75			Harada *et al.*, 1972
Hakone, Japan	28	50, rooting[a]	15.01	2.54	2.32			Harada *et al.*, 1972
Pinus elliottii, Japan	8	50, rooting[a]	2.48	0.66 (0.06)	3.76 (0.30)	3.52 (0.25)	1.38 (0.26)	Akai *et al.*, 1970
P. sylvestris, England	47	70, rooting	7.31	(0.11)	(0.25)	(0.44)	(0.30)	Ovington, 1962
P. taeda, Japan	8	50, rooting[a]	2.13	0.81 (0.04)	3.08 (0.27)	2.70 (0.22)	1.06 (0.32)	Akai *et al.*, 1970
P. taeda, Japan	34	50, rooting[a]	3.71	0.16 (0.05)	2.92 (0.2)	0.93 (0.31)	24.26 (0.1)	Akai *et al.*, 1972
		100, total[a]	5.57	0.22 (0.1)	6.70 (0.35)	1.28 (0.40)	54.53 (0.42)	
Pseydotsuga menziessii								
Vancouver Island, B.C.	18	40, rooting	2.04	1.85	(0.08)	(0.7)	(0.04)	Weber, 1973
		56, total	3.37	3.35	(0.13)	(0.96)	(0.07)	
Upper Pack, Wa.	30	30, rooting	1.41		(0.15)			Heilman, 1961
		30+, total	2.14					
Cedar River, Wa.	36	45, rooting	2.44	3.34	(0.20)	(0.66)	(0.10)	Cole *et al.*, 1968
		60, total	2.81	3.88	(0.23)	(0.74)	(0.11)	
Whidbey, Wa.	52	30, rooting	1.05		(0.26)			Heilman, 1961
		30+, total	1.60					
Quercus sp., mixed, Belgium	34	40, rooting	4.48	0.92	26.8 (0.16)	133.0 (13.6)	6.46 (0.15)	Duvigneaud and Denayer-DeSmet, 1970
Quercus ilex, France	150	40, rooting	8.64	3.87 (0.46)	58.62 (1.28)	65.44 (39.91)	24.46 (0.58)	Rapp, 1971
Quercus petrea, England	21	60, rooting	5.10	(0.004)	(0.14)	(0.27)	(0.19)	Ovington, 1962

[a] a hot HCl soluble

The studies of Harada (1972) on *Cryptomeria japonica* ecosystems indicate that the nutrient quantities in the biological portion of a forest ecosystem may be relatively independent of the soil nutrient capital, except when the nutrient is limiting.

(ii) Tree

In the study of the nutrient distribution of the tree component of an ecosystem there are three major aspects to be considered: mass (biomass or phytomass), nutrient concentration, and variability in the estimation of both of these variables. The various methods that have been used in stand biomass estimation have been reviewed by Art and Marks, 1971; Madgwick, 1970; and Olson, 1963.

The mean or modal tree method was the first main approach to tree biomass estimation. In this method a tree of mean stand dimensions was harvested and weighed and stand biomass was then estimated by multiplying this weight by the number of trees per unit area. This method was used extensively in earlier studies, especially in Europe, but it now is used less frequently (Ovington, 1956, 1957). The stands on which this method were used were usually uniform, such as plantations or even regrowth.

A modification of the mean tree approach was to stratify the stand and select a tree of mean dimension for each stratum. The selection of strata was usually on the basis of size class or species and the method was still usually applied to uniform stands. Most European and American researchers have tended to convert to unit area by multiplying by the number of individuals in each strata and then adding together the total number of strata (Forrest and Ovington, 1970; Keay and Turton, 1970; Ovington and Madgwick, 1959; Switzer *et al.*, 1966; Wright and Will, 1958), while the Japanese researchers have generally used the method of basal area allocation using the calculation, $Y = Y'(\frac{G}{G'})$, where Y = biomass per unit area, Y' = tree biomass, G = tree basal area, and G' = total basal area (Ando, 1965; Tadaki *et al.*, 1967 a and b, 1963, 1970; Satoo, 1968).

The main problem associated with biomass estimation using the mean or stratified mean tree technique is the identification of the mean tree. This is usually done by selecting a tree of mean diameter, but such a tree may not be a tree of mean biomass, as shown in Table 3. This selection involves a subjective decision.

Total area cropping in which all trees are removed and weighed on an area is another method of estimation. The main limitation is that the area can be used only once, but this method is valuable for testing or comparing other methods (Baskerville, 1966; Ovington *et al.*, 1967; Satoo, 1967 a and b; Cole *et al.*, 1968).

A regression, relating the tree biomass or a tree component to an easily measurable parameter or parameters such as diameter, height, or basal area is the most generally used technique. Because Kittredge (1944) used logarithmic transformed data in his regressions this was originally called an allometric relation and this terminology has been carried on until the present. This is a misnomer, as, instead of relating one dimension of an organism to another dimension over time as in the true allometric relation, the biomass regressions relate the dimensions of different organisms in space. Logarithimic transformations may also require correction terms because of the biasing in the double transformation (Baskerville, 1972; Madgwick, 1970).

Table 3. Estimates of stand oven dry biomass based on selection of various expressions of the mean tree (kg/ha) from Baskerville, 1965.

Base of estimation	Foliage	Branches	Cones	Stemwood	Stem bark	Total above-ground	Roots	Total tree
1. Total tree estimation	5,029	4,738	188	19,376	2,823	32,154	9,260	41,414
2. Tree of mean height	1,833 (-63.5)	1,962 (-64.3	77 (-59.0)	10,617 (45.2)	1,480 (-47.5)	15,699 (-51.2)	4,861 (-47.5)	20,560 (-50.2)
3. Tree of mean diameter	2,835 (-43.6)	2,622 (-44.6)	119 (-36.7)	14,626 (-24.5)	2,051 (-27.3)	22,553 (-30.8)	6,779 (-26.8)	29,032 (-29.8)
4. Tree of mean basal area	3,816 (-24.1)	3,488 (26.4)	158 (-16.0)	17,993 (-7.1)	2,550 (-9.7)	28,805 (-12.9)	8,357 (-9.8)	36,362 (-12.2)
5. Stand table	4,946 (-1.6)	4,641 (-2.0)	183 (-2.6)	18,894 (-2.5)	2,807 (-0.6)	31,471 (-2.1)	9,532 (+2.9)	41,003 (-1.0)
6. Tree of mean volume	4,392 (-12.7)	4,132 (-12.8)	183 (-2.6)	20,210 (+4.3)	2,878 (+1.9)	31,795 (-1.1)	9,636 (+4.1)	41,431 (+0.1)
7. Average co-dominant tree	7,136 (+42.4)	7,078 (+49.4)	298 (+58.5)	28,780 (+48.5)	4,178 (+48.0)	47,497 (+47.7)	13,772 (+48.7)	61,269 (+47.8)

[1] Values in parentheses are the deviations from estimate 1 expressed as a percentage of estimate 1

The method involves two stages. The first stage is the selection of trees of different sizes, which are measured, cropped and weighed. From these trees regression equations are developed relating a measured parameter to the component of interest. The trees on a plot of known area are measured and the equation applied. Errors may be quite high depending upon how closely the parameter selected for measurement is related to the component of interest. The use of this method has become quite general as the equations can be applied to an area without the need for destructive sampling, thus changes in biomass can be estimated over a period of time.

There is some indication that generalized equations may be developed for species or groups of species thus eliminating for many types of study the tedious process of resampling (Baskerville, 1965).

Table 4 compares the unit area method with the regression technique, and while the individual regression equations may have high standard errors, ranging from 52% for foliage to 15% for bole wood, there is a compensatory effect on a total area basis, so that errors are in practice relatively low. A further comparison is shown in Table 5 between the regression technique, the mean tree method and the stratified mean tree technique.

The biomass of tree leaves has received attention in past studies because of its relation to stand productivity, the large nutrient mass it contains, its effect on the chemical content of incoming water and its effect on other ecosystem components such as understory. Tadaki (1966) indicated that a stable foliar biomass level is generally attained as shown in Figure 4, and this was shown to be true for Douglas-fir (Long and Turner, 1974).

Table 4. A comparison of the unit area biomass estimation technique and the regression method estimate for Douglas-fir (kg/ha, even dry weight), from Dice, 1970.

Component	Unit area	Regression	% Difference
Older foliage	7107	6963	-2.0
Total foliage	9097	7802	-14.2
Total branches	13,886	11,210	-19.3
Dead branches	8145	5753	-29.4
Older bole wood	114,202	124,148	+8.7
Total bole wood	121,687	134,370	+9.4
Bole bark	18,728	18,543	-1.0
Total aerial	171,543	176,148	+2.7
Roots	204,529	204,765	+0.1

Table 5. A comparison of the mean tree, stratified mean tree, and regression (allometric) techniques for biomass estimation (kg/ha, oven dry weight) Ovington and Madgwick, 1959a.

Component	Mean tree	Stratified mean tree	Regression
Leaves	340	370	380
Living branches	630	700	720
Dead branches	430	490	470
Boles	5940	5960	6030
Roots	1470	1630	1640
Total	8390	8890	9020

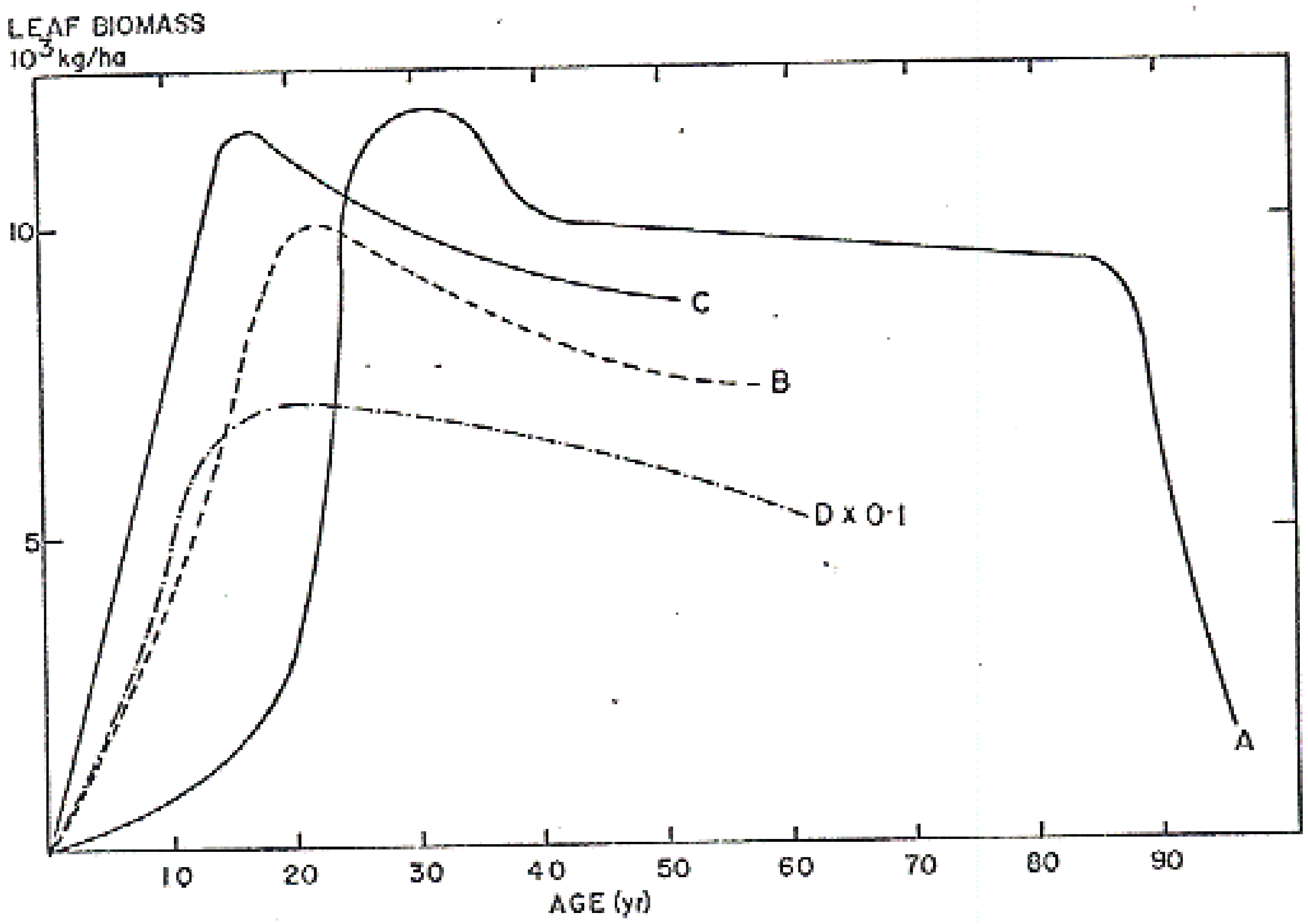


Figure 4. Long term trends of leaf biomass in forests: (A) *Abies veitchii-A. mariesii* forest (oven dry); (B) *Pinus sylvestris* (oven dry); (C) *Pinus densiflora* (fresh weight); (D) *Cryptomeria japonica* (x 0.1, oven dry).

Table 6 shows some estimates of per area biomass for various coniferous species throughout the world. Examples were chosen to display a range of different species, ages, and locations. It should be noticed that, except for *Abies veitchii* and *Tsuga heterophylla* which were selected specifically for their high standing biomass foliar biomass does not rise above 14,000 kg/ha and usually averages approximately 9,000 kg/ha. Another coniferous species not included in this list, *Cryptomeria japonica*, may have foliar biomasses in excess of 20,000 kg/ha (Tadaki and Kawasaki, 1966) but in the case of this species the needles have reverted to bracts and the twigs are the photosynthetic organ. Branch weight, as shown in Table 6, is also fairly uniform and for a given species on a given site there is usually a fairly well defined ratio of foliage to branch biomass.

Fujimori's (1971 a and b) studies on *Tsuga heterophylla* referred to in Table 6, represents an attempt to estimate the maximum productivity and standing biomass for forest ecosystems. This hemlock stand represented one of the highest productivities with the productivity of foliage, branch and wood being 6, 4, and 20 thousand kg ha^{-1}yr^{-1} respectively. The highest estimated accumulations reported by Fujimori (1972) were for Pacific Coast *Sequoia sempivirons* and *Pseudotsuga menzieissi* and Japanese *cryptomeria japonica*.

Table 6. A series of biomass values for coniferous species (10^3kg/ha, oven dry weight).

Species	Country	Age	Foliage	Total crown	Bole wt.	Total aboveground	Reference
Pinus contorta	U.S.A.	100	14.0	37.3	151.0	183.3	Johnstone, 1971
Pinus nigra	U.K.	18	3.1	9.4	17.0	25.3	Wright and Will, 1958
Pinus nigra	U.K.	48	5.5	16.5	93.5	110.0	Wright and Will, 1958
Pinus radiata	Australia	12	9.5	28.2	89.5	117.7	Forrest and Ovington, 1970
Pinus resinosa	U.S.A.	32	11.3	34.4	85.6	120.0	Xydias, 1964
Pinus strobus	Japan	41	10.1	24.2	180.0	204.2	Akai *et al.*, 1971
Pinus sylvestris	U.K.	17	9.0	20.9	16.2	35.4	Ovington, 1957
Pinus sylvestris	U.K.	18	6.1	18.9	35.0	53.9	Wright and Will, 1958
Pinus sylvestris	U.K.	33	7.3	31.0	118.8	149.8	Ovington and Madgwick 1959a
Pinus taeda	Japan	34	9.5	33.5	168.0	226.5	Akai *et al.*, 1972
Pinus taeda	U.S.A.	40	7.70	--	72.7	114.4	Switzer *et al.*, 1966
Pseudotsuga menziessii	U.S.A.	30	8.0	15.6	22.8	38.5	Heilman, 1961
Ps. menziessii	U.S.A.	52	12.0	41.4	174.6	215.7	Heilman, 1961
Ps. menziessii	U.S.A.	75	10.8	27.3	144.5	171.7	Paddock, 1962
Abies balsamea	Canada	40-50	9.1	17.2	51.8	74.0	Baskerville, 1965a
A. sachalinensis	Japan	29	13.4	29.2	48.1	77.3	Yamamoto and Sanada, 1970
A. veitchii	Japan	25	17.6	33.1	107.6	140.7	Tadaki *et al.*, 1970
A. veitchii	Japan	60	18.8	51.1	205.7	256.7	Tadaki *et al.*, 1970
Tsuga heterophylla	U.S.A.	26	21.1	41.8	150.9	192.7	Fujimori, 1971

Having estimated the forest biomass, the next stage is to determine the nutrient concentration of the tissue and hence the nutrient content, *i.e.*, the stand nutrient content = biomass x nutrient concentration = Σ(component biomass x component nutrient concentration). One of the main problems involved is that of sampling to account for the variation of concentration in the tissue of the tree. The major difference to be considered is the nutrient concentration difference between tissue types. Generally the trend shows foliage > bark > twigs > branches > wood, but this may vary slightly, *e.g.*, with twigs higher than bark, according to different nutrients and species. Some typical figures for the various tissues for a poor site Douglas-fir stand are shown in Table 7. Nutrient contents of the components of forests generally follow the trend of the biomass distribution but the differences between tissue nutrient concentrations, amounting to an order of magnitude, is sufficient to alter this trend.

Table 7. Nutrient concentrations (%) for the tissues of naturally regenerated, poor quality Douglas-fir, age 38 years (Heilman, 1961).

Nutrient	Needles	Live Branches	Dead Branches	Bark	Wood
N	0.980	0.255	0.241	0.252	0.050
P	0.346	0.055	0.020	0.042	0.005
K	0.908	0.230	0.033	0.186	0.035

Many studies have been carried out on nutrient variability of foliage and other tissue in an attempt to estimate the optimum time and position to sample for diagnostic purposes (Van den Driesshe, 1969,1973; Evers, 1972; Fortesque, 1973; Gagnon, 1964; Hohne, 1967; Humphreys and Kelly, 1962; Lavender and Carmichael, 1966; Lowry and Avard, 1965; Peterson, 1961; Rapauch *et al.*, 1971). From these and other studies a summary table of the main causes of nutrient variation between samples of a tissue type was constructed and is shown in Table 8.

For any tissue of interest, and needles have been emphasized in past studies, many of the factors in Table 8 will interact and will apparently, or actually, be the same. For non deciduous species, when the seasonal variation is integrated, an estimate of needle age class differences will be obtained. The studies carried out for diagnostic work usually indicated a time during the year, a period of several weeks, together with a postion or positions on the tree where samples could be obtained to achieve the greatest sensitivity. Sampling for nutrient distribution studies may take several months and an estimate of the whole is required so that minor variations, those for those arising from pathogens, diurnal variation, exposure, and genetic variability can probably be ignored. For the budget type study, which is limited to one species in a fairly limited location, the major differences resulting from geographical location, climate, soil, and tree species can be ignored although it is realized that these can have a dramatic effect on nutrient concentrations (Young and Carpenter, 1967; Yamamoto and Sanada, 1970; Harada and Sato, 1966; Harada *et al.*, 1969.

The critical factors that appear to be important for budget type of nutrient cycling study are nutrient differences between years, seasonal differences, tree age, foliage age, crown class, and the position of the

Table 8. Reasons for differences in tissue concentration of forest trees. The references selected for examples are for coniferous species.

---

1. Nutrient variation arising from tree location.
   - i Geographical location (in relation to the coast, altitude, etc.). Turner and Kelly; 1973, Hohne, 1963.
   - ii Variation because of soil differences. Safford and Young, 1968.

2. Nutrient variation arising from time and tree age.
   - i Nutrient variation between years. Humphreys *et al.*, 1971; Turner and Kelly, 1973; Leaf *et al.*, 1970; Miller, 1966.
   - ii Nutrient variation during the year (seasonal). Tamm, 1955; Will, 1957; Lavender and Carmichael, 1966; Miller, 1966.
   - iii Nutrient variation during the day. Khashes, 1972.
   - iv Nutrient variation caused by tree age. Raupach *et al.*, 1969; Askew, 1937; Hohne, 1967.
   - v Nutrient variation caused by foliage age. Beaton *et al.*, 1965 a and b; Will, 1957; Heiberg and White, 1950.

3. Nutrient variation arising from tree physiology and morphology.
   - i Nutrient variation between tree species. Young and Carpenter, 1967.
   - ii Nutrient variation caused by differences in crown classes. Lavender, 1970; Wright and Will, 1958.
   - iii Nutrient variation arising from different positions on the tree. Brackett, 1964; Gagnon, 1964; Hall and Raupach, 1963.
   - iv Nutrient variation arising from branch aspect. Peterson, 1961; White, 1954; Humphreys and Kelly, 1962.
   - v Nutrient variation arising from foliage exposure.
   - vi Nutrient variation arising from the presence of fruits. Brackett, 1964; Gessel, 1962.
   - vii Nutrient variation arising from the presence of pathogens. Rennerfelt and Tamm, 1962.
   - viii Nutrient variation arising from genetic variability. Driessche, 1973.

---

sample on the tree. There are consistent trends involved for many nutrients depending upon the chemical properties and the biological utilization of the nutrient. Mobile nutrients, such as K, will tend to decline as the tissue becomes less physiologically active (*i.e.*, as a result of aging of the tissue, as the position changes further into the crown as a result of growth, or in suppressed trees), while for immobile nutrients such as Ca or Mn the opposite trend is true (Curlin, 1970). The mobile-immobile definitions are as in Epstein (1972). Some nutrients appear to be intermediate (N and P) and so will be retranslocated on some occasions and remain stable or accumulate on others. This may partly arise because of deficiency. From the biomass and nutrient concentration, the nutrient content of the stand can be obtained. An example of a nutrient distribution in a poor quality 20-year-old Douglas-fir stand is shown in Table 9 (Webber, 1973). This data demonstrates how the concentration differential between tissues significantly influences the nutrient distribution pattern. While the foliage represents 14% of the total tree standing biomass, foliar nutrient contents for N, P, K, Ca, and Mg represents at least 50% of the total elemental content, alternatively the wood representing 54% of the biomass contains only 13% of the N, and less than 10% of the total for every other nutrient.

(iii) Forest floor

The forest floor includes all the dead organic matter in the layer over the mineral soil (surface organic matter in Ovington, 1962). The forest floor has been separated into components which generally reflect

Table 9. Biomass and nutrient distribution in a 20-year-old Douglas-fir stand (Webber, 1973).

Component		Biomass	N	P	K	Ca	Mg
Foliage	kg/ha	10,874	163	35	75	153	25
	%	14.2	58.7	64.6	52.6	53.7	60.7
Live	kg/ha	12,995	42	9	30	64	6
Branch	%	16.9	15.3	15.7	20.8	22.3	14.5
Dead	kg/ha	2,485	7	1	1	13	2
Branch	%	3.2	2.4	1.1	0.3	4.4	3.9
Wood	kg/ha	41.725	35	5	9	17	4
	%	54.4	12.7	9.0	6.1	6.1	9.7
Bark	kg/ha	8,652	30	5	29	39	5
	%	11.3	10.9	9.6	20.2	13.5	11.2
Total	kg/ha	76,731	277	55	143	286	40
	%	100	100	100	100	100	100

fairly uniform chemical and phsyical properties. There have been various nomenclature systems for these components (*e.g.*, L, F, H; or Aoo, Ao, 01, 02, etc.),but for nutrient cycling studies it is probably easiest to characterize the forest floor in terms of its wood, litter, and humus composition. The wood can be considered in terms of wood which originated from previous stands, and large and small wood from the existing stand. The litter comprises leaves, needles, and other fine materials which are still recognizable as to source, while the humus is stable, fairly uniform in chemical composition and is unidentifiable as to source.

As many estimates have been made of the quantity of organic matter on the surface of the soil, because of its importance and ease of sampling, examples (Table 10) will be limited to Douglas-fir to reduce the amount of tabular material. These estimates have been arranged so as to indicate some of the variables affecting the weight and nutrient composition, for example, the understory species in the study of Youngberg (1966), age in the study of Heilman (1961), and density in the study of Paddock (1962). As the various understory species may reflect different site qualities, Youngberg's (1966) study may be considered an indirect study of site quality.

Studies on the dynamics of the forest floor have involved comparing the inputs into the forest floor (litterfall) to the actual weight of the forest floor to get a decomposition factor as follows,

$k = \frac{\text{litterfall}}{(\text{forest floor} + \text{litterfall})}$, on the assumption that the forest floor biomass is in steady-state (Jenny *et al.*, 1949; Olson, 1963; Ando, 1970), but this assumption has been questioned (Minderman, 1968).

Table 10. Douglas-fir forest floor weights and nutrient contents (kg/ha oven dry weight).

Stand Description	Biomass		N	P	K	Ca	Mg	Ref.
	total	total-wood						
No understory (dense)		22,932	199	48	63	200	76	Youngberg (1966)
U.S.- Ocean spray -salal		23,905	208	21	31	251	60	
U.S.- Vine maple -salal		24,394	180	34	32	214	77	
U.S.- Salal		29,272	208	40	68	255	60	
U.S.- Salal-sword fern		29,394	300	41	34	246	73	
U.S.- Sword fern		30,736	370	45	36	193	48	
U.S.- Vine maple-sword fern		34,007	364	63	63	306	140	
U.S.- Sword fern-oxalis		66,838	501	78	77	217	132	
U.S.- Salmonberry -sword fern		85,865	1,305	120	170	354	203	
30-year-old, U.S.-salal	61,264	42,011	372	37	57			Heilman (1961)
32-year-old, U.S.-salal	34,933	22,960	183	27	22			
38-year-old, U.S.-salal	62,798	33,920	273	54	52			
38-year-old, U.S.-salal	46,805	23,710	267	32	36			
52-year-old, U.S.-salal	117,219	74,390	657	134	132			
Burnt area, U.S.-salal	17,699		125	18	13			Paddock (1962)
12-year-old sparse U.S.-salal	22,252		168	24	15			
12-year-old, dense U.S.-salal	23,442		165	28	15			
30-year-old, sparse U.S.-salal	13,763		105	16	11			
30-year-old, dense U.S.-salal	23,621		289	32	20			
30-year-old, dense U.S.-salal	24,372	17,582	187	27	34			Balci (1964)
39-year-old, sparse U.S.-salal	12,055		85	22	14			Paddock (1962)
75-year-old, U.S.-salal	23,604		180	33	21			

The weight of the forest floor and the nutrients contained in it have been considered in several studies on the assumption that as the stand develops the forest floor will immobilize more and more nutrients, thus on marginal sites progressive nutrient deficiency can develop, especially N (Tamm *et al.*, 1960; Weetman, 1962; Heilman, 1966; Viro, 1967; Miller, 1966).

In the study by Williams (1972) of spruce plantations in England, significant quantities of N were found to be tied up in the forest floor. Treatments which increased the decomposition rate, *i.e.*, discing, narrowing the C/N ratio from 47, or raising the pH, affected the mineralization rate and made more N available for growth. These results are supported by the study of Adams and Dickson (1973) comparing good and poor spruce stands. In the poor stands 100 kg/ha more N (594 *vs* 493 kg/ha N) was immobilized in the forest floor, an amount considered sufficient to aggrevate the already poor nutrient regime.

(iv) Understory

The importance of the understory in the forest ecosystem depends upon the location, species, age, stocking, and site quality (Baskerville, 1966). Cole *et al.* (1968), Baskerville (1966), Ovington and Madgwick (1959) all showed that the understory generally represents a minor component of the ecosystem (Table 11). Very dense stands have an almost nonexistent understory (Youngberg, 1966).

Table 11. Estimates of understory aboveground biomass and nutrient content in some selected temperate forests (kg/ha oven dry weight).

Stand	biomass	N	P	K	Ca	Mg	Ref.
Douglas-fir	1,010						Cole *et al.*, 1968
Abies amabalis	1,770	16					Turner and Singer,1974
Old growth Douglas-fir							
Large	5.438	25	5	12	31		Grier *et al.*, 1974
Small	3,426	33	2	11	13		
Alnus rubra							
36 years	6,400						Henderson, 197
51 years	7,700						
Fraxinus excelsior	2,400						Madgwick, 1965
Betula alba	2,194						Ovington, 1955
Alnus incana	2,147						
Douglas-fir (6 stands)	70-9,000	2-47	1-7	1-65			Paddock,1962
Douglas-fir (12 stands)	70-11,000	1-60	1-8	1-65			Heilman, 1961

There are two main situations where the understory becomes a very significant component of the stand biomass. The first is in the early stages of stand development. In this situation there will be a rapid growth of the understory and also rapid species changes (Dyrness, 1973) followed by decline in growth and species changes as the overstory develops (Long, 1973). This process may include a succession of understory species (Dyrness, 1973; Long and Turner, 1974).

The second situation is associated with the decline of the overstory and subsequent understory development as a result of the deteriorating overstory (Henderson, 1970). In these situations the understory may consist of two classes of species. One is the usual understory species (ferns, shrubs, annuals, geophytes, etc.), and the second is the tree species which may develop into the new stand. An example of this is the *Alnus incana* stand of Van Cleve *et al.* (1971) in Alaska, which as the stand developed the understory also increased. The stand would eventually become all spruce.

Many understory species may accumulate nutrients in excess of those found in the overstory, so they may play a disproportionate role in the nutrient distribution (Likens and Borman, 1970). If the understory has many tree species there may not be such biasing.

(b) Nutrient Transfers

The nutrient transfers that have attracted most interest are litterfall, throughfall, and stemflow together with a few studies on forest floor losses. Uptake has been studied in a variety of ways usually with doubtful success and these will be discussed below.

(i) Tree litter production

Many studies have been carried out on the litter production by forest stands (Bray and Gorham, 1964). Organic matter and nutrient return by litterfall has been considered important in relation to stand productivity and also as a measure of stand nutrient uptake by assuming equilibrium between uptake and return. Some estimates of organic matter return to the forest floor in Douglas-fir forests are summarized in Table 12. Needle litter, typically between 2000 and 3000 kg/ha/yr, represents about 70% of the total litter production. Few estimates of large wood (stems) return have been made so this is not included in the table. Large branch production increases with the age of the stand possibly due to its deterioration. Foliar mass of the stand divided by the average time of needle retention results in a gross estimate of the average annual foliar mass. This value is approximately equal to the needle litter production indicating that the needle litter is approximately equivalent to a discrete year's foliage. There are flaws in this approach as indicated by the foliar distribution patterns of Silver (1962) and Smith (1972) but it is the best estimate of this type available covering a range of forest conditions.

The data of Table 12 indicate that leaf litter tends towards a constant level of production and is probably related to the steady-state reached in foliar biomass (Figures 5 and 6).

Table 12. Summary of annual mean litter production by Douglas-fir in the Pacific Northwest (kg $ha^{-1}yr^{-1}$ oven dry weight)

Stand age[a] (yr)	Length of study (yr)	Location	Total litter	Range	Needle litter	Ref
30	1	Cedar River	2,110	-	-	1
30	1	Pack Forest	2,110	-	1,300	
30	8	Pack Forest	1,450	300-3,610	1,120	3
32	1	Darrington	1,300	-	960	2
36	9	Pack Forest	2,320	1,590-2,950	1,830*	3
37	4	Pack Forest	1,540	1,300-1,690	1,010	3
38	1	Pack Forest	2,580	-	2,130	2
38	1	Matlock	2,440	-	1,800	2
38	6	Voight Creek	1,764	1,110-3,550	-	2
39	3	Cedar River	3,112	2,828,3780	2,600	5
40	9	Pack Forest	3,590	1,540-6,600	2,690*	3
40	4	Pack Forest	2,140	1,890-2,510	1,550	3
50	9	Lee Forest	2,900	1,980-4,890	2,260	3
50	8	Pack Forest	2,591	1,827-3,680	1,900	3
52	1	Whidbey	2,465	-	1,800	2
160	8	Pack Forest	3,200**			
			(3,620)	1,900-5,720	2,880	2
450	1	Andrews, Or.	6,138		2,002	6

* mean needle litter estimate

** adjusted for a very large branch

[1] Rahman, 1964.

[2] Heilman and Gessel, 1963.

[3] S.P. Gessel, unpublished data.

[4] Dimock, 1958.

[5] D.W. Cole, unpublished data.

[6] Abee and Lavender, 1972.

Table 13 shows some typical quantities of nutrients returned to the forest floor by litter assuming no leaching in the litter traps. These data indicate considerable variability in the nutrient return. This high variability may be a result of leaching losses especially in the case of potassium which is very mobile in the ecosystem.

Table 13. Annual nutrient quantities returned to the forest floor in litterfall by Pacific Northwest Douglas-fir stands (kg/ha).

Age (yr)	N	P	K	Ca	Mg	Reference
30	11	2	3			Heilman, 1961
32	8	1	2			Heilman, 1961
38	14	4	5			Heilman, 1961
38	15	3	3			Heilman, 1961
52	11	5	6			Heilman, 1961
40	19	1	2	47	5	Gessel and Turner, 1975
450	22	4	6	71	1	Abee and Lavender, 1972

(ii) Understory litter production

Understory litter production may be significant in stands where the understory itself represents a significant proportion of the stand biomass, for example, stands in early or late stages of development. The presence of annuals, deciduous species, geophytes, and ferns in the understory may return a disproportionate amount of litter in relation to biomass of the understory and tree.

As previously mentioned, the understory species can accumulate greater nutrient levels relative to the overstory (Gerloff *et. al.*, 1966; Likens and Borman, 1970) and this will be reflected in the nutrient return to the forest floor, thus the understory may play a biased role in the return or nutrients, especially for trace elements (Scott, 1954).

(iii) Throughfall and stemflow

Throughfall (crownwash) is that solution which has passed through the stand canopy of the stand and hence its nutrient content is a sum of input by precipitation, plus nutrients leached from the canopy (leaves and twigs) and/or by the removal of dust and tree organic matter from the surface. Loss from the solution may occur by foliar re-absorption (Rapp, 1970). Stemflow is the solution channelled down from the branches to the stem and then flows down the bole of the tree. The nutrient content of stemflow then is partially a result of precipitation, crown wash, and the washing of the tree trunk. The net quantity of nutrients reaching the forest floor in solution is the sum of the throughfall plus stem flow, while the net quantity removed from the tree surface (off the surface or from within), is the throughfall plus stemflow minus the precipitation.

Abee and Lavender (1972) reported leaf wash from an old growth coniferous stand in Oregon and the results were, with input by precipitation in parentheses, 2.1(1.3), 2.5(0.2), 21.6(0.1), 2.3(2.1) and 0.9(1.3) kg ha^{-1}yr^{-1} for N, P, K, Ca, Mg, and Mn respectively. Stemflow represented 5 - 30% of these figures depending upon the nutrient. Rapp (1971) indicated that some of the nitrogen introduced in rainfall was absorbed by the foliage so that there was a net loss of 0.7 kg ha^{-1}yr^{-1} in the throughfall.

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 and bacause of the higher concentration of organic compounds in the solution it appears to have a greater impact on soil nutrient leaching (Gersper and Holwaychuck, 1971). By passing down the tree trunk the stemflow solution may bypass the forest floor and be channelled directly to tree roots (Reyonolds, 1966), thus causing the roots to be absorbing from a higher concentration soil solution than generally assumed.

(iv) Total return to the forest floor

The total return to the forest floor is the sum of the inputs from throughfall, stemflow, and litterfall. This division has been made in the past on the basis of sampling procedure, but in terms of obtaining a better understanding of the system the nutrients should be sorted into a spectrum related to their size or form of return. Results from two different stands will illustrate this concept. One is a 30-year-old Douglas-fir stand studied by Rahman (1964) and the other is a 450-year-old stand of Abee and Lavender (1972). These results are shown in Figure 5.

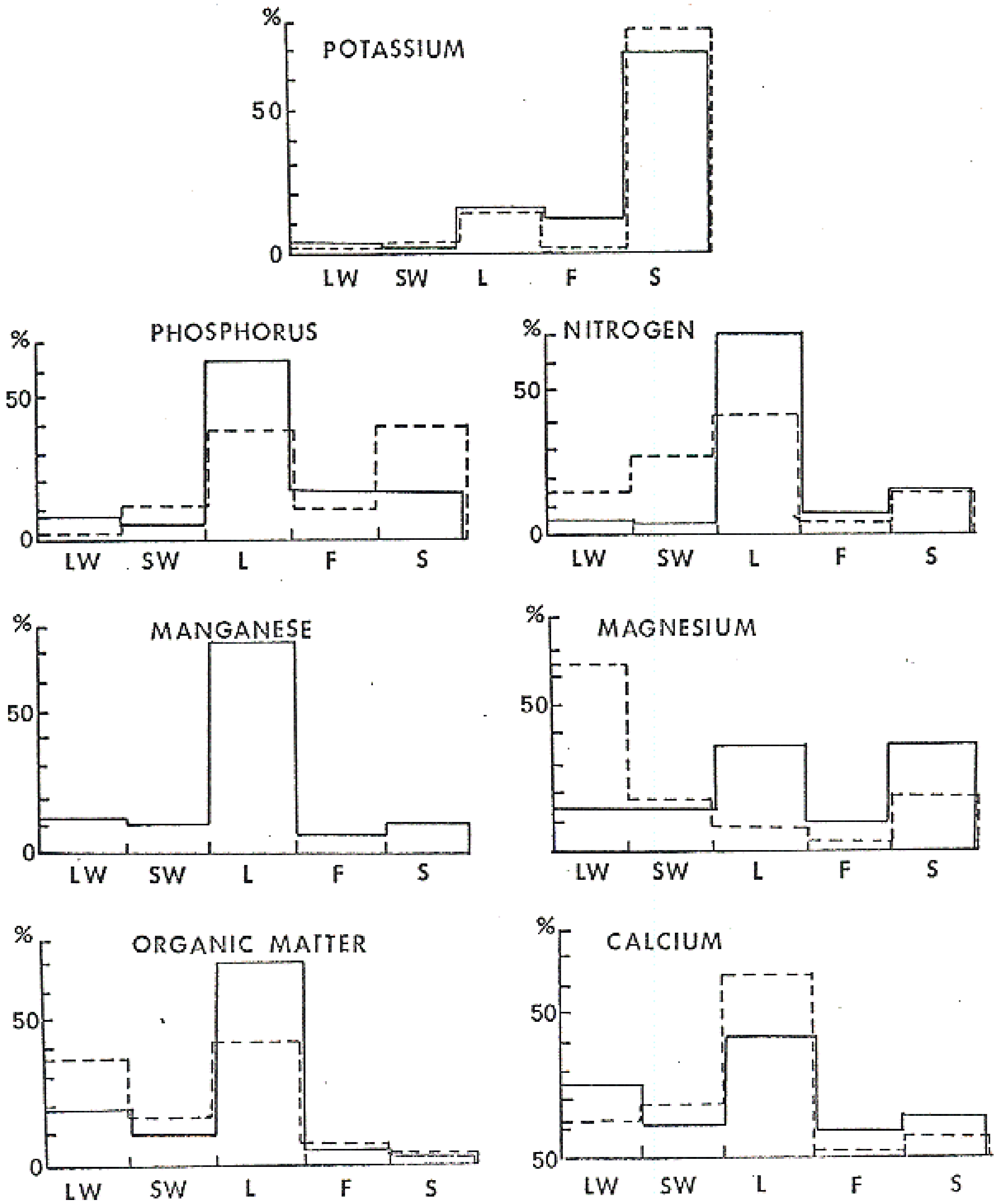


Figure 5. The proportion of potassium, phosphorus, nitrogen, manganese, magnesium, organic matter, and calcium returned to the forest floor by the large wood (LW), small wood (SW), leaf(L), fine material (F), and the solution (S). The solid line represents data from the 36-year-old stand, and the broken line is the 450-year-old stand.

The divisions made in this case were large wood, small wood, needles, fine materials, and solution. These categories can undoubtably be improved but they will be sufficient for illustration. Generally the various nutrients follow similar trends in both stands with some exceptions. What these diagrams illustrate is the carriers for the various nutrients. Carbon (organic matter) has a high proportion transported in the woody components whereas most other nutrients are transported in the needles or fine material. Potassium, a very mobile nutrient, is almost independent of organic matter being almost entirely dependent upon the hydrological cycle.

In a study on the total return to the forest floor by Corsican Pine treated with different levels of fertilizer, H.G. Miller (pers. commun.) gave figures of 39, 3, 23, 26, and 11 kg $ha^{-1}yr^{-1}$ for N, P, K, Ca, and Mg respectively. These were averaged over the treatments.

These categories also have importance in relation to nutrient availability for plants. Nutrients in the fine material or solution form would not require very much microbial decompostion to transform them to the available form. Thus potassium is mainly in the available form. Large wood components will take a considerable period of time to undergo microbial decomposition and thus release the nutrients, while small wood and needles will be intermediate.

(v) Plant uptake

Many problems have been associated with the study of nutrient uptake into trees. One of these has been the definition of uptake, which in this review is the quantity of nutrients taken from the soil and translocated into the tree (Switzer and Nelson, 1972; Mead, 1971). Uptake measurements have been attempted in several ways, one method being that of Switzer and Nelson (1972). This study involved estimating nutrients accumulated in the current tissue, the quantity leached and the proportion contributed by redistribution. The remainder is assumed to be uptake. H.G. Miller (pers. commun.), using similar methods as the present study, gave uptake figures of 17-181, 4-9, 11-33, for N, P and K respectively in Corsican pine. These are typical uptake estimates for forest stands. This range is a result of increasing quantities of applied N fertilizer.

In the past the term uptake has been applied to parameters which are actually estimates of mean accumulation or loss. For example, the crudest method used was that of Rennie (1955) who estimated the quantity of nutrients in the standing crop and divided this by the age, thus obtaining a mean accumulation rate. Ovington (1962) estimated the standing crop at two different ages, took the difference, divided by the number of years and then added the litter loss. This gave a mean accumulation rate which was probably nearer to uptake than Rennie (1955), but still ignored throughfall and redistribution. Rodin and Bazilevich (1967) assumed steady-state existed and therefore the uptake equalled the losses. The losses from the tree were assumed to be entirely by way of litter. This again ignored throughfall, redistribution and annual accumulation.

Various attempts have been made to estimate temperate forest uptake by using isotopes (Riekerk, 1967; Mead, 1971), but with limited success.

(c) Integrated Nutrient Cycles

While the data gathered on the individual ecosystem components and transfers are important, of more importance is the total nutrient cycle. By study of integrated cycle the relationship between the various components can be ascertained. Further, by comparing the cycles of different ecosystems, relationships can be developed and the cycles checked for inconsistencies (*e.g.*, very high losses, etc.). Very few complete forest nutrient cycles have been published, but based on some of those available, summaries of the organic matter and nitrogen cycles are given in Table 14. Most of the stands listed are of low site quality. It is interesting to note how consistent many of the results are, the main difference in the cases of the N cycles being that *Alnus rubra* is a nitrogen fixing species. By comparing the red alder (36 years old) and the 36-year-old Douglas-fir stand, the effect of the nitrogen fixation can be readily seen, especially considering the standing biomasses are very similar. The red alder and the old growth Douglas-fir stands both have relatively high understory biomasses. In both cases it is because of the decline of the overstory but for red alder the understory development is fern, while for the Douglas-fir it is an ingrowth of tree species. When analyzing the nutrient cycle of a forest, the species, quality and stand structure are important as is the role of succession.

Zinke (1969) while not having all ecosystem cycling components, has been attempting to explain differences in nutrient cycles of forest ecosystems. In Ponderosa pine he found a three fold increase of N content

Table 14. Summary of total organic matter and nitrogen cycles of selected forest ecosystems. Distribution in kg/ha and nutrient transfers in kg $ha^{-1}yr^{-1}$. Root turnover and weathering not included.

Component	Douglas-fir[1] 36 years		Douglas-fir[2] 450 years		*Abies amabalis*[3] 175 years		*Quercus ilex*[4] 150 years		*Alnus rubra*[5] 36 years	
	O.M.	N	O.M.	N	O.M.	N	O.M.	N	O.M.	N
Distribution										
Tree foliage	9,097	102	8,906	75	17,600[a]	189	7,000	93	4,056	100
branch	22,031	61	48,543	49	17,710	18	27,000	153	19,376	20
wood	121,687	77	(472,593	189	392,720	141	(235,000	517	127,584	128
bark	18,728	48			38,710	13			23,549	165
root	32,986	32	74,328	62			55,000	155	35,230	176
total	204,529	320	604,370	375			324,000	918	209,438	589
Understory	1,010	7	10,264[b]	60[b]	1,770	16	-	-	9,526	102
Forest Floor										
wood	6,345	14	55,200	132	10,000	79	4,182	29	20,713	166
litter	4,428	40	(43,350	(434	13,010	174	7,990	85	24,415	350
humus	11,999	121			30,510	397	4,936	12	21,216	361
total	22,772	175	98,750	566	53,520	650	13,311	125	66,344	376
Soil rooting	103,597	2,438			205,200	3,555	180,150	8,640	138,360	5,348
total	111,552	2,809	79,250	4,300	243,960	15,855			158,507	5,447
Nutrient Transfers										
Geochemical Cycle										
input		1.1		1.3		1.3		14.7		1.0
output		0.6		1.0		2.7		1.0		5.6

Biological Cycle										
crown leachate		1.5		2.0		1.3		14.9		2.8
stem flow		0.2		-		-		1.2		0.2
total litter	2,000	13.6	6,138	30.7	3,100	16.3	?	32.8	4,056	94.2
total return		16.4		34.0		18.9		63.6		97.2
loss from										
forest floor		4.8	-	-	-	10.3	-	1.4		?
uptake		21.3				11.9		13.2		97.6
redistribution		17.8				12.4		-		77.7

---

[1] 36-year-old Douglas-fir stand studied by Cole et al. (1968), growing at Cedar River, Wa. precip. approx. 140 cm.

[2] 450-year-old Douglas-fir stand studied by Grier *et al.* (1974) growing at the Andrews Site, Or., precip. approx. 240 cm.

[3] 175-year-old *Abies amabalis* stand studied by Turner and Singer (1975), growing at Findley Lake, Wa., precip. approx. 270 cm.

[4] 150-year-old *Quercus ilex* stand studied by Rapp (1971), growing in Mediterranean France, the precipitation is 120 cm.

[5] 36-year-old *Alnus rubra* stand studied by Turner (pers. files) growing at Cedar River, Wa., precip. approx. 140 cm.

[a] includes lichen

[b] understory includes trees up to 15 cm.

[c] includes understory

(kg/ha) of the system when the rainfall increased from 37 to 135 cm. Differences in available nutrients from parent material were dramatic (two fold) but whether there was a change depended upon the parent materials and the species under study.

5. Manipulation of Forest Stands

Of the manipulations carried out in forest stands, such as addition of fertilizers, thinning or clearcutting, fertilization is the main treatment of interest in this study. Forest fertilization has become a general practice in many areas because of the increased wood production obtained (Gessel *et al.*, 1965; Gentle and Humphreys, 1967; Baule and Fricker, 1970; Bengtson, 1968). The studies have mainly concentrated upon the production of utilizeable wood and response measurement, rather than the ecological or nutrient cycling consequences.

Many fertilizer studies have indicated an increased concentration of a nutrient or nutrients in tissue (usually needles), (Heilman, 1961; Raupach *et al.*, 1969; T.V.A., 1968; Gessel *et al.*, 1965; Baule and Fricker, 1970), but as this is the monitoring of only one aspect of the stand components, it tells very little about the total ecosystem.

Heilman (1961) studied the effect of multiple N additions on five low site quality Douglas-fir stands, representing different age classes and provenances. Results of N additions were an increased biomass and tree N, P and K content, with the forest floor weight remaining constant or slightly decreasing. To obtain an increase in wood production, *i.e.*, a response, there has to be an increase in foliar biomass and/or an increase in needle efficiency. While both of these appear to be involved in this study, if either of these features occur it does not necessarily imply that a growth response will be obtained. The only transfer measured in Heilman's (1961) study was litterfall, and for this there was an increase. By comparing leaf litterfall to the standing foliar biomass, on the assumption that the leaf litter is equivalent to a discrete year's foliar production, there was apparently an increase on both leaf production and the length of time of needle retention (Table 15).

Table 15. Comparison of needle litter and foliage weight of Douglas-fir in the fertilizer trial of Heilman (1961).

Location and Description	Foliage biomass (kg/ha)	% increase	Leaf litter (kg/ha)	% increase	n*	wood** response %
Upper Pack, 30 years						
unfertilized	8,019	64	1,298	32	5.2	+45
fertilized	13,149		1,707		6.7	
Darrington, 32 years						
unfertilized	5,309	81	958	35	4.5	+79
fertilized	9,610		1,467		5.6	
Lower Pack, 38 years						
unfertilized	7,997	77	2,128	20	2.8	+24
fertilized	14,168		2,546		4.6	
Matlock, 38 years						
unfertilized	8,982	80	1,802	34	4.0	-20
fertilized	16,152		2,149		5.7	
Whidbey, 52 years						
unfertilized	11,950	16	1,482	42	7.1	-30
fertilized	13,854		2,101		5.6	

* n = number of years of needle retention = $\left(\frac{\text{foliage biomass}}{\text{needle litter}} - 1\right)$.

** wood response = wood biomass of fertilized plot divided by wood biomass of the control. More correctly it should be based upon the wood increment since fertilization but these figures were not available.

In some studies on fertilization effects, litterfall decreased immediately after treatment, as a result of increased needle retention by the tree. Thus, Miller (1966), studying Corsican pine in Scotland, found that a year after N application, litterfall decreased in proportion to the N added, as shown in Table 16. Leaf litter included wood, so removing this may have an even more obvious effect on leaf litter, *i.e.*, if 30% (820 kg/ha) of the control level litterfall is wood content, and this quantity is assumed constant in all treatments, then the high N treatment will have produced about 50% of the control level. Similarly, in a study on Yezo spruce, Shiozaki and Nagaoke (1971) found decreased leaf litter immediately after fertilization, followed by an increase 5 years later, at this stage paralleling Heilman's results. They also found a 20% decrease in the total forest floor weight as a result of increased decomposition, especially in the humus layer where there was a 50% weight loss.

Table 16. The effect of the addition of N-fertilizer on litter production and returned N in Corsican Pine, one year after treatment (Miller, 1966).

N added (kg/ha)	Litterfall (kg/ha)	% of control	N returned (kg/ha)	% of control
0	2,740	100	11.8	100
84	2,180	80	10.2	86
168	2,030	74	9.3	79
336	2,060	75	9.5	81
504	1,940	71	9.2	78

This forest floor weight loss noted by Shiozaki and Nagaoke (1971) can be caused by any disturbance or treatment that will increase microbial activity such as the narrowing of the C/N ratio, improved aeration, or improved pH condtions. This loss in forest floor weight will be accompanied by nutrient release which become available for tree growth. Conversely widening of the C/N ratio or a more adverse pH or aeration may cause further accumulation within the forest floor.

Crane (1972) studies the movement and loss of urea in a forest soil with and without irrigation, using tension lysimeter plates. His results indicated that very little nitrogen was lost from the system by leaching, supporting the previous results of Cole and Gessel (1965). Soil reactions, especially the mobilization of chelating agents, caused the loss from the upper soil horizons of other nutrients, for example Fe and Mn. Kelly (1973), also using tension lysimeters, studied nutrient losses of P and N after fertilization of the forest floor. Again there appeared to be little loss from the system.

SITE AND METHODS

General Description

The forest stands used for intensive study were located in and around the University of Washington's Allen E. Thompson Research Center in the City of Seattle's Cedar River Watershed, 35 miles southeast of Seattle. This site has been used for nutrient cycling and process studies since 1960, hence information is available over a considerable time span.

The climate, geology, soils, and vegetation of the site used for initial studies were described originally by Cole and Gessel (1968). In summary, the Research Center was located in a plantation of Douglas-fir (*Pseydotsuga menziessii* (Mirb.) Franco) established in 1931, at 6x8 ft. spacing, following a series of wildfires in the 10-20 year period after logging of the original forest between 1910 and 1920. Details of this stand are shown, together with those of other stands used in this study, in Table 17. The principal understory species were salal (*Gaultheria shallon* Pursh.), Oregon grape (*Berberis nervosa* (Pursh.) Nutt.), bracken fern (*Pteridium aquilinum* (l) Kuhn var. *pubescens* Underw.), red huckleberry (*Vaccinium parvifolium* Smith) and a scattering of twin flower (*Linnea borealis* L. var. *americana* (Forbes) Redher). There are several species of mosses, the predominant species being *Eurynchium oreganum* (Sull.) Jaeg. The species authority used was Hitchcock and Conquist (1973).

The climate is typical of the western foothills of the Cascades at an elevation of 210 meters. Climatic data gathered at Landsberg, approximately two miles from the site, is shown in Table 18 for the years 1973 and 1974. The soil is Everett series developed from glacial outwash terraces, formed during the recessional stage of the Fraser glaciation about 12,000 years ago. The Everett series belongs to the Brown Podzolic Group and is classified as a typical Haplorthod, coarse loamy over sandy, skeletal mixed mesic (Schlichte, 1968).

To monitor nutrient cycling on an age sequence of Douglas-fir stands, the area in and around the A.E. Thompson site was surveyed (making use of previous studies (Long, 1973)) for vegetation types and ages. A map of the area locating the various study sites is shown in Figure 6. Criteria for selection of a plot included close proximity to an access road and preferably to other plots to enable easier servicing and sample collection.

Four stands were selected for intensive study of systems in which no treatments had been applied, with three other stands available for less intensive data collection. Within a stand, a plot site was selected for its uniformity of stocking, how typical it was of the area, absence of disease or other factors causing breaks in the canopy, and the availability of space for a plot buffer strip.

The ages of the intensive study plots were 30, 42, 73, and 95 years, while the less intensively studied stands had ages of 9, 22, and 49 years. In these latter stands, no lysimeter plates were installed. The four intensive study plots were located relatively close to one another (Figure 6). Cores taken from trees on these plots indicated fire scars (from the previously mentioned fires) in the older stands and charcoal was found below the litter layer on the soil. The plots, described in Table 17, showed decreasing numbers of stems, and increasing tree mean dbh with

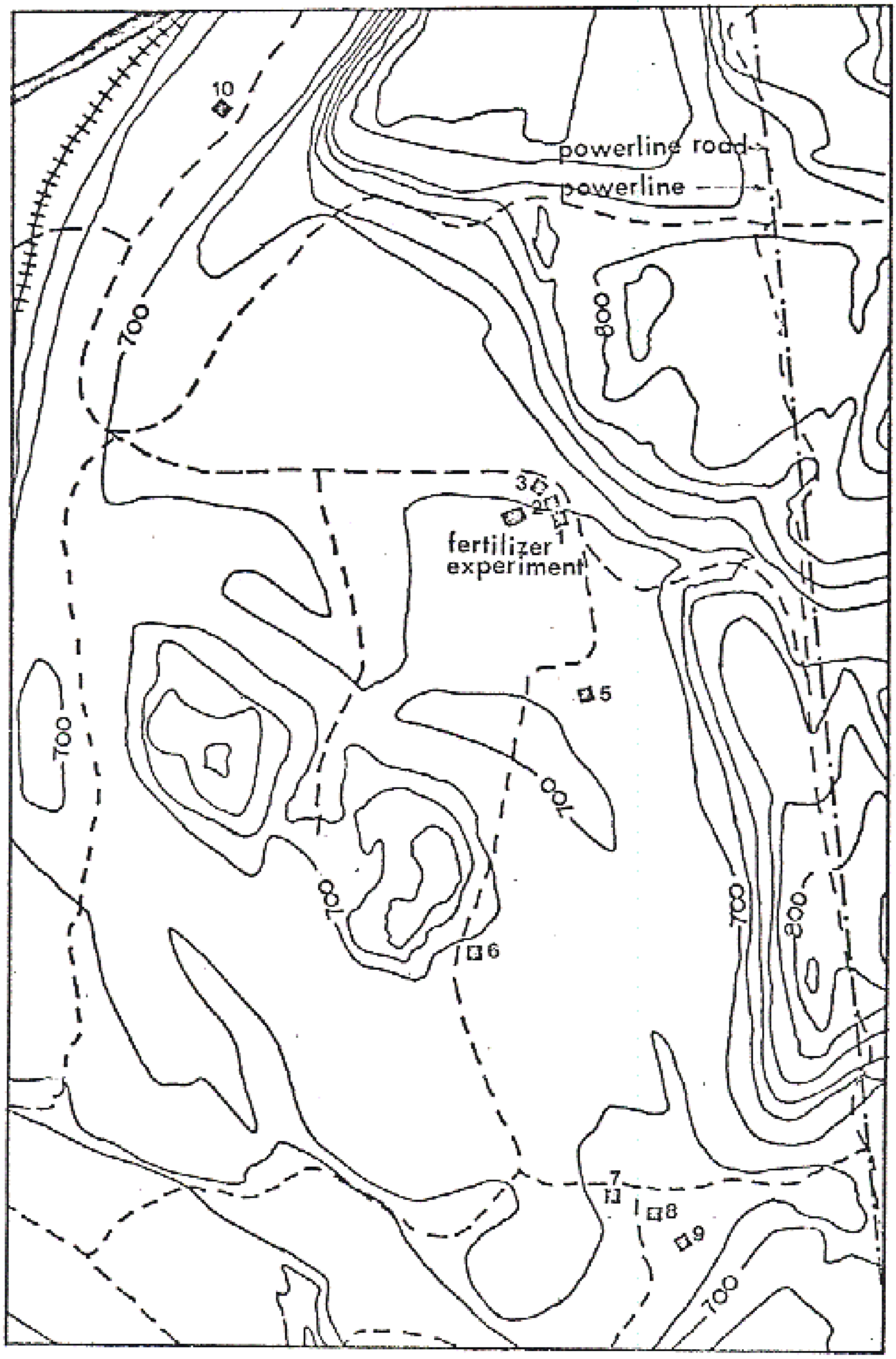


Figure 6. Location of study plots in the Cedar River Watershed. Contour interval is 20 feet and the scale is approximately 5 inches to the mile. Broken lines represent roads while the black squares are study plots. Numbers indicate plot numbers.

Table 17. Location and characteristics of the stands used for nutrient cycling studies in the Cedar River Watershed.

No. on Fig. 1	Total age of tree (yr)	Mean diam.[a] and inc. (cm)	Density (st./ha)	S.Q.	Location[b]	Data and Comments
Plantation						
3	9	-	2,022	mid IV[c]	plot 3	Nutrient distribution and above ground cycling.
2	30	14.13 (0.36)	1,800	mid IV	plot 2	Organic matter distribution plus some cycling data
5	36	15.6	1,490	mid IV	plot 5	Complete nutrient cycle (Cole *et al.*, 1968)
2	42	19.20 (0.31)	1,289	mid IV	plot 2	complete cycle
10	49	19.29 (0.30)	1,067	high IV	1 mile from plot 2	Nutrient distribution and some cycling data
Naturally Regenerated						
11	22	9.35 (0.39)	2,756	mid IV	"	Nutrient distribution and above ground cycling.
7	30	11.38 (0.30)	2,346	low IV	"	Nutrient distribution and above ground cycling
6	42	20.12 (0.33)	822	mid IV	"	Nutrient distribution and above ground cycling.
8	73	17.41 (0.22)	1,889	mid IV	"	Nutrient distribution and above ground cycling
9	95[d]	28.64	644	low III		Nutrient distribution and above ground cycling

[a] Mean diameter and increment, breast height

[b] Plot numbers as in Cole and Gessel (1968)

[c] This Site Quality assumed from the surrounding stands

[d] Hemlock comprises 31% of this stand, mean diameter 14.3 cm, increment 0.22 cm and maple comprises 20% of the stems with mean diameter 21.32 cm and increment 0.19 cm.

Table 18. Climatic data for 1973 and 1974, monitored at the Landsberg weather station. Figures in parentheses are deviations from the long term mean.

Month	Temperature (°C)			Precipitation (cm)	
	Average	Av. Max.	Av. Min.	Total	Snow
1973					
January	2.1 (-0.7)	5.9	5.8	13.9 (-3.8)	13.5
February	5.7 (1.4)	11.4	0.0	7.3 (-7.0)	0
March	6.0 (-0.3)	10.9	1.1	7.5 (-7.2)	Trace
April	8.1 (-1.3)	16.3	0.9	5.7 (-4.5)	0
May	12.1 (0.0)	19.1	5.1	9.1 (0.9)	0
June	12.8 (-0.5)	18.9	8.2	14.3 (5.9)	0
July	16.9 (0.2)	24.9	8.8	0.7 (-2.7)	0
August	14.3 (-2.0	21.9	6.8	1.6 (-2.6)	0
September	14.3 (0.1	21.4	7.1	9.1 (0.5)	0
October	9.3 (-0.8)	14.3	4.4	13.4 (-1.3)	0
November	3.8 (-2.0)	7.3	0.3	24.7 (6.2)	1.0
December	4.6 (0.5)	7.6	1.5	27.3 (6.7)	0
Annual	9.3 (-0.5)	-	-	134.6 (-8.9)	14.5
1974					
January	1.5 (-1.1)	5.5	2.1	8.8 (-8.9)	14.0
February	4.3 (-0.4)	8.0	0.6	16.5 (2.1)	Trace
March	5.4 (-0.6)	10.0	0.7	7.7 (3.2)	Trace
April	8.1 (-0.3)	12.7	3.5	12.2 (0.9	0
May	10.0 (-1.6)	15.5	4.5	9.2 (0.8	0
June	14.5 (0.1)	21.5	7.6	8.7 (0.7)	0
July	16.9 (-1.0)	23.6	10.3	6.3 (4.3)	0
August	17.1 (1.1)	19.2	9.6	1.9 (-2.8)	0
September	16.5 (2.2)	25.1	7.3	1.2 (-7.2)	0
October	10.1 (0.2)	17.5	2.7	5.3 (-8.9)	0
November	5.8 (-0.1)	9.8	1.9	24.4 (5.5)	0
December	4.6 (0.9)	8.1	1.1	23.5 (3.4)	12.7
Annual	9.6 (-0.2)			125.7 (-17.8)	26.7

Table 19. Some gneral physical properties of the soils on the study stands. Textural classes are based on the International system.

Age (yr)	Depth (cm)	Texture (%)						% of 2mm fraction			ERD* (cm)	LOI
		>6.4mm	2-6.4mm	<2mm	sand	silt	clay	sand	silt	clay		
22	0-15	55	27	18	14.8	2.2	1.1	82	12	6	32	10.72
	15-30	67	20	13	12.0	0.5	0.5	92	4	4		6.28
	30-60	68	19	13	11.7	0.9	0.4	90	7	3		2.20
30	0-15	50	20	34	28.5	4.1	1.4	84	12	4	28	9.62
nat.	15-30	47	23	30	24.6	4.5	0.9	82	15	3		5.98
	30-60	49	22	29	27.6	1.3	0.1	95.2	4.5	0.3		2.45
42	0-15	51	17	32	24.9	5.0	2.1	78	16	6	40	7.22
nat.	15-30	53	15	32	26.0	4.8	1.2	81	15	4		4.77
	30-60	54	23	23	21.0	1.5	0.5	91	7	2		2.22
49	0-15	39	24	37	29.2	5.9	1.9	79	16	5	46	10.21
	15-30	58	19	23	18.4	3.9	0.7	80	17	3		7.66
	30-60	61	21	18	16.9	0.9	0.2	94	5	1		2.86
73	0-15	47	19	34	28.2	5.1	0.7	83	15	2	32	10.65
	15-30	62	14	24	21.6	2.2	0.1	90	9	0.5		7.53
	30-60	82	7	11	10.7	0.3	0.03	97	3	0.3		2.92
95	0-15	42	19	39	33.9	3.9	1.2	87	10	3	50+	11.21
	15-30	69	11	20	17.8	1.8	0.4	89	9	2		7.05
	30-60	65	16	19	17.3	1.5	0.1	91	8	0.5		3.05

* Effective rooting depth

increasing stand age. This was less obvious in the 49 and 73-year stands because of hemlock and cedar ingrowth.

The understory vegetation of the 22, 30, 42, and 73-year-old naturally regenerated stands, described by Long (1973), was generally similar to that of the plantation for the dominant vascular species, with some moss species becoming more important in the older stands. There was a change with age in the dominant understory species, from salal in the younger stands to moss in the older stands.

Soils of the study stands were all related to, or were Everett series but, as seen by the descriptions in Table 19, there was some between plot variation, especially in the depth of rooting and the stone content.

Plot Layout and Biomass Estimation

Plots were 0.045 ha (0.1 acre) in area, in order to make them equivalent to the intensive study plots previously established by Cole and Gessel (1968). The plots were square and established using a compass and tape. Each tree was numbered using tags and the breast height diameter (dbh) taken to the nearest 0.05 inch (0.13 cm). Stand dominant height (tallest ten trees per plot) was estimated and this estimate used to determine the stand site quality. Using an increment corer, cores were taken on ten trees per plot to determine total stand age. On each tree a shallower core was taken to estimate the previous five year increment.

To estimate stand biomass, Dice's (1970) regression equations ("Cedar River Model") were used, after first testing them with eight additional trees sampled over a range of diameter classes. For certain components of the trees, for example branches, large errors may be incurred, possibly related to the structure of the stands, but the time involved in collecting further samples to lower the error precluded improvement of their estimation in this study. A Fortran IV program was written to carry out the biomass calculations and as Dice's (1970) equations included logarithmic (log-log) transformations, allowance was made for a bias correction term (Madgwick, 1970). By remeasurement of stands, mortality and growth could be estimated and average annual values for productivity estimated from the increment core and remeasurement data.

Understory biomass was estimated by species from six 1-m^2 quadrats and estimates of understory productivity were also made (Long, 1973; Long and Turner, 1974). Forest floor weights (organic matter over the mineral soil) were determined using eight 613 cm^2 round cores per plot and sorted into components after drying. Large logs, obviously from the previous stands, were ignored, so that the estimated forest floor weight had some relationship to the organic matter produced by the existing stand. Bulked soil samples from each plot by depth were taken, and returned to the laboratory for analysis.

Nutrient Transfer Estimation

The selection of methods for the measurement of nutrient transfer was made so that the data would be comparable to previous studies, and also, considering the large quantity of data to be collected, for convenience. A series of methods was used for determining the transfers and conceptually these can be better understood by referring to Figure 7.

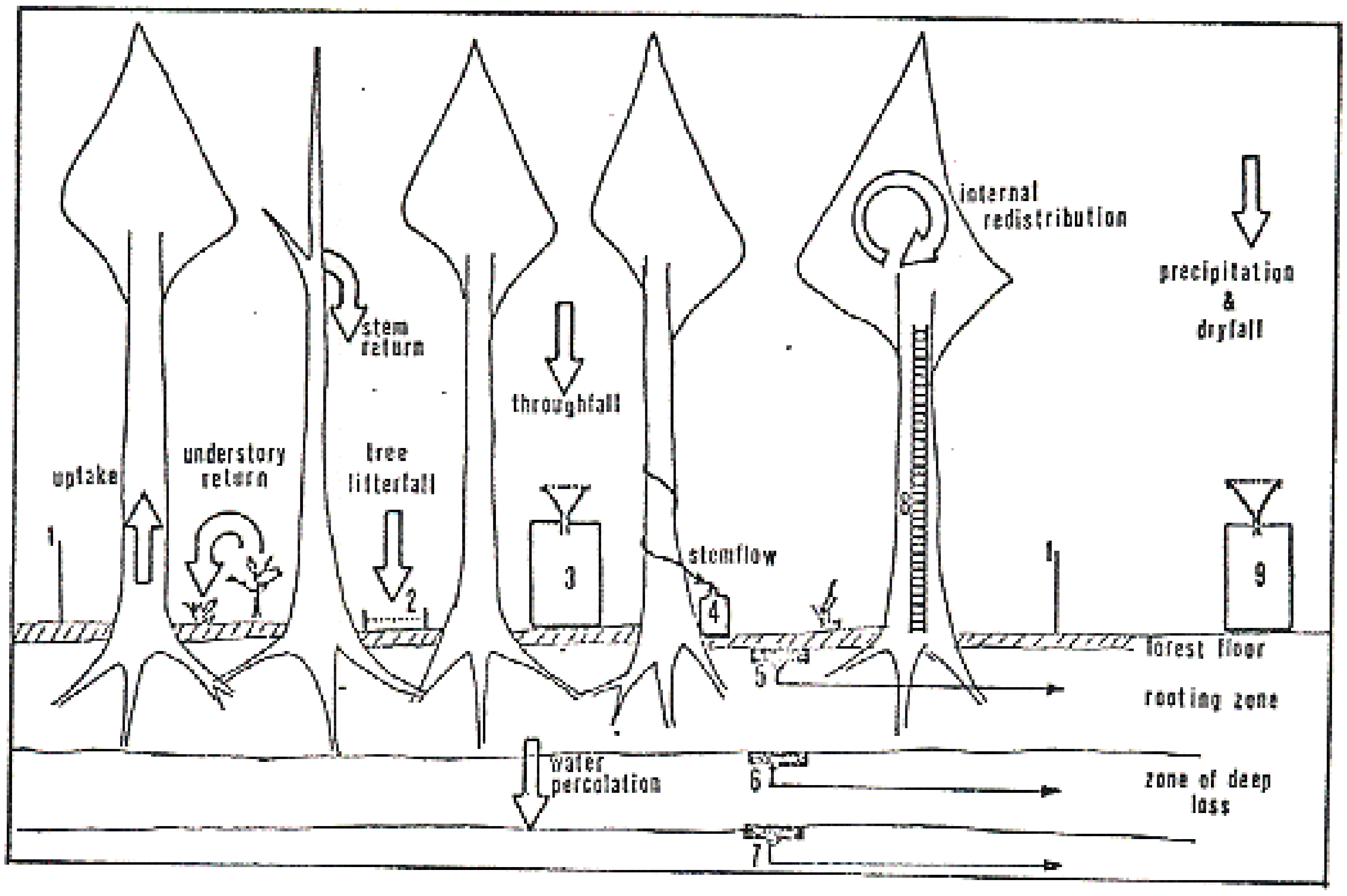


Figure 7. Schematic diagram of data collection for a forest nutrient cycling budget. Main transfers are named on the diagram. Numbers denote a method of collecting the transfers: 1--plot boundary (tree tally), 2--litter trap, 3--throughfall collector, 4--stemflow, 5--forest floor lysimeter plate, 6--rooting zone lysimeter plate, 7--deep loss lysimeter plate (the lysimeter plates being used for leachate collection), 8--ladder for tissue collection for uptake and internal redistribution (understory is also sampled), 9--input collectors.

To estimate tree litter production, four 18 x 18 inch litter traps (0.209 m^2) were randomly located within each plot and collections made on or near the 20th day of each month. After being dried at 70°C, the samples were sorted into Douglas-fir needles, other leaves, twigs and branches, cones and other material. This "other material" included bud scales, grass, fragmented material and unidentifiable litter, but these were not differentiated. Subjective notes on the appearance of the litter were also made especially in the case of unusual events. Large wood litter was estimated by assuming all mortality at the time of remeasurement was returned to the forest floor as large wood. Understory litter was estimated from the standing biomass. All annuals and leaves of deciduous understory species, as well as a proportion of the perennial understory foliage were assumed returned. This proportion was based on the length of life of the foliage estimated from subsamples. This subsampling method was also used for estimating the return by the mosses. The length of segment life from one species, *Hylocomium splendens*, in which the length of frond retention was about four years (J.N. Long, pers. commun.), was estimated and this estimate was applied to the other moss species.

Nutrients transferred by the throughfall was estimated from three collectors per plot, consisting of an 11" diameter (613 cm^2) funnel fixed into a 20 gallon plastic trash barrel. The funnel had a fine screen placed over the funnel to eliminate the accumulation of large material in the solution. The mesh of this screen was the same as that used for the litter traps so that no particle size was lost as a result of differences in screen mesh. Samples were collected at the same time as the litter. Stemflow was collected using rubber strips around the tree as in Cole and

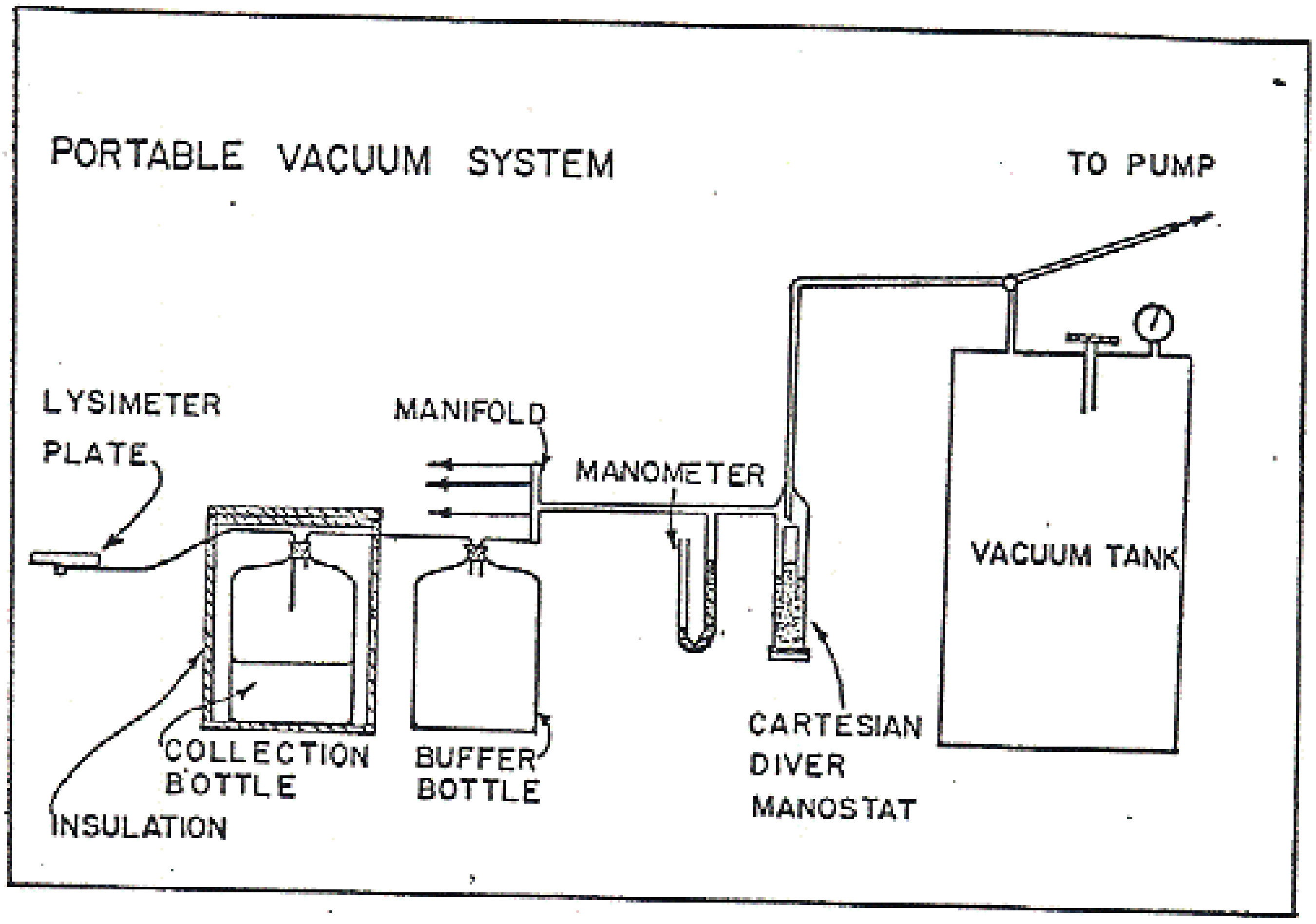


Figure 8. Portable vacuum system used for collection of leachates from the lysimeter plates away from the main intensive study site and its related vacuum system.

Gessel (1968). These samples were less than satisfactory owing to the extensive and repeated damage to the collectors by squirrels. Precipitation input was measured in a collector similar to that used for throughfall, set out in the open.

To monitor nutrient transfer in water percolating through the soil, tension lysimeter plates were installed. The system was the same in principle as that of Cole and Gessel (1968) but the plates were modified as in Crane (1972), which meant that the plates were coated with a resin rather than haveing a rubber backing stretched over them. The plates were either 6" or 11" in diameter. Suction (0.1 atm.) was supplied by the system shown in Figure 8. The vacuum tanks were evacuated by hand pump or by using the carburetor advance on a motor vehicle. Plates were installed below the forest floor, below the rooting zone, and in some cases at one meter depth, nutrients moving through these lowest plates being considered lost from the system. Owing to the cost of the plates, the limitations on the small vacuum systems and the limitations of analytical capacity, only two plates at each depth in each plot could be run continuously, but for short periods of time four plates were installed to enable estimates of water volume variability to be obtained. Some of these results are shown in Table 20, together with some comparable data of Cole and Machno (1969).

Within Tree Transfers

Within the tree and understory components, three nutrient variables of interest were requirement, redistribution and uptake. These three terms are defined as follows:

Table 20. Variability of the quantities passing through tension lysimeter plates, expressed as coefficient of variation.

Soil Depth and Stand	C.V.[a]	Reference
Plantation, forest floor	34	Cole and Machno, 1969
42-year-old plantation forest floor (collected 12/19/73)	23	present study
30-year-old natural stand forest floor (collected 12/19/73)	29	present study
42-year-old natural stand forest floor (collected 12/19/73)	22	present study
73-year-old stand, forest floor (1/19/74)	47	present study
95-year-old stand, forest floor		
(collected 1/19/74)	77[b]	present study
(collected 2/20/74)	32[c]	
Plantation, rooting zone	69	Cole and Machno, 1969
42-year-old natural stand, rooting zone (collected 11/20/74)	49	present study

[a] C.V. - coefficient of variation

[b & c] are the same location excet that (c) had a lysimeter plate moved from the base of a tree because it had been located under the direct influence of stemflow.

(a) Requirement is the nutrient content of the current tissue and specifically, in this study, is the sum of the nutrients in the current foliage, branches and wood. This is assured to be the "requirement" for current growth.

(b) Redistribution is the quantity of nutrients retranslocated within the tissues of the tree and understory. Optimally this would be estimated by analyzing the tissue when it was current, then when it was one year old, two years old, etc., until it was dropped from the tree. Because of time considerations, it was assumed that the concentration of the older tissue when it was current was the same as that of the present current tissue.

Changes in the concentration, as the tissue matures, are attributed firstly to leaching and secondly to retranslocation. Leaching is assumed only to occur from foliage (rather than twigs and foliage) and is probably an overestimate as it consists of not only leaching but surface washing and removal of particulate organic matter from the tree. Changes in wood and and branches are assumed to be all retranslocation. Accumulation is calculated as negative retranslocation.

(c) Current Net Uptake is the quantity of nutrients removed from the soil humus complex by the trees and understory. It is calculated as the difference between requirement and retranslocation (adjusted for leaching) and can be written as:

$$N_{uptake} = N_c + N_t - N_r \quad \ldots\ldots\ (1)$$

where

N_c = total nutrient content of the current tissue (requirement)

N_t = loss from leaching

N_r = quantity of nutrients retranslocated (positive or negative).

(d) Average annual uptake is used in the studies on net accumulation and is taken over a longer period of time than the net uptake (*e.g.*, the length of time of needle retention). This is essentially the difference between the inputs and outputs of the vegetation and hence differs from the current net uptake in that litterfall needs to be taken into account.

These are theoretical considerations, the practicalities of which are discussed in the Results and Discussion section. In the loss by leaching, stemflow was ignored as it was assumed, on the basis of the literature (Mahendrappa and Ogden, 1973), that it was predominantly the result of washing of the outer surface of the bark. Equation (1) was also used for the understory but leaching had to be ignored owing to the problems of measuring it.

Fertilizer Experiment

To test some of the hypotheses of nutrient cycling in regard to ecosystem stability, a field experiment involving fertilizer addition was

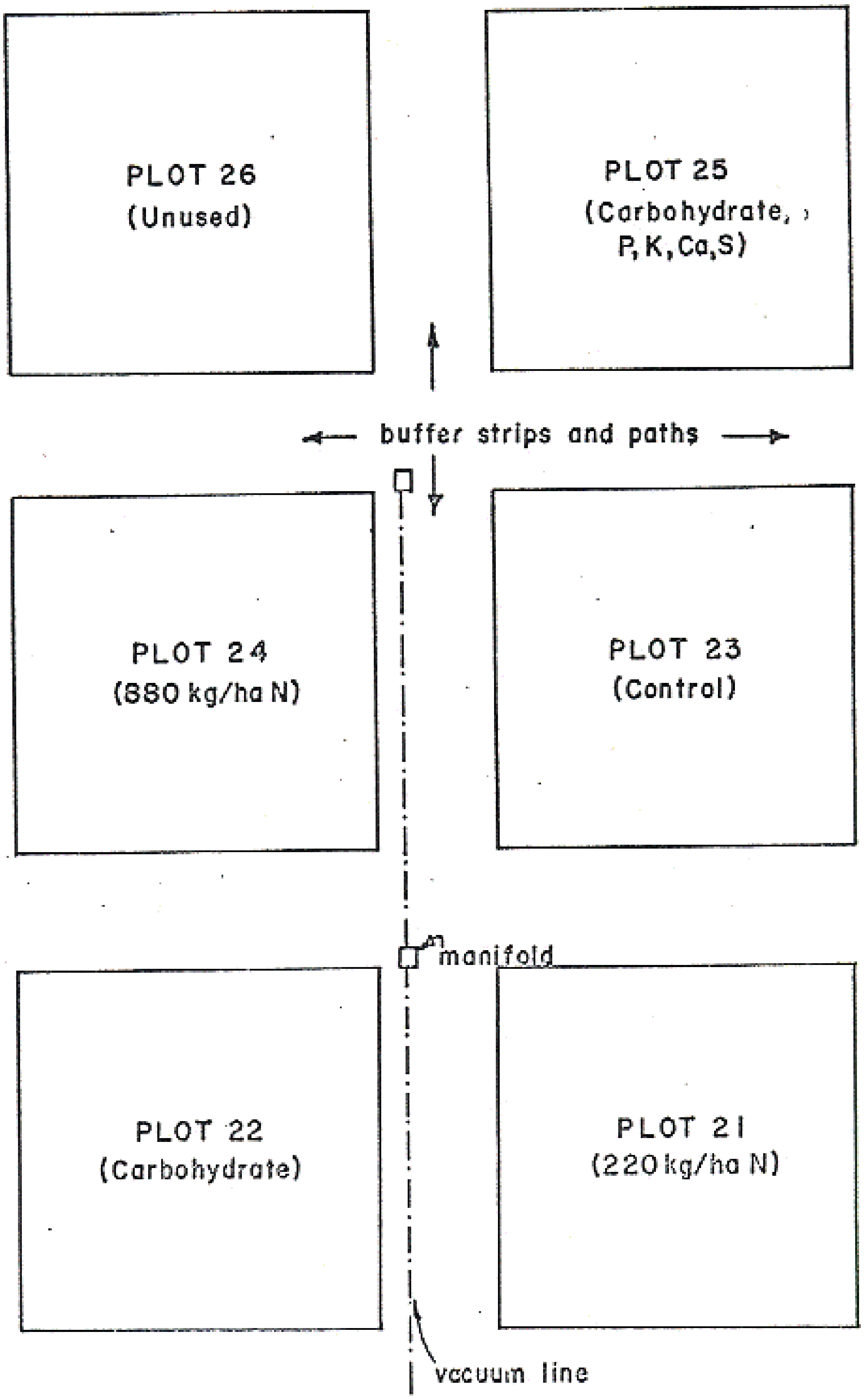


Figure 9. Plot layout for the fertilizer experiment.

established. The aim of this experiment was to investigate nutrient transfer internal to the tree compared to that external to the tree. The layout involved five plots, each 0.05 acre (0.023 ha), as shown in Figure 9. The treatments and time of application are shown in Table 21, together with some of the plot variables. The aim of the design was to give gradation of nitrogen availability, from overabundance (880 kg/N/ha), to stress conditions (carbohydrate applied to widen the C/N ratio). Measurements were essentially as in the previously described plots, but there was more intensive sampling in the crowns of the trees, and, because of the damage caused by the application of the treatments, the understory was ignored.

Sample Preparation

Plant tissue samples from the tree, understory and forest floor were dried at 70° C, sorted into components, and where necessary, weighed. Samples for analysis were then ground in a Wiley mill (40 mesh) and stored in glass screw-top jars.

Water samples were filtered and stored temporarily in glass bottles at 2°C. One liter had 2.5 ml sulphuric acid and 30% hydrogen peroxide added and the solution digested and evaporated down to 2.5 ml. This remainder was then made up to one liter with distilled water and a 100 ml. subsample taken for analysis.

Soils were dried, sieved and stored using standard methods (Piper, 1944).

Table 21. Treatments used in the fertilizer experiment in order of expected decreasing nitrogen availability.

Plot No.	Mean dbh (cm)	Stems (St/ha)	Treatment and time of application
24	15.5	2,133	Broadcast 880 kg/ha N as urea Applied 2/22/74.
21	15.5	2,000	Broadcast 220 kg/ha N as urea Applied 2/22/74
23	14.1	2,267	Control, no treatment
22	14.9	2,041	Broadcast 8,000 kg/ha sugar, applied 2/22/74, plus approximately 10,000 kg/ha sawdust (see below) on 5/21-22/74.
25	15.8	1,778	Broadcast 8,000 kg/ha sugar, applied 2/22/74, plus approximately 10,000 kg/ha sawdust on 5/23-24/74. 22 kg/ha of P as superphosphate and 110 kg/ha as KCl were applied 2/22/74.

Footnote: The sawdust was a cedar-alder mixture. The analysis of the sawdust showed 0.09, 0.095, 0.092, 0.183, 0.110 and 0.017 percent of N, P, K, Ca, Mg, and Mn respectively, which was equivalent to 9, 1, 9, 18, 11, and 2 kg/ha of these nutrients respectively. The C/N ratio of the sawdust was 61 (approximately) and with the addition of the sugar the ratio was raised to 110. Solubilization and decomposition of the sugar reduced this, so for most of the duration of the experiment the C/N ratio was 70-80.

Chemical Analyses

The chemical analyses were generally carried out using standard methods of the laboratory and the errors involved in analysis were considered much less than the field sampling variability. Nitrogen concentrations in plant material were estimated using either macro- or micro-Kjeldahl methods (Jackson, 1958), depending upon the amount of sample available. Soil N was estimated by the macro-Kjeldahl method (Jackson, 1958), and the analyses for nitrogen on the digested water samples were carried out on an auto-analyser IL353.

A 0.5-1.0 g sample of plant material was dry ashed at 420°C in a muffle furnace and then dissolved in dilute HCl and made up to 200 ml. (Piper, 1944). Potassium, Ca, Mg, and Mn were determined by atomic absorption on a Scientific Instruments Atomic Absorption Spectrophotometer II, as were the soil extracts and the water samples. In some instances where there was insufficient plant material for the dry ashing procedure, the solutions from the micro-Kjeldahl digests were used for cation and P analysis. Phosphorus was determined on all waters, digests and extracts by the Osmond method (a phosphomolybdenum blue complex) with ascorbic acid as a reducing agent, on the Technicon Auto-Analyzer.

Exchangeable K, Ca, Mg, and Mn in the soil were estimated by use of a pH 7 ammonium acetate extracting solution (Jackson, 1958). Available P was estimated using a sodium bicarbonate extract (Jackson, 1958), while total P, K, Ca, Mg, and Mn were determined by dissolving a soil sample in HF and HNO_3 (Brown pers. commun.).

RESULTS AND DISCUSSION

1. Organization of Results

(a) Hypotheses and Definitions

In order to fulfill the original aim of this study (*i.e.*, the determination of the applicability of the results on nutrient cycling obtained from the Thompson Research Center to other forest stands), a sequence of hypothese was developed. The methods used to test these hypotheses are outlined in this section.

Firstly, the original study of Cole *et al.* (1968) is discussed in further detail, including two additional nutrients and more nutrient transfers. This is done to more fully describe the type of data that is being collected to define nutrient cycling and to present some interpretations of these data. Secondly, several other age classes from the same plantation as the study of Cole *et al.* (1968) are investigated, to determine whether a steady-state situation develops during stand maturation. Use of the plantation allowed aspects of the development of a single stand to be assessed (*i.e.*, organic matter and nutrient accumulation and cycling), independent of the problems of variability associated with variations in site quality and stocking usually found in this form of study.

Thirdly, other stands from the same location, with approximately the same site quality, are also incorporated. These stands vary from the previous stands (in the plantation), in that they are naturally regenerated, and, so, individually, they have more variable stocking and age distributions. However, accepting this increased variability, it is thus possible to extend the available stand age range. Stands of Douglas-fir of similar site quality, which were studied by other investigators, are also included where possible, to give some estimate of the range of data involved in other studies and attempt to attach more general applicability to the results of the hypotheses being tested. A final section will investigate the effects of manipulations on the nutrient cycle in forests and discuss the stability or flexibility of the nutrient cycle.

An understanding of distribution, and changes in distribution, of organic matter (biomass) in the forest ecosystem was considered an essential prerequisite to this study, as one assumption was that the distribution of the nutrients N, P, K, Ca, Mg, and Mn in the ecosystem was dependent upon the organic matter distribution, and that nutrient cycling was a modulation of the organic matter-hydrologic cycles. Previous studies, mentioned in the literature review, plus other studies carried out by the author (Long and Turner, 1975) have shown the foliage to be the most critical of the stand components, because of its direct influence upon tree productivity, understory biomass, and forest floor biomass. The foliage also contained a high proportion of the nutrient content of the tree component of the ecosystem. Emphasis was therefore placed upon this component, it being considered basic to an understanding of the whole nutrient cycle.

One of the main problems associated with this study was that of testing the statistical significance of the results. With so many related variables, critical differences could well be masked. For many variables, measurement difficulties precluded the collection of sufficient replicates for adequate statistical analysis. As this thesis was essentially an overview study, *i.e.*, an attempt to assess the critical changes in the nutrient cycle of the stand as it increased in age, it was considered that in the interest of obtaining sufficient stands of different age classes, replication within each age class would not be possible. This meant that, where possible, measured stand parameters were analyzed using analysis of variance, or trends were assessed using regression analysis, but for many aspects of the nutrient cycle only critical observation could be employed. It was assumed that, if the individual components of the ecosystem were in steady-state, then the total ecosystem was in steady-state, but if one component changed significantly, then the ecosystem changed proportionally.

(b) Terminology

In the hypotheses several terms are used, and some principles implied, which will be defined here in further detail. The main hypothesis was that as the Douglas-fir ecosystem developed in time (matured), the nutrient cycle would reach a steady-state situation. This meant that, in general, the nutrient pools would remain constant in quantity over time, as would the transfers into and out of these pools. Steady-state, as used in this study means that a component of the stand (tree foliage, humus, total organic matter on the soil, understory, etc.) remains constant in mass of organic matter and nutrients over a long period of time. This allows for small scale fluctuations over the space of a year or several years, but long term cyclic changes have been ignored.

A stable condition implies that if a disruption is caused in the steady-stae condition, for example, as a result of thinning, defoliation, or fertilizer addition, the ecosystem, or the directly affected component, will tend to equilibrate to a steady-state condition. If the treatment does not alter stand site quality, *e.g.*, thinning, the post-treatment steady-state will probably equal pre-treatment steady-state, whereas, if the treatment alters the site quality, *e.g.*, fertilization, the new steady-state level may be different.

While not intending to cover them in this study, it is worth noting the alternatives in studying stability, these being: (a) stability, where the new steady-state level is equivalent to the old, (b) bounded stability, where the new stead-state level is lower or higher than the old, and (c) instability, where after disruption no new steady-state level is attained.

Examples of stability are easy to conceive, for example, if a stand is thinned, after a period of time the crown will probably obtain the pre-thinning level. Similarly with bounded stability, if the stand is fertilized, a new level of foliar biomass may be attained and maintained.

Instability is more difficult to visualize, and because of this some of the limits of the definitions can be conceived. If the treatment is clearcutting of a stand, it could be argued that the components of the old stand did not readjust adquately, so a new ecosystem was established, and thus the first ecosystem was unstable. For example, the removal of Douglas-fir and its replacement by red alder may imply the Douglas-fir ecosystem was unstable. Alternatively, it could be argued that the old system was stable, and after clearcutting, given enough time, the old ecosystem would reappear.

In the definitions involving stability a time period must be included. Thus, if the ecosystem is not tending towards a stable situation in, for example, ten years, then it may be termed unstable. If steady-state is never originally achieved, unstable situations may also occur. For example, red alder components change rapidly and none appear to reach steady-state before the stand degenerates and disappears (Zavitkovski and Newton, 1972).

Another method for analyzing stead-state is the use of ratios, such as the ratio of the input or output to the pool size, thus indicating a proportional loss or gain over a period of time (Jordan and Kline, 1972). Two nutrient transfers may be compared to a ratio which may represent rates of change or efficiency. This was used here to express the efficiency of nutrient utilization or retention by the trees, *e.g.*, uptake/requirement, loss requirement. These ratios are related, *i.e.*, a lowering of the uptake ratio may result from a raising of the internal redistribtuion ratio, thus the ratios may indicate a more efficient nutrient utilization strategy. An appropriate study of the efficiency of nutrient utilization requires that there be a deficiency in the nutrient or nutrients in question (in the present case, N), so that there is not the complicating factor of luxury consumption.

2. The Original Study at the Thompson Research Center (Cole *et al.*, 1968).

(a) Data Presentation

The nutrient cycle synthesized for Douglas-fir by Cole *et al.* (1968) involved the results derived from the Thompson Research Center, and provided the initial base for this thesis. Table 22 shows a revised

Table 22. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 36-year-old Douglas-fir ecosystem (Cole et al. 1968).

Component		Organic matter	N	P	K	Ca	Mg	Mn
TREE								
Foliage	- current	1,990	24	5	16	7	3.0	1.6
	- total	9,097	102	29	62	73	15.0	13.7
Branches	- current	513	4	1	3	2	0.7	0.2
	- total	13,886	44	10	35	67	2.4	44.3
	- dead	8,145	17	2	3	39	2.7	2.6
Wood	- current	7,485	10	2	10	4	3.5	0.4
	- total	121,687	77	9	52	47	11.3	5.3
Bark		18,728	48	10	44	70	7.4	5.5
Total Aboveground		171,543	288	60	196	196	44.0	31.6
Roots		32,986	32	6	24	37	6.0	2.4
Total tree		204,529	320	66	220	333	50.0	34.0
SUBORDINATE VEGETATION		1,010	7	1	7	9	2	1
FOREST FLOOR								
Branches		1,423	5	1	4	8	1	1
Needles		3,005	35	4	5	27	5	3
Wood		6,345	14	2	8	17	3	2
Humus		11,999	121	19	15	85	32	9
Total		22,772	175	26	32	137	41	15
SOIL								
Total Estimate								
0 - 15 cm		38,372	809	1,167	12,030	26,325	14,216	1,843
15 - 30 cm		36,935	868	1,195	17,673	20,735	24,242	1,690
30 - 45 cm		28,290	761	980	19,910	30,878	30,014	2,708
45 - 60 cm		7,955	371	536	21,910	20,878	38,014	2,709
Total soil		111,552	2,809	3,878	71,523	98,816	106,486	8,950
Exchangeable or available quantity								
0 - 15 cm				40	79	313	37	25
15 - 30 cm				37	66	196	35	10
30 - 45 cm				32	52	152	25	6
45 - 60 cm				32	37	80	12	5
Total exchangeable				141	234	741	109	46
TOTAL "ACTIVE" ECOSYSTEM					493	1.220	201	92
TOTAL ECOSYSTEM		339,863	3,310	3,971	71,782	99,295	106,579	9,000

Table 23. Annual transfers of N, P, K, Ca, Mg, and Mn (kg/ha) between components of the Douglas-fir ecosystem (Cole *et al.*, 1968).

Transfer	N	P	K	Ca	Mg	Mn
Input (precipitation)	1.1	trace	0.8	2.8	0.5	0.1[a]
Uptake by forest[b]	38.8	7.23	29.4	24.4	7.1	2.2
Total return to forest floor	16.4	1.4	15.8	18.5	8.0	3.9
Leached from forest floor	4.8	0.95	10.5	17.4	6.1	0.8
Leached beyond rooting zone	0.6	0.02	1.0	4.5	0.9	0.1

[a] estimate from different year to the rest of the study.

[b] uptake is as defined by Cole *et al.*, 1968), and in the present context is actually stand requirement.

Table 24. Annual uptake and return of N, P, K, Ca, Mg, and Mn (kg/ha) by the second growth Douglas-fir ecosystem (Cole *et al.*, 1968).

Component	N	P	K	Ca	Mg	Mn
Annual Uptake[a]						
foliage	24.3	4.7	16.2	17.8	2.9	1.6
branch	4.2	0.8	2.7	2.6	0.7	0.2
bole	10.3	1.7	10.5	4.0	3.5	0.4
Total	38.8	7.2	29.4	24.4	7.1	2.2
Annual Return						
litterfall	13.6	1.0[b]	2.7	11.1	3.4	3.6
stemflow	0.2	0.1	1.6	1.1	0.5	0.1
leaf wash	1.5	0.3	10.7	3.5	2.2	0.2
Total	15.3	1.4	15.0	15.7	6.1	3.9
Total return to forest floor (+precipitation)	16.4	1.4	15.8	18.5	7.0	4.0

[a] uptake as defined by Cole *et al.* (1968), and in present context is actually stand requirement.

[b] recalculated, original figure of 0.2 was low.

version of the distribution of organic matter and nutrients within the 36-year-old Douglas-fir ecosystem. In the original presentation of the study, the nutrients Mg and Mn were not included, but they have been added here (Dice, 1970, plus S.F. Dice, pers. commun.).

As the soil data originally included only total P and the exchangeable cations, further analyses were carried out to determine available P and total cations. These latter estimates reinforced the fact that the biological component plus the soil available components of the ecosystem (in which this study is specifically interested) were very small compared to the total soil nutrient pool. However, it is this small quantity of nutrients which controls the continued productivity of the ecosystem.

Table 23 indicates the transfers between the major components of the ecosystem. Further details on uptake and return to the forest floor are shown in Table 24 (Cole *et al.*, 1968, plus the data for Mg and Mn from Dice, 1970). As the estimate of Mn in the precipitation was not available, an estimate from a subsequent year was included to indicate the magnitude of the input. In Tables 23 and 24 the "uptake" is actually the quantity of nutrients contained within the current tissue, and as such is really stand requirement (Switzer and Nelson, 1972). The precipitation was not originally included in the return but was incorporated here to indicate the total quantity of nutrients reaching the forest floor. The understory has been ignored for the uptake and return estimates of this stand, as insufficient data was available for further calculation including this component.

The features of this stand which are considered of importance in characterizing this nutrient cycle are (1) the species was Douglas-fir,

(2) it was of poor site quality (S.Q. IV based on King, 1966), (3) the age is 36 years and (4) it was planted. Being planted it is uniformly stocked and of uniform age, whereas a naturally regenerated stand may tend to be less uniformly spaced and have a greater age distribution. In the original study the method of tree biomass estimation was by total area cropping, while the present study employed regression techniques, thus there may be some variation as a result of differences in estimation methods.

(b) Calculations Based on the Data of Cole *et al.* (1968).

Using the nutrient concentration differences in the tissue, estimates of the nutrient requirement for growth were calculated (data from S.F. Dice, pers. commun.). An estimate of internal redistribution was then made, and hence, by subtraction, uptake could be calculated. The results of this recalculation are shown in Table 25, and indicate that almost half of the stand's N requirement for new growth was obtained from sources within the tree (redistribution), while over 70% of the P was from the same source. These two nutrients are retained in relatively high proportions, indicating they may be retranslocated relatively efficiently. This high efficiency of redistribution does not necessarily imply a low efficiency of acquisition from the soil, but rather indicates exploitation of the most efficient strategy to fulfill requirements for growth.

The trees appeared to have obtained less than one third of their K requirement from internal redisribution. This may be because of high loss from crown leaching. There may in fact be a high amount of K translocated but the estimation method used in this study (balancing of net

Table 25. Requirement, translocation, and uptake of N, P, K, Ca, Mg, and Mn in a second growth Douglas-fir forest (kg $ha^{-1}yr^{-1}$).

Component	N	P	K	Ca	Mg	Mn
Foliage						
requirement	24.3	4.7	16.2	7.0	2.9	1.6
translocation	9.7	3.9	7.9	2.7	-1.6	-6.3
uptake	14.9	0.9	10.3	15.8	4.5	7.9
Branches						
requirement	4.2	0.8	2.7	2.6	0.7	0.2
translocation	2.5	-0.1	0.9	nil	0.5	0.05
uptake	1.7	0.9	1.8	2.6	0.2	0.15
Bole						
requirement	10.3	1.7	10.5	4.0	3.5	0.4
translocation	5.6	1.4	1.3	1.1	3.0	0.0
uptake	4.7	0.3	9.2	2.9	0.5	0.4
Total current uptake	21.3	2.1	21.3	21.3	5.2	8.45
% uptake/requirement	55	29	72	157	73	384
Difference between uptake and return (excluding precipitation);						
from Cole *et al.*, 1968	23.5	5.8	14.4	8.7	1.0	-1.7
from adjusted values	4.9	0.7	5.5	2.8	-1.8	4.5

Table 26. Various estimates of annual accumulation in a second growth Douglas-fir ecosystem (kg $ha^{-1}yr^{-1}$).

Accumulation	very mobile				very immobile	
	K	N	Mg	P	Ca	Mn
From equation 1	7.9	7.2	0.9	1.0	8.7	4.6
Equation 1 -T.F.[a]	2.8	5.7	-1.3	0.7	5.2	4.4
Summed from woody tissue	11.0	6.4	0.7	0.5	5.5	0.65

[a] T.F. is throughfall

annual nutrient contents) would not indicate it. However, comparing the N values to those for K, there was twice as much K as N in the crown, but six times more K than N was leached from the crown. Calcium and Mn were accumulated in the foliage, resulting in uptake being much greater than requirement.

At this stage two points can be made. The first is that the biological cycle is many times greater, in terms of quantities of nutrients transferred, than the geochemical cycle. Secondly, the difference between uptake and return to the forest floor is much less for N, P, K, and Ca than for the estimates of Cole *et al.* (1968), indicating better estimation of the relative roles of cycling internal and external to the tree.

In estimating uptake by using current tissue requirement and redistribution, needle nutrient accumulation was treated as permanent storage, similar to wood, when in fact, in terms of the time scale we are interested in, it was only temporary (*i.e.*, 4 - 5 years). When uptake was calculated over the length of the needle life, leaf litter can be taken into account and an average annual accumulation rate was obtained which should theoretically equal the estimate calculated as the difference in the stand nutrient content over some time period divided by that time period minus mortality. This latter estimate of accumulation was often cited as the stand uptake (Mina, 1955; Smirnova and Gorodentsa, 1958; Sonn, 1960; Ovington, 1962; Rodin and Bazilevich, 1967).

In these calculations leaching from the crown (throughfall) presented a problem in that it could be treated either as a permanent loss from the tree or as a quantity which is constantly being replaced by the tree. In either case, since all throughfall was treated as physiologically active in relation to the tree, two sources of error are possible. One is that throughfall is not totally leaching but is at least partly the washing of exterior surfaces (dust, removal or organic material by rainfall impaction, etc.), or increased aerosol sieving by the leaves, as suggested by Mayer and Ulrich (1974). Secondly, the nutrient elements will vary in their replaceability depending upon the demand by the tree and the mobility of the nutrient in question. The equation used to calculate accumulation,

i.e., accumulation = uptake - (litterfall + throughfall),... (1)

uses throughfall a second time (it was previously used for the calculation of uptake), and thus in this equation, it has been removed from the calculations. This means that calculating accumulation in this way will give accurate results for nutrients relatively independent of the hydrological cycle, but it will be necessary to further account for throughfall to make it applicable for the nutrients highly dependent upon the movement of water (*e.g.*, K).

This method attempts to treat the cycling of a nutrient according to its physio-chemical relationship to the ecosystem. The results of the various methods of calculation are summarized in Table 26 and they indicate that in most cases throughfall should be treated as a non-replaceable loss. As a refinement, throughfall should be divided into leaf wash and leaf leaching by use of filters in the field collectors but this was not done in the present study. On a stand basis, tree mortality will also affect the accumulation pattern of nutrients, but no data were avaiable from the study of Cole *et al.* (1968).

In Table 26, using the accumulation of nutrients in the older woody tissue as the standard, the two estimates that are most in error can be pinpointed. These are the most mobile (K) and the most immobile (Mn) probably because of the leaching problems in the former and the continuing accumulation in the case of the latter.

The use of this single stand for intensive study indicated the minor role of the geochemical cycle in relation to the biological cycle, the importance of the cycle internal to the tree, the relationships of the various nutrients (mobile versus immobile), and the relative importance of the nutrients. No information can be obtained on long term rates of change as for this more than one stand is required.

3. Studies Within the Plantation.

(a) Assumptions Used in the Plantation Study.

The optimum method of studying long term changes in nutrient cycling in a forest ecosystem would be to monitor a stand over a long period of time, for example, fifty years. As this is generally impractical, an alternative method is to take a series of stands of different ages and assume they are simultaneous expressions of the same stand. The stands should be selected so that only the age will differ, but this is rarely true as spatial, environmental, and growth variability will all affect the final results.

By using stands of the same site quality, the assumption is made that there is no change in site quality over the life of a stand. Thus, a site quality IV stand at age 30 years will still be site quality IV at 90 years. There is no way of testing this assumption in the present study.

Both the above mentioned methods have been incorporated in this study by using measurements taken over a twelve year period in one stand, augmented by a 9-year-old replanted area in the same stand, and a 49-year-old part of the plantation. The details of the plots within the plantation were summarized in Table 19.

(b) Plantation Data.

Table 27 shows the organic matter distribution of the 30-year-old plantation, and the organic matter and nutrient distribution of the 42-year-old plantation (the control plot of Cole and Gessel, 1968). The organic matter and nutrient distribution of the 49-year-old plantation are shown in Table 28. Some components of the older stand appear to be at or near steady-state (36 through 49-year-old).

One of these was the critical component of tree foliage, and it was found that the foliar biomass reached steady-state some time after crown closure of the stand. This does not mean that the biomass is completely constant on an annual basis, but allows for flucturation caused by mortality and ingrowth. Thus if a single plot was monitored continuously for several years there may be a gradual increased in the foliar biomass for a period, followed by a reduction (mortality), and then a further increase. The foliar biomass of the plantation at 30 years was 6,540 kg/ha which increased to 9,4440 kg/ha by the time it reached 42 years, and then declined to 9,390 kg/ha at 49 years.

Table 27. Organic matter distribution of the 30-year-old Douglas-fir plantation, together with the organic matter and distribution of N, P, K, Ca, Mg, and Mn in the same plantation at the age of 42 years (kg/ha).

Component	30 year organic matter	42 year						
		Organic matter	N	P	K	Ca	Mg	Mn
TREE								
Foliage-current	2,100	2,440	26	5.2	19.4	9.2	3.0	2.0
-total	6,540	9,440	98	21.1	66.7	73.1	14.6	16.8
Branch-current	540	480	4	0.3	2.7	1.9	0.7	0.3
-total	10,160	13,720	49	9.3	28.7	70.5	7.4	4.6
Stem -current[a]	4,980	3,650	6	0.5	4.0	1.8	2.2	0.3
-total wood	128,540	182,630	97	10.4	63.1	91.3	18.6	7.5
-bark	17,360	23,610	72	13.7	43.9	123.2	12.5	12.8
-total	145,900	209,890	169	24.1	107.0	214.6	31.1	20.5
Total aboveground	162,590	229,400	307	59.0	202.4	358.2	53.0	43.1
UNDERSTORY								
-vascular		2,380	21	2.7	17.2	19.7	4.1	3.6
-fern		120	2	0.3	0.9	0.9	0.3	0.1
-moss		890	5	1.6	6.0	4.6	1.3	1.0
-total		3,390	29	4.6	24.1	25.1	5.7	4.8
FOREST FLOOR								
-wood	6,880	3,480	15	2.2	2.6	14.8	2.0	1.4
-litter	4,000	6,911	62	8.4	12.4	34.2	15.4	14.8
-humus	11,280	16,280	146	19.8	29.1	80.5	36.3	34.8
-total	22,170[b]	26,670[b]	223	30.3	44.1	129.5	53.6	50.9

No estimates were made of the soil in these stands as it was considered that with the limited number of samples possible, the error would be too great to detect and changes.

a ... Based on total stem increment, so may contain some bark.

b ... may be slight differences in totals because of rounding errors.

Table 28. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 49-year-old Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage - current	2,200	26	5	19	7	3	2.0
- total	9,390	108	25	66	69	15	16.0
Branches - current	420	3	0.3	2	2	1	0.2
- total	13,560	43	8	30	25	7	4.5
- dead	6,200	12	1	2	20	2	2
Wood - current	3,300	5	0.4	4	2	3	1
- total	178,350	101	13	58	83	17	8
Bark	22,840	67	12	42	109	11	11
Total aboveground	230,390	333	61	201	356	52	41
SUBORDINATE VEGETATION							
- vascular	2,480	21	2	16	18	4	3
- fern	140	2	0.4	1	1	0.3	0.2
- moss	810	5	2	6	4	1	1
- total	3,430	28	4	23	23	5	5
FOREST FLOOR							
Wood	7,370	25	2	4	21	1	2
Litter	7,230	70	10	13	51	13	15
Humus	18,390	178	26	34	131	32	39
Total	32,990	272	38	51	203	46	57
SOIL							
Total estimates							
0 - 15 cm	45,899	920	1,270	11,010	22,320	18,520	2,110
15 - 30 cm	38,583	820	1,330	15,720	18,900	26,220	1,760
30 - 60 cm	24,237	1,370	1,580	40,040	49,720	71,040	6,200
Total soil	108,729	3,110	4,180	66,770	90,940	115,780	10,070
Exchangeable estimates							
0 - 15 cm			42	81	299	42	32
15 - 30 cm			39	67	180	41	11
30 - 60 cm			71	82	212	37	12
Total exchangeable			152	230	691	120	55

(c) Supporting Data from the Literature.

An important consideration is how great a fluctuation can be allowed in the foliar biomass without considering that the stand (1) has not reached steady-state, (2) is undergoing some change in stability, or (3) belongs to a different statistical population. Ovington (1957) studying *Pinus sylvestris*, considered steady-state to exist with fluctuations of up to 20% occurring in the foliar biomass. Ovington's (1957) study included stands which had been thinned and therefore may not yet have stabilized. Tadaki *et al.* (1970) allowed variations of 15% from the mean in their study on *Abies veitchii*, as did Harada *et al.* (1972) in *Cryptomeria japonica*. Again these were managed stands, and some of them may not have adjusted to treatments.

In the 42-year-old plantation at Cedar River, six 0.05 acre (0.0225 ha) plots were established systematically (for the fertilizer experiment) and the foliar biomass estimated to obtain some idea of the spatial variation. The mean foliar biomass was 8,430 ± 550 kg/ha (representing a standard error of 6.5%), with a range of up to 11% from the mean. Taking all of these values into account, and not being able to use statistical analysis, steady-state will be assumed to exist if the stands vary less than 11%, although based on results from the literature, variations up to 20% may be accepted.

The other factor to be taken into account is the error involved in the estimation of biomass, as small differences between stands will be meaningless if the error involved in the estimation method is sufficiently high. Typical values of the standard error of the estimation equation are 56.4, 43.5, 15.9, 20.4, and 20.9% for the foliage, branch, wood, bark, and total tree respectively (Dice, 1970), which is much wider than the 11% margin stated above. When the equations, with the above errors, are used to estimate the biomass of a stand, *i.e.*, on a per area basis, the errors tend to be compensatory, leading to a much lower overall error. Thus, comparing the complete area estimation to the regression technique (Table 4) the errors are now 2.0, 14.2, 19.3, 9.4, 0.9, and 0.12% for the older foliage, total foliage, branch, wood, bark, and total tree respectively, which represent a considerable reduction in error. The arbitrary value of 11% is quite meaningful under these circumstances.

With the 36-year-old stand as the base level, the ranges of the estimate were 8,190 to 10,010 kg/ha, and12,040 to 14,710 kg/ha for the foliage and branch biomass respectively. Thus, within this system there appeared to be steady-state for the foliage and branch biomass (and therefore the total crown) in the 36-49 year age range, and there did not appear to be any increasing or decreasing trend. The 30-, 36-, and 49- year-old stands' current foliage were essentially similar but the current foliage of the 42-year-old stand was outside the 11% limit. It is possible to have significant variations in inputs and outputs of a compartment for short periods, without seriously affecting the steady-state nature of the compartment itself. Such variations in current foliage or litter may, for example, represent adjustment after mortality.

The wood biomass cannot have such limits applied as it is an accumulating organ. There was some variation in this compartment, especially at 36 years, but again this may be the result of mortality and/or a different method of estimation in this particular stand. The current wood production had a trend with age which followed the typical wood volume production curve (Assman, 1970), and over the age range studied there was declining production (*i.e.*, 4,900 kg $ha^{-1}yr^{-1}$ at age 30, and 3,300 kg $ha^{-1}yr^{-1}$ at age 49 years). While the current wood production of a single living tree will always be a positive value (ignoring internal decomposition), on a stand basis there can be a net decrease because of mortality, and as the individual tree production declines, this possibility has a higher probability of occurring.

The understory biomass was variable but appeared fairly constant from 42 to 49 years of age. The 36-year-old stand understory biomass was low, especially when the results of the 9-year-old stand (Table 29) were included for comparison. This may be because the moss was not included and also because of the smaller number of samples taken for the estimation. There is probably the further effect of different sampling seasons. To obtain a better understanding of the changes that occur in the understory, other stands are required and these are available in later sections.

(d) Nutrient Content of the Plantation

The nutrients contained in the tree component of the 36-,42-, and 49-year-old stands generally followed the organic matter distribution so that trends noted for the tree organic matter were also applicable to the nutrients. To extend the range of data further, the results from the 9-year-old plantation are included (Table 29). These data are in contrast to those of the previously discussed older plantation, as the 9-year-old stand is still in the early stages of development and none of the components are near steady-state. In this young stand the aboveground biomass

Table 29. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 9-year-old Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage - current	360	4.8	0.7	3.5	1.2	0.4	0.3
- total	1,040	12.8	2.5	7.9	6.3	1.2	1.7
Branch	1,820	7.1	2.0	9.3	11.3	2.0	1.1
Stem	7,110	13.5	1.0	42.3	25.6	7.6	4.0
Bark	700						
Wood	6,410						
Total aboveground	9,940	33.5	6.2	59.8	43.2	10.8	4.4
Roots	930	2.3	0.9	1.5	2.1	0.3	0.2
Total tree	10,870	35.8	7.1	61.3	45.3	11.1	4.6
SUBORDINATE VEGETATION							
Salal - current	1,530	12.4	2.1	15.8	9.5	3.7	0.8
- older	2,906	21.8	3.6	23.0	29.1	8.5	3.0
- stem	1,774	5.7	4.3	3.6	6.4	1.7	2.1
Oregon grape	110	1.0	0.2	0.9	0.4	0.1	0.03
Bracken fern	430	4.3	1.0	7.7	2.5	1.1	0.06
Moss	60	0.5	0.1	0.4	0.2	0.1	0.03
Other	50	0.5	0.1	0.5	0.2	0.1	0.03
Total aboveground	6,860	46.1	11.3	51.9	48.0	15.3	6.1
Roots	2,560	6.4	2.6	4.1	5.9	0.8	0.6
FOREST FLOOR	3,860	28.0	6.2	10.8	30.9	6.6	4.6
SOIL							
0 - 15 cm	29,820[a]	895[a]	1,320[a]	91	320[b]	43[b]	
15 - 30 cm	30,370	875	1,220	88	259	28	
30 - 45 cm	28,461	782	820	65	171	15	
45 - 60 cm	8,200	355	430	42	87	14	
Total soil	96,851	2,907	3,790	286	837	100	
TOTAL ECOSYSTEM	121,001	3,023	3,817	414	919	119	

N.B. Some of the subtotals were estimated on the non-rounded figures, so there may be some slight discrepancies.

a... total estimates.
b... exchangeable estimates.

of the tree represented only 59% of the total aboveground biomass (*i.e.*, tree + understory) and a smaller proportion of many nutrients, *e.g.*, 46% of the aboveground N was in the tree component, while the comparable figures for the 36-year-old stand were 99% for the organic matter and 98% for the N.

If it is assumed at age zero that all vegetative materials above the mineral soil were removed and/or decomposed, the changes involved over the total age span (50 years) can be observed. Some of the organic matter trends are indicated in Figure 10. It is obvious that while the tree components of the older stands (36 through 49 years) have reached, or are reaching, a steady-state level for some components, specifically foliage, and the wood production (current wood) was levelling off, the 9-year-old stand has yet to reach the period of greatest change, (*i.e.*, the period of maximum productivity. The rapid decline appearing immediately after the 36-year old stand is probably a result of the method of estimation, plus an actual decline in wood production (current wood), so that the true rate of decline in wood productivity is not as sharp as depicted in Figure 10.

(e) Forest Floor Studies.

Both the humus and total forest floor had increasing weights with increasing stand age plotted in Figure 11. The forest floor of the 9-year-old stand was very poorly developed and there was no obvious humus layer. There was a layer of decomposing organic matter which could be described as a fermentation layer, but this was not separated out in the

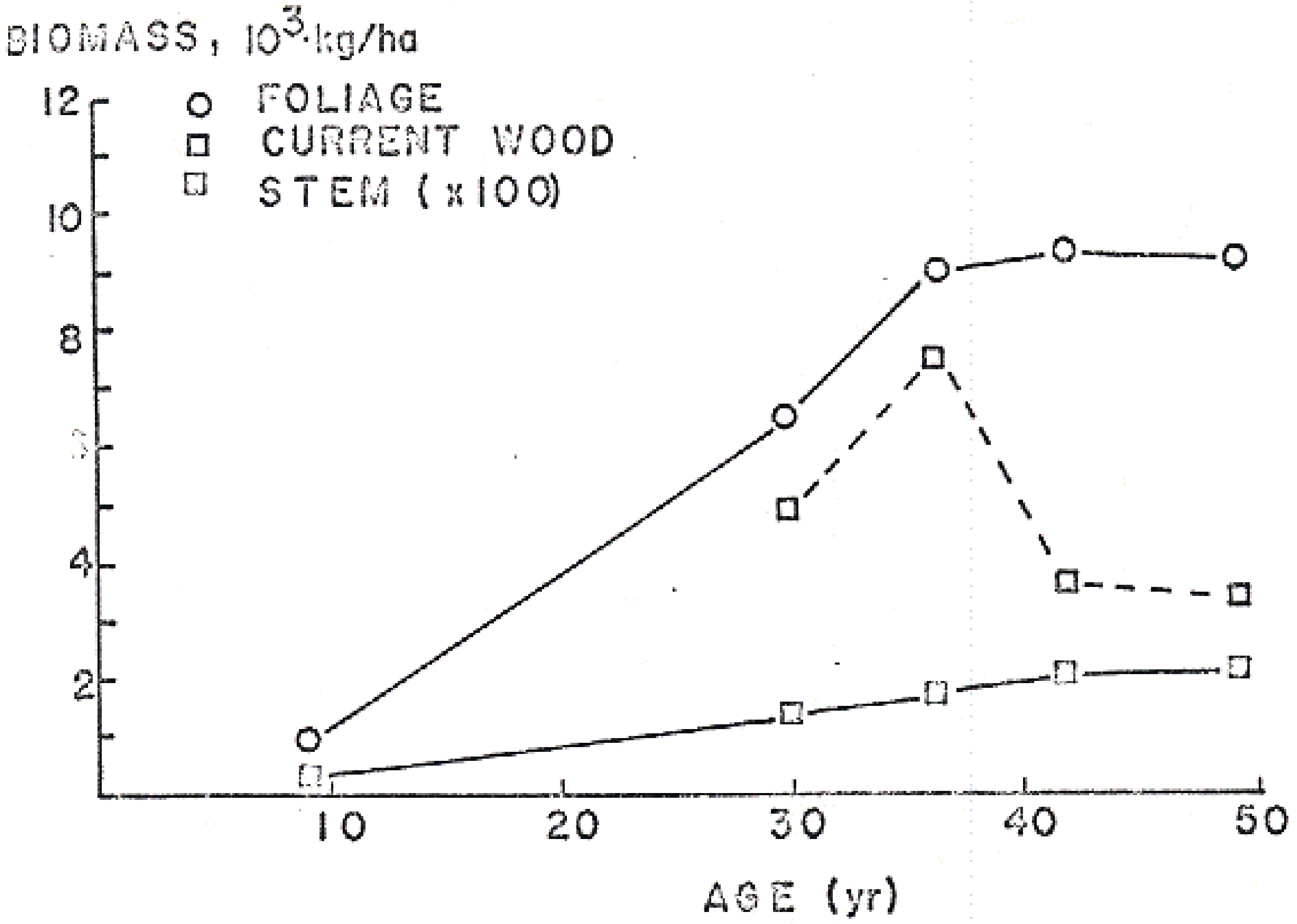


Figure 10. Foliar biomass, current wood, and total wood plotted against stand age in the Cedar River Douglas-fir plantation.

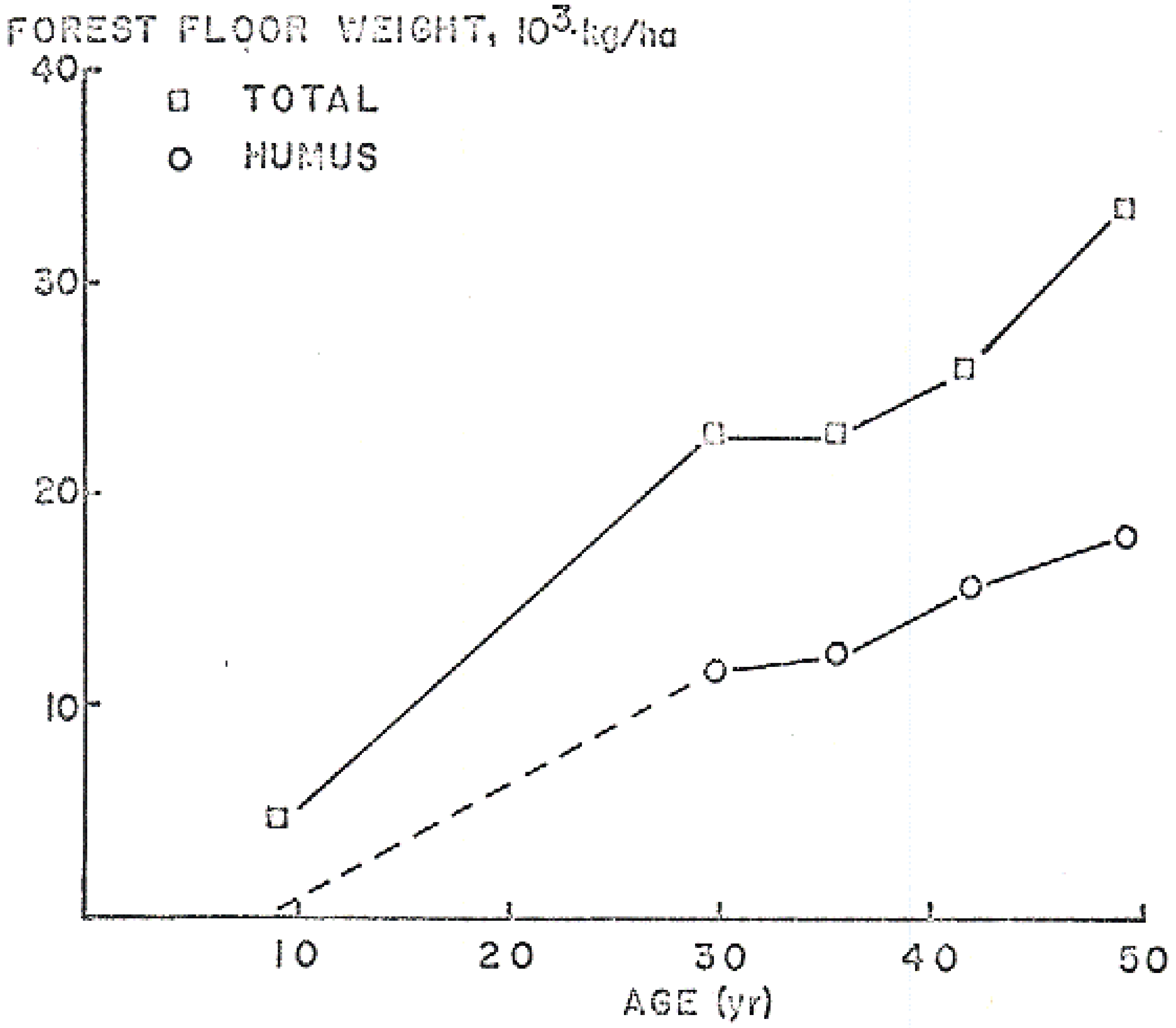


Figure 11. Changes in the total forest floor and humus biomass with increasing stand age in the Cedar River Douglas-fir plantation.

sampling procedure. Using the replicate samples from the plots, regression lines of forest floor weight against stand age were calculated, and these are shown in Table 30. When the value "9 years" was substituted into equation 1 the calculated result was 3552 kg/ha, while the measured mean result was 3860 kg/ha (8% error), which was considered a fairly good prediction. All the calculated equations were fairly similar in slope and they imply a constant increase in forest floor weight with time. Using the equation 3 it was found that the total forest floor organic matter was accumulating at the rate of 540 kg ha^{-1} yr^{-1}. The humus, from equation 4, had an accumulation rate of 210 kg ha^{-1}yr^{-1} of organic matter. Equation 4 gave a humus weight, in the 9-year-old plantation, of 1800 kg/ha which was small and was probably the reason it was not estimated.

Table 30. Regressions of the forest floor weight (minus wood), and humus, against age (years) for the plantation.

No.	Stands used in the calculation	Equation	r^2	S.E.%
Total Forest Floor				
1	30-, 36-, 42-, 49-year-old	$Y = 550.63X - 1403.42$	0.978	8.55
2	9-, 30-, 36-, 42-, 49-year-old	$Y = 555.95X - 1226.09$	0.965	9.79
3	0-, 9-, 30-, 36-, 42-, 49-year old	$Y = 537.82X - 512.35$	0.979	11.1
Humus				
4	0-, 30-, 36-, 42-, 49-year-old	$Y = 374.256X - 161.84$	0.988	6.63

Nutrient accumulation rates can be calculated from: (a) the previous equations (Table 30) multiplied by the nutrient concentrations of the forest floor, (b) calculation of independent equations from the actual forest floor nutrient contents, and (c) by subtracting the outputs from the inputs out of and into the forest floor.

While there was considerable variation in these estimates, depending upon the method employed, they indicated that the forest floor was constantly accumulating and thus causing progressive immobilization of nutrients with increasing age of the stand. Many aspects of nutrient cycling affect or are affected by this nutrient immobilization but only three will be mentioned here and these will not be discussed in any detail. The first involves the reason why accumulation occurs in the forest floor. Possible reasons for accumulation include the widening C/N ratio, increased proportion of wood in the litterfall as the stand increases with age, cooling of the forest floor associated with energy interception by the tree crown as the stand matured, insulating effect of the moss as discussed by Van Cleve *et al*. (1971), possible chemical inhibition, and the changing chemistry of the litterfall.

The second important aspect is the possible effects of this accumulation. If the forest is growing on a marginal site in relation to a particular nutrient (in the case of this study, N) the continued immobilization of the nutrient may be causing progressive increased deficiency of N, thus causing changing patterns in the uptake and cycling (both internal and external to the tree) of the nutrient. This has been hypothesized by Heilman (1966), Miller (1966, and Viro (1967).

Table 31. Nutrient accumulation rates (kg $ha^{-1}yr^{-1}$) in the forest floor based on (a) modulation of organic matter accumulation regression, (b) nutrient content regression, (b2) nutrient content regression including the forest floor wood, and (c) as a difference of inputs and outputs. The figures in parentheses are the percentage of uptake removed from the forest floor.

Method	N	P	K	Ca	Mg	Mn
a	5.3	0.81	0.81	3.9	1.24	0.48
b	4.47	0.67	0.67	3.3	1.03	0.33
b2	4.86	0.72	0.89	3.8	1.14	0.42
c inputs & outputs						
9-year-old	7.5	1.0	5.1	10.6	1.32	1.82
	(14)	(1)	(16)	(25)	(2)	(28)
36-year-old	11.6	0.45	5.3	1.1	1.7	3.8
	(31)	-	(21)	-	(10)	(40)
42-year-old	16.2	1.5	14.0	15.2	1.4	6.5
	(57)	(30)	(69)	(41)	(4)	(72)

The third aspect is the reaction of the tree to the changing distribution of the substrata nutrients (from soil to forest floor). In Table 31, the measured forest floor accumulation rates are shown (methods a and b) and an estimate based on inputs and outputs (method c) is also shown. Method c does not include the effect of tree uptake from the forest floor, but by using method b2 for the accumulation rate, the uptake from the forest floor can be approximated by difference as follows:

Inputs = Outputs + Accumulation,

and Outputs = Lysimeter plate losses + uptake from the forest floor by plants.

Rearranging these equations, Uptake from the forest floor = Inputs - Accumulation - Leaching (lysimeter plates), which amounts to the difference between methods b2 and c in Table 31. This can be calculated for each age of the study where all data are available, and while there are some obvous discrepancies (specifically P and Ca for the 36-year-old stand), the trees are removing 6.7, 4.4, 0.5, and 3.4 kg $ha^{-1}yr^{-1}$ from the forest floor for N, K, Mg, and Mn respectively for the 36-year-old stand. As Table 31 indicates these figures represent 31, 21, 10, and 40% of the uptake of these four nutrients respectively.

(f) Nutrient Transfers of the Plantation

To complete the nutrient cycles, the summary data of the nutrient transfer estimates for the 42- and 49-year-old stands are shown in Tables

32 and 33. No lysimter plate data are available for the 49-year-old stand. The stands are fairly similar in most respects, but there are some obvious differences, for example, the greater mortality in the 49-year-old stand.

In comparing the 42 and 49 year-old stands to the 36-year-old stand the nutrient transfers are generally higher in all regards except K. Table 34 lists all transfers measured in the 9-year-old stand. The nutrient return to the forest floor in this stand was almost the same as in the older stands, mainly because of the high return by the understory in the younger stand. The annuals, ferns, and geophytes in the 9-year-old stand were all returned to the forest floor each year, so that a high proportion of the understory standing biomass was returned annually. Tree leaching was not measured in this young stand so that an estimate was made on the proportion of leaf biomass to the 22-year-old stand. This is probably a minimum value, especially as the understory leaching was ignored.

(g) Transfers of Nutrients Internal to the Tree.

When the estimates of requirement, redistribution, and uptake were made, the 36-, 42-, and 49-year-old stands showed very great similarity. This is not surprising as these estimates are based very much on the standing biomass and nutrient contents, leaf leaching being the main random factor. These three stands were over the peak of production and the requirement for all nutrients except Mn was decreasing, *i.e.*, from 39 kg $ha^{-1}yr^{-1}$ at 36 years to 34 kg $ha^{-1}yr^{-1}$ at 49 years for N (a reduction of approximately 12%.

Table 32. Nutrient transfers within the 42-year-old Douglas-fir plantation (kg ha^{-1} yr^{-1}).

Transfer	Organic Matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree - leaf	2,556	20.2	2.6	8.9	30.7	3.7	7.2
- branch	594						
- stem	2,458	2.1	0.2	1.2	1.1	0.5	0.1
Understory - vascular	313	2.2	0.3	1.6	5.2	1.2	1.0
- moss	230	0.9	0.2	0.8	3.5	0.6	1.1
- total	543	3.1	0.5	2.4	8.7	1.8	2.1
Total litter	6,151	25.4	3.3	12.5	40.5	6.0	9.4
Solution							
- leaf wash		0.5	0.8	10.3	5.2	0.3	0.1
- stemflow		0.03	0.01	0.25	0.18	0.03	
- total (with precip.)		2.2	1.1	12.8	7.6	0.8	0.2
Total return to forest floor	6,151	27.6	4.4	25.3	48.1	6.8	9.6
Loss from forest floor		7.3	2.2	14.6	24.0	3.6	
Loss from rooting zone		3.4	0.6	13.4	12.1	2.3	
Loss from system		1.6	0.1	4.5	10.5	3.2	
Within Tree							
Foliage - requirement	2,440	26.4	5.2	19.4	9.2	3.0	2.0
- translocation		11.0	2.4	-1.7	-19.7	-3.1	-5.9
- uptake		15.4	2.8	20.1	28.9	6.1	7.9
Branch - requirement	480	4.0	0.3	2.7	1.9	0.7	0.3
- translocation		2.4	-0.03	1.9	-0.6	0.5	0.1
- uptake		1.6	0.33	0.9	2.5	1.2	0.4
Wood - requirement	3,650	5.5	0.5	4.0	1.8	2.2	0.3
- translocation		3.6	0.2	2.8	nil	1.8	-0.2
- uptake		1.9	0.3	1.2	1.8	0.4	0.2
Total tree requirement		35.9	8.0	26.1	12.9	5.9	2.6
Total tree uptake		19.8	2.6	22.2	28.0	7.4	8.4
% uptake/requirement		53	44	85	217	125	322
Within Understory							
- requirement	891	9.9	1.8	8.1	4.2	1.3	0.6
- translocation		3.7	1.0	3.2	-8.9	-0.7	-1.8
- uptake		6.2	0.8	4.9	13.1	2.0	2.4
Total stand uptake		26.0	3.4	23.8	41.1	9.4	10.8
Return to forest floor-loss		20.3	2.2	10.9	24.1	3.2	
Stand uptake-return to forest floor		-1.6	-1.0	-1.1	-7.0	2.6	1.2

Table 33. Nutrient transfers within the 49-year-old Douglas-fir plantation ($kg\ ha^{-1}\ yr^{-1}$).

Transfer	Organic matter	N	P	K	Ca	Mg	Mn
<u>Litterfall</u>							
Tree - leaf	1,780	17.8	2.6	6.6	27.6	2.3	5.3
- branch	500						
- stem	5,772	4.4	0.5	2.2	3.4	0.6	0.1
Understory - vascular	316	2.2	0.3	1.6	5.2	1.2	1.1
- moss	210	0.9	0.2	0.8	3.2	0.6	1.0
- total	526	3.0	0.5	2.4	8.4	1.8	2.1
Total litter	8,578	25.2	3.7	11.2	39.4	4.7	7.4
<u>Solution</u>							
- leaf wash		1.8	0.5	9.0	4.0	1.4	0.2
- stemflow							
- total (with precip.)		3.5	0.8	11.2	6.2	1.9	0.3
Total return to forest floor		28.7	4.4	22.4	45.6	6.6	7.7
Loss from forest floor							
<u>Within Tree</u>							
Foliage - requirement	2,200	25.9	4.9	19.0	7.4	3.0	1.7
- translocation		9.2	3.1	-0.5	-19.5	-3.1	-4.4
- uptake		17.5	2.3	19.5	30.9	7.5	6.2
Branch - requirement	420	3.2	0.3	2.4	1.7	0.6	0.2
- translocation		1.9	0.0	1.5	-0.7	0.4	0.1
- uptake		1.4	0.3	0.9	2.4	0.2	0.1
Wood - requirement	3,300	4.8	0.4	3.6	1.7	2.5	0.8
- translocation		3.0	0.2	2.6	0.2	2.2	0.7
- uptake		1.8	0.2	1.0	1.5	0.3	0.1
Total tree requirement		33.9	5.6	25.0	10.8	6.1	2.7
Total tree uptake		20.7	2.8	21.4	34.8	7.0	6.4
% uptake/requirement		60	50	86	322	115	242
<u>Within Understory</u>							
- requirement	970	11.0	1.9	7.1	4.3	1.9	1.0
- translocation		4.0	1.0	3.1	-9.1	-1.1	-1.9
- uptake		7.0	0.9	4.0	13.4	3.0	2.9
Stand uptake - return		-1.0	-0.7	2.0	2.6	3.4	1.6

Table 34. Nutrient transfers within the 9-year-old Douglas-fir plantation (kg ha^{-1} yr^{-1}).

Transfer	Organic matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree	360	2.5	0.3	1.4	3.4	0.3	0.7
Understory	2,055	12.3	0.8	12.3	22.6	2.3	3.1
Total litter	2,415	14.8	1.1	13.7	26.0	2.6	3.8
Solution							
- leaf wash[1]		0.2	0.03	1.2	0.4	0.3	0.02
Total (with precip.)		1.9	0.2	3.4	3.7	0.8	0.12
Total return to forest floor		16.7	1.3	17.2	29.7	3.4	3.9
Loss from forest floor		9.2	0.3	12.1	19.1	2.0	2.1
Within Tree							
Foliage - requirement	360	4.8	0.7	3.5	1.2	4.4	0.3
Woody - requirement	750	2.4	1.8	8.0	5.9	1.5	0.8
Total requirement	1,110	7.2	2.5	11.5	7.1	5.9	1.1
Total translocation		1.7	0.7	3.2	-0.8	0.2	-1.0
Total uptake		5.7	1.8	9.5	8.3	5.9	2.1
Within Understory							
- requirement - salal	1,530	12.4	2.1	15.8	9.5	3.7	0.8
- oregon grape	30	0.4	0.7	0.5	0.1	0.04	0.01
- bracken fern	430	4.3	1.0	7.7	2.5	1.1	0.1
- moss	15	0.2	0.02	0.1	0.1	0.02	0.01
- other[2]	50	0.5	0.1	0.5	0.2	0.1	0.03
- total	2,055	17.8	3.9	24.6	12.4	5.0	0.9
- translocation		7.3	2.1	8.2	-6.2	0.5	-2.0
- uptake		10.5	1.7	16.8	18.6	4.5	2.9
Total stand uptake		16.2	3.4	26.3	26.9	10.4	5.1
% stand uptake by tree		35	40	32	31	57	42
% uptake/requirement(tree)		79	72	83	117	100	188
% stand uptake/requirement		72	64	73	138	95	244
Return - forest floor loss		7.5	1.0	5.1	10.6	1.4	1.8
Uptake - return		-0.5	-0.4	0.4	11.1	-1.1	-1.0

---

[1] Based upon proportional leaching of foliar mass of the 22-year-old stand.

[2] Mainly annuals.

The % uptake/requirement estimate gave an indication of where the trees were obtaining the nutrients to fulfill these requirements, *i.e.*, from within the tree or from the soil-humus complex. A high figure indicates that the soil-humus complex is the major supplier, while a low figure indicates that the tree is internally redistributing a high proportion of its requirement. These figures must be looked at in relation to the magnitude of the leaching of a particular nutrient. A ratio of over 100 indicates that the nutrient is probably being accumulated in luxury amounts. Over this sequence of ages from 9 to 49 years, the trees were generally increasing their efficiency of redistribution of N and P. Potassium remained relatively constant over this age sequence, while Mg, Ca, and Mn were accumulated. Some differences appeared in the 36-year-old stand and these originated in the lower estimate of leaching from the crown (throughfall) than in the other stands. Within these ecosystems there was no apparent deficiency for the trees of K, Ca, Mg, and Mn, and probably there was an overabundance of these nutrients considering the quantity of nutrients within the soil. Nitrogen was limiting and may become more so, and P, while not limiting for growth may require less energy for redistribution than for removal from the soil because of bonding by sesquioxides.

Over this 50 year period in the life of the stand, there has been a great change in the role of the understory component of the ecosystem. In the 9-year-old stand the understory component was taking up 70, 60, 78, 73, 43, and 58% of the total stand uptake for N, P, K, Ca, Mg, and Mn respectively, while in the older stands the understory component was taking up less than 5% of all nutrients. There was a similar relationship in the return of nutrients to the forest floor by the understory.

4. Extension to the naturally regenerated stands within the watershed (and inclusion of those reported in the literature).

(a) Data Organization

Data from the naturally regenerated stands of Douglas-fir within the watershed, and of approximately the same Site Quality as the plantation, were included to:

(a) extend the age range,

and (b) within the same age range, compare these stands to those of the plantation, especially in regard to stand density. Data available from other studies on nutrient distribution in stands of similar Site Quality were included to indicate how typical the Cedar River data was of Site Quality IV stands.

An augmented age range within the Cedar River Watershed included a 73-year- and a 95-year-old stand. The 95-year-old stand had the complicating factor of a slightly higher Site Quality than other stands in the study but it was considered similar enough to use in determining trends over time. Also, this was the only stand available of this age range. A younger stand was also included, 22 years old, which was considered to be near the period of maximum tree productivity for these stands (*i.e.* located in the time series between the 9- and the 30-year-old stands). The 42-year-old naturally regenerated stand was selected for its stand density, which was much lower than that for the plantation (822 versus 1289 stems/ha).

The inclusion of naturally regenerated stands increased variation in regard to stand structure and this may have an effect upon nutrient cycling. This variation arose because the stands were probably not initiated with uniform or near optimum spacing, so that stands have irregular spacing with a range of ages.

(b) Tree Organic Matter Distribution

The biomass and nutrient distribution of the naturally regenerated 22-, 30-, 42-, 73-, and 95-year-old stands are listed in Appendix 1. The data do not include estimates for dead branches, and while lichens were observed on the branches and boles of the 73- and 95-year-old stands no estimates were made of their biomass. As it is difficult to assess the data while in tabular form, portions have been plotted on graphs (Figures 12 through 21), which also include the data of the plantation, and where possible the data of other workers (Heilman, 1961; Paddock, 1964; Webber, 1973; and Long, 1973). Because of the insensitivity of measurement, and the present concentration upon the biological changes within the stand, the soil nutrient content has not been included here. The magnitude of the soil nutrient pool was similar in the range of stand.

The foliage biomass data (Figure 12) indicate a levelling off, as was hypothesized, except for the case of the 95-year-old stand which had a slightly higher site quality. Using the 11% limit as described for the plantation, the 73- and 95-year-old stands were higher than permissible for steady-state. Based on this single year estimate for the 73-year-old stand, it appeared that the hypothesis was false, but when the 73-year-old stand was re-estimated after two years, mortality had brought it within the 11% limit (9,900 kg/ha). If a 15% limit had been used, the original figure would have been within the limits. The 73-year-old stand estimate, being within the limits, was supported by the estimate from Paddock's 75-year-old stand. It is argued here that the 95-year-old stand would have been within similar limits if it had had a lower site quality.

While the estimates of the foliar biomass are relatively uniform, the wood accumulation showed more variation, especially when the data of other investigators are included (Figure 13). The data of the Cedar River Watershed (both plantation and naturally regenerated stands) indicated a steady increase in wood accumulation which may be described by the regression line,

$Y = 3164.25X + 15041.94$, where Y = wood biomass (kg/ha) and
X = age in years ($r = 0.969$ and S.E. = 16.68).

This implies a constant rate of wood production of approximately 3200 kg $ha^{-1}yr^{-1}$, belied by the estimate of current wood which ranges from 7,500 to 2,500 kg $ha^{-1}yr^{-1}$ (if the 9-year-old stand is ignored), but the difference can be explained by tree mortality. The data of other studies do not fit so well, especially that of Heilman (1961). The reason for this could be ascribed to stand history. The foliage is a non-accumlating organ, *i.e.*, it reaches a stead-state, while the wood is accumulating with time. The foliage will not reflect the stand history in that there will be a similar steady-state level for a stand of a given site quality independent of the initial conditions of the stand. The wood on the other hand, will be quite sensitive to stand history, so that a dense stand accumulating wood rapidly from stand initiation will have a much higher standing wood biomass (and probably higher wood mass on the floor

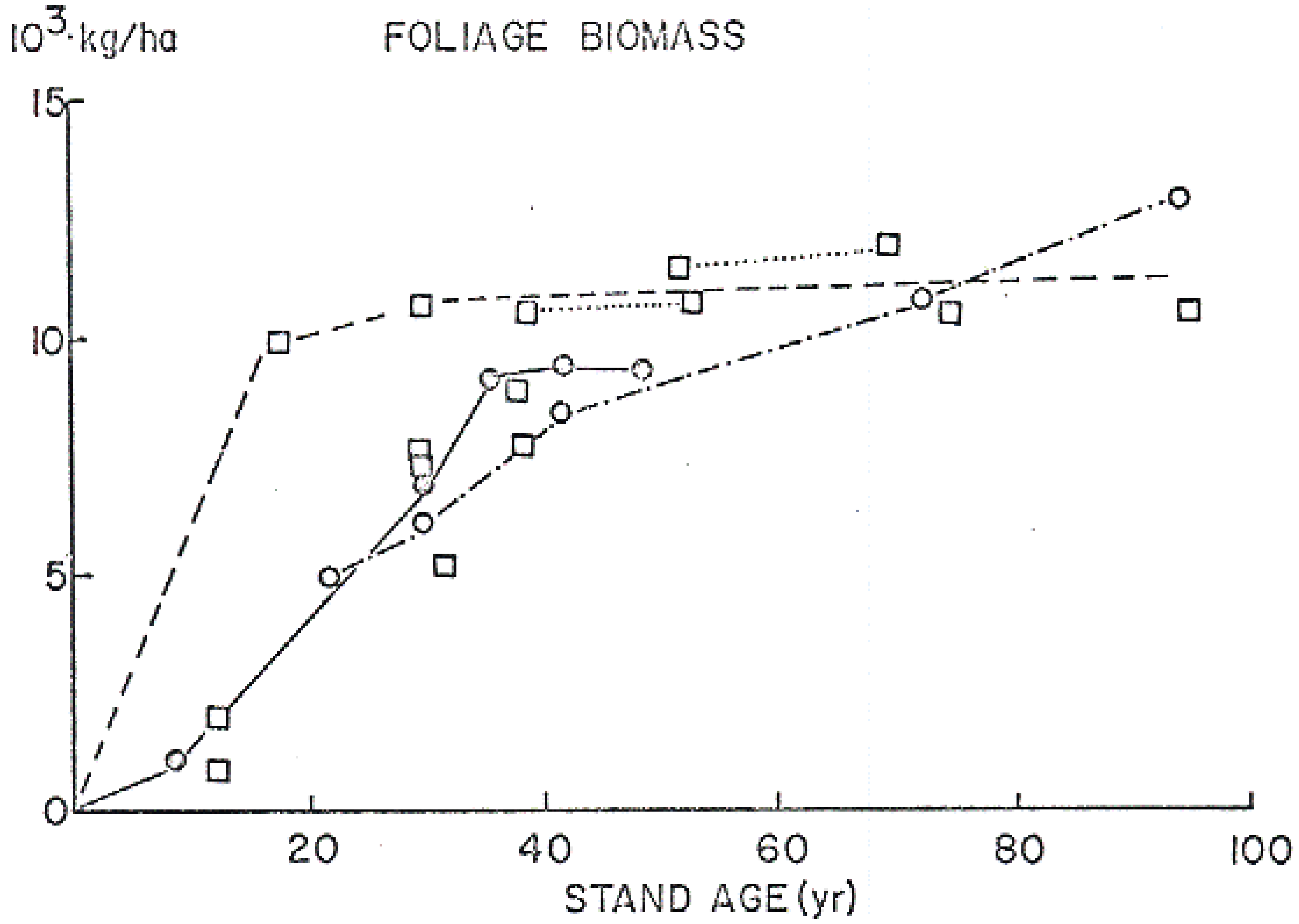


Figure 12. Foliar biomass in relation to stand age in Site Quality IV Douglas-fir stands. Data are from the Cedar River plantation and naturally regenerated stands, and from other workers reported in the literature.

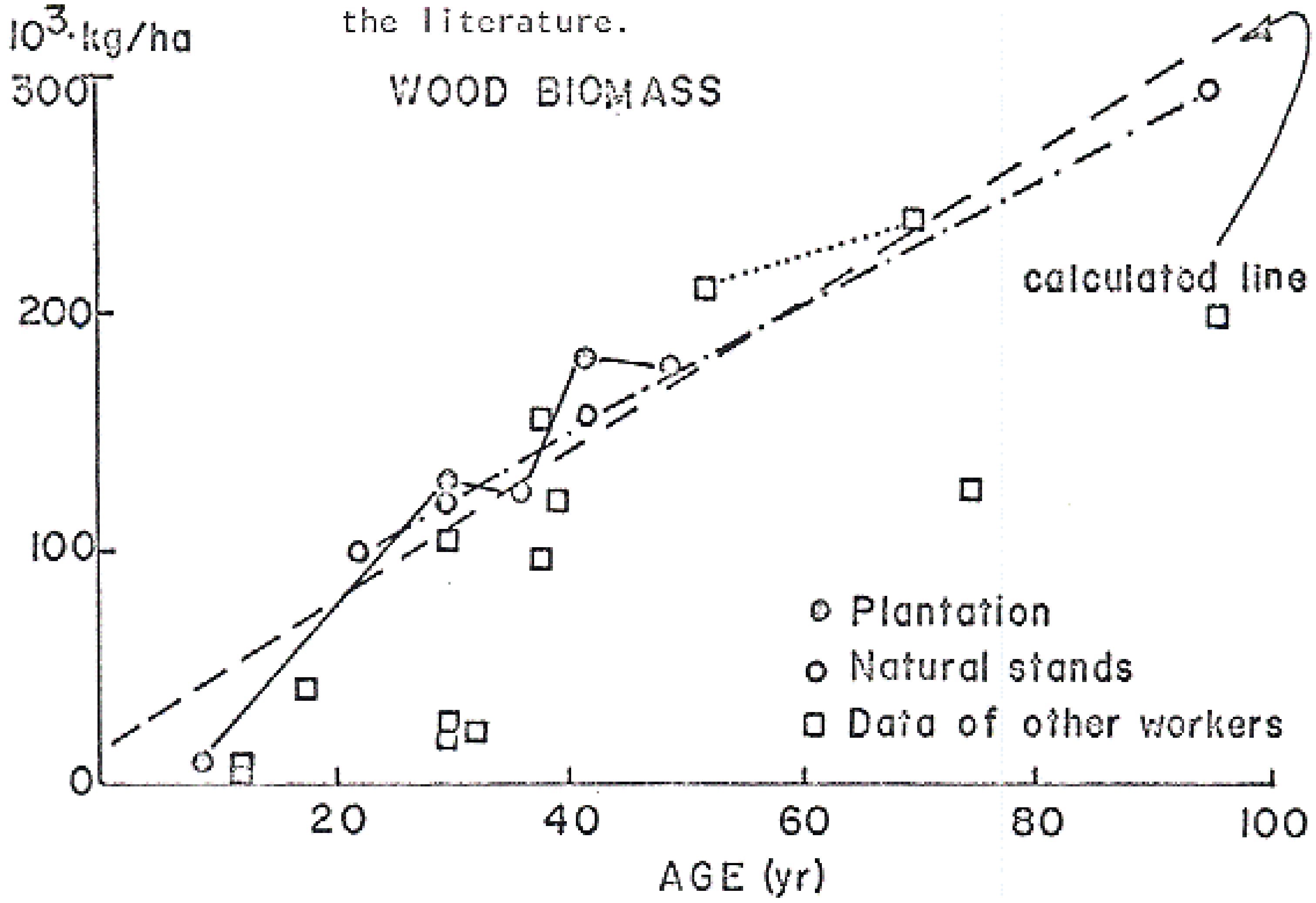


Figure 13. Wood biomass of Douglas-fir stands plotted against stand age. Stands include the Cedar River plantation and naturally regenerated stands, together with the data of other workers. The calculated line is based only on the Cedar River Data.

reflecting mortality) than a sparsely stocked stand in which the trees are only just beginning to actively compete. This was one reason why the study of the plantation was important as it removed the variables associated with stand history.

(c) Understory Relations

Figure 14 indicates the importance of the understory in the early period of the stand life and its declining importance after stand crown closure (Long, 1973). It also gives some indication of the increasing importance of moss after crown closure. The 36-year-old stand of Cole *et al.* (1968) appears to have had a very poor estimate of understory biomass, probably being 4-5 times lower than would be expected based upon the data of other stands. This is, in part, a result of not estimating the moss and there may be a seasonal effect involved as previously discussed.

The understory data from the studies of other workers indicate a trend similar to the present study but generally with lower levels of biomass. The dominant vascular understory species was salal (*Gaultheria shallon*) and its biomass was shown to be inversely correlated with overstory foliar biomass (Long and Turner, 1975). Thus the present trend of decreasing total understory biomass with age was expected. Many stands, plotted in Figure 14, below 400 kg/ha were very dense and the understory was almost entirely moss.

The line connecting the Cedar River data (including that of Long's (1973) 5-year-stand) is drawn through zero implying that the areas were totally cleared before stand establishment, either by fire, in the case of

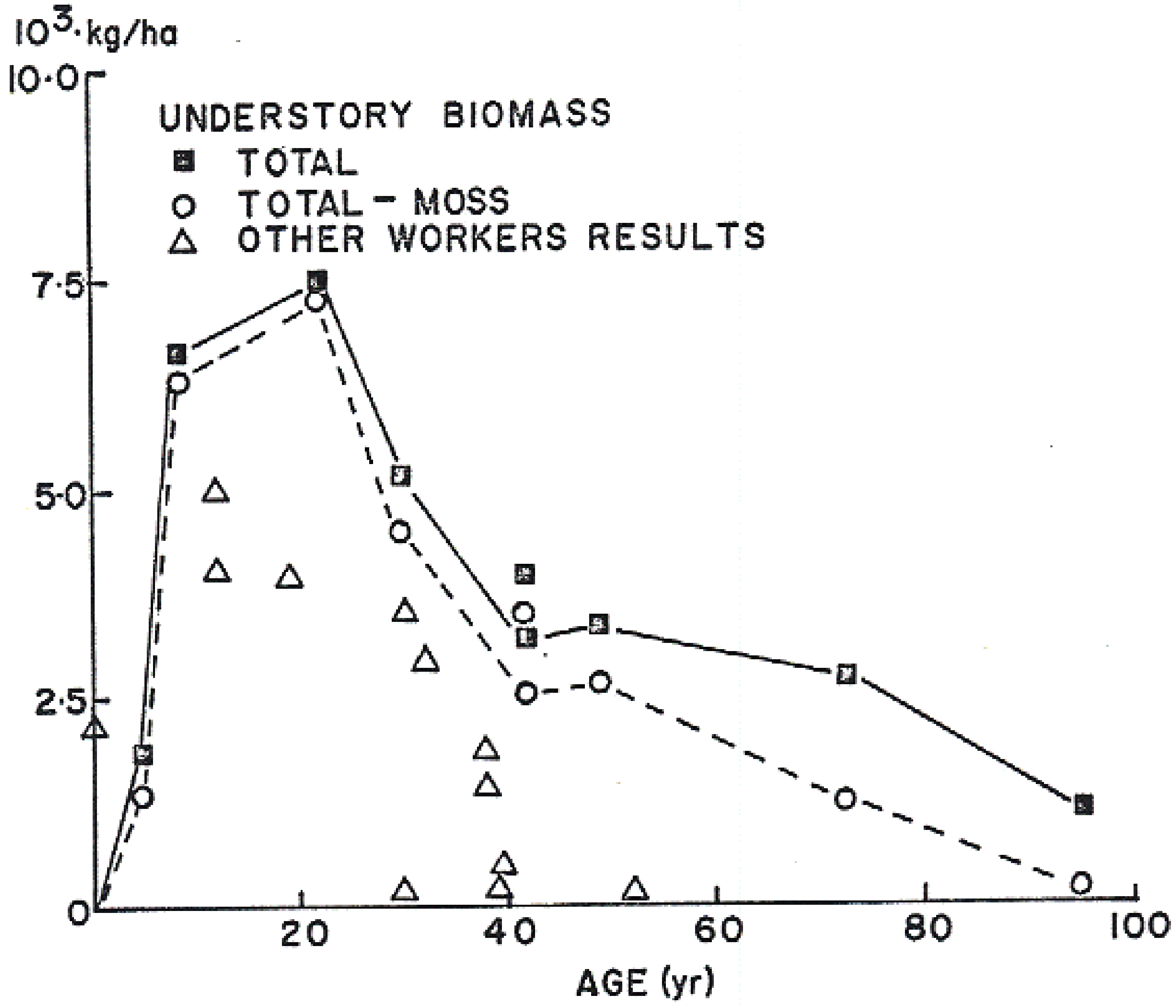


Figure 14. Changes in understory biomass with increasing age of the stand. The solid line connects the total understory biomass of the stands in the Cedar River Watershed and the broken line the total understory minus moss. The triangles represent the data of Heilman (1961) and Paddock (1962).

natural stands, or by man, in the case of plantations. If an area is lacking in seed source, or does not re-establish to trees for some other reason the understory may predominate. This can be seen in the stand studied by Paddock (1964) which, when plotted at time zero, as there were no trees, did have an understory species biomass of approximately 2,200 kg/ha. This is mentioned to indicate that overstory and understory establishment may not occur at the same time so that on Figure 14, the alternative to time referring to tree age may be the ecosystem age, something which is rather harder to define.

(d) Forest Floor Studies.

In Figure 15 the forest floor weights are plotted, separated into humus and total forest floor components. The humus shows a constant increase in weight with age and this can be described by the regression,

$Y = 371.98X - 263.92$ ($r^2 = 0.995$, S.E. $= 6.3$), where Y = humus biomass and X = age in years.

The total forest floor also increases with age but it is more variable, mainly because of wood content. This quantity of wood on the forest floor will be related to the stand structure as discussed for the wood production. For example, comparing the 42-year-old plantation to the sparse 42-year-old stand, the sparse stand had negligible wood on the forest floor while the plantation had 6,900 kg/ha.

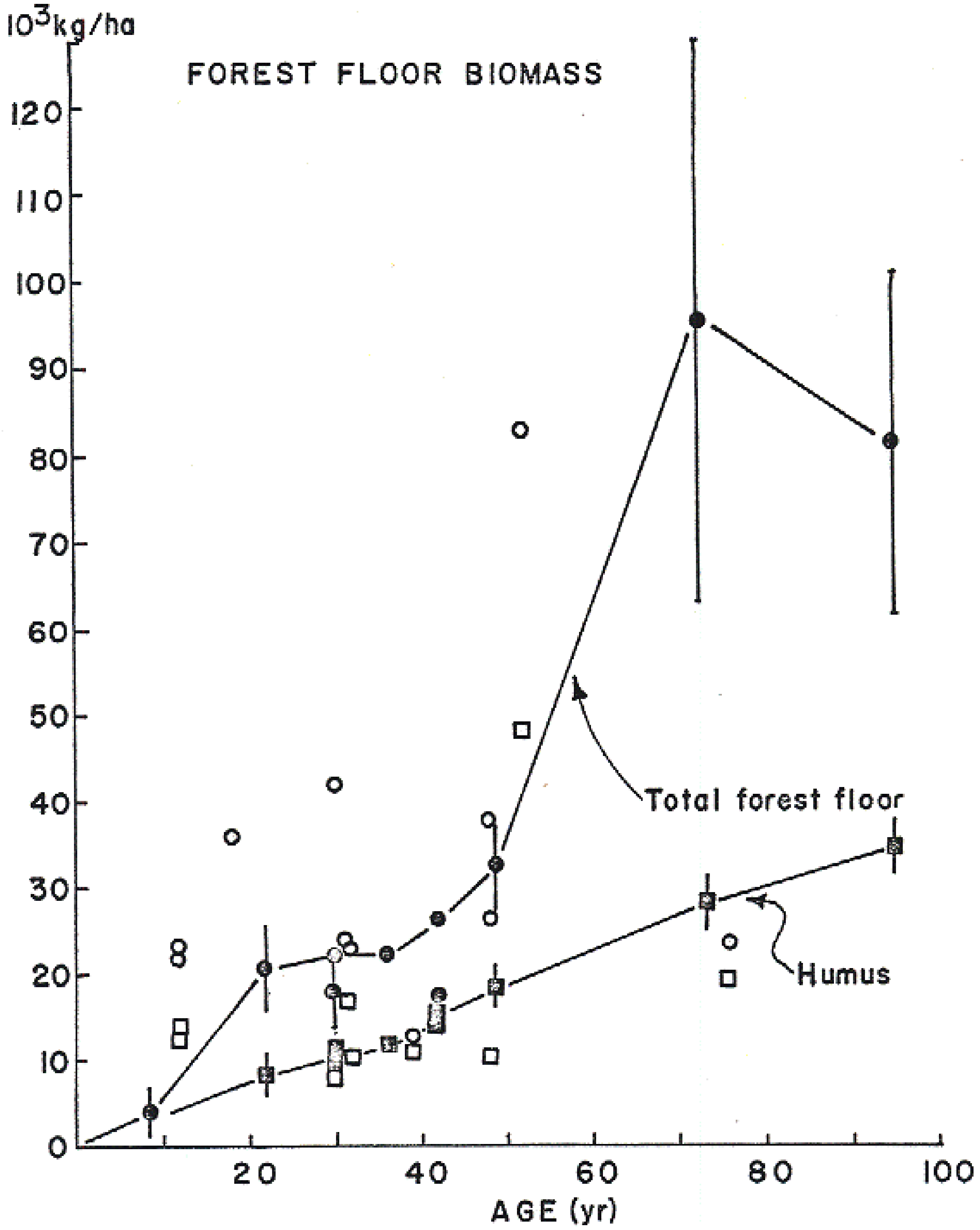


Figure 15. Total forest floor (circles) and humus (squares) biomass plotted against the age of the stand. Solid squares and circles are data collected from the Cedar River Watershed, while the open squares and circles are data from the literature.

It was originally hypothesized that all major components of the stand, except wood, would, shortly after crown closure, reach steady-state and that most of the transfers would subsequently reach a comparable or parallel steady-state level. What actually appears to happen is that the foliage and total crown do reach steady-state and this depends on the time of crown closure, which is, in turn, an age-density, rather than a strictly age, relationship. This can be described by the three dimensional diagram shown in Figure 16, indicating that the denser the stand, the faster the foliar biomass development. From the few data available (Heilman, 1961; Turner, personal files) the height of the surface appears to be controlled by site quality, *i.e.*, the higher the site quality, the higher the surface (hence the higher foliar biomass of the 95-year-old stand). This figure also shows that a steady-state level has actually been attained. When all the data are pooled after crown closure, and the 95-year-old stand is ignored, no significant relationship between foliar biomass and age is evident. The surface is not entirely flat but is made up of a series of fluctuations arising from productivity and mortality as discussed for foliar stability in the plantations.

(e) General Conclusions and Hypothesis Modifications.

The foliage and total crown appear to be the only organic matter compartments of the ecosystem which are reaching steady-state. The wood, humus, and hence total forest floor appear to be increasing steadily while the understory is decreasing. It may be that in the understory the

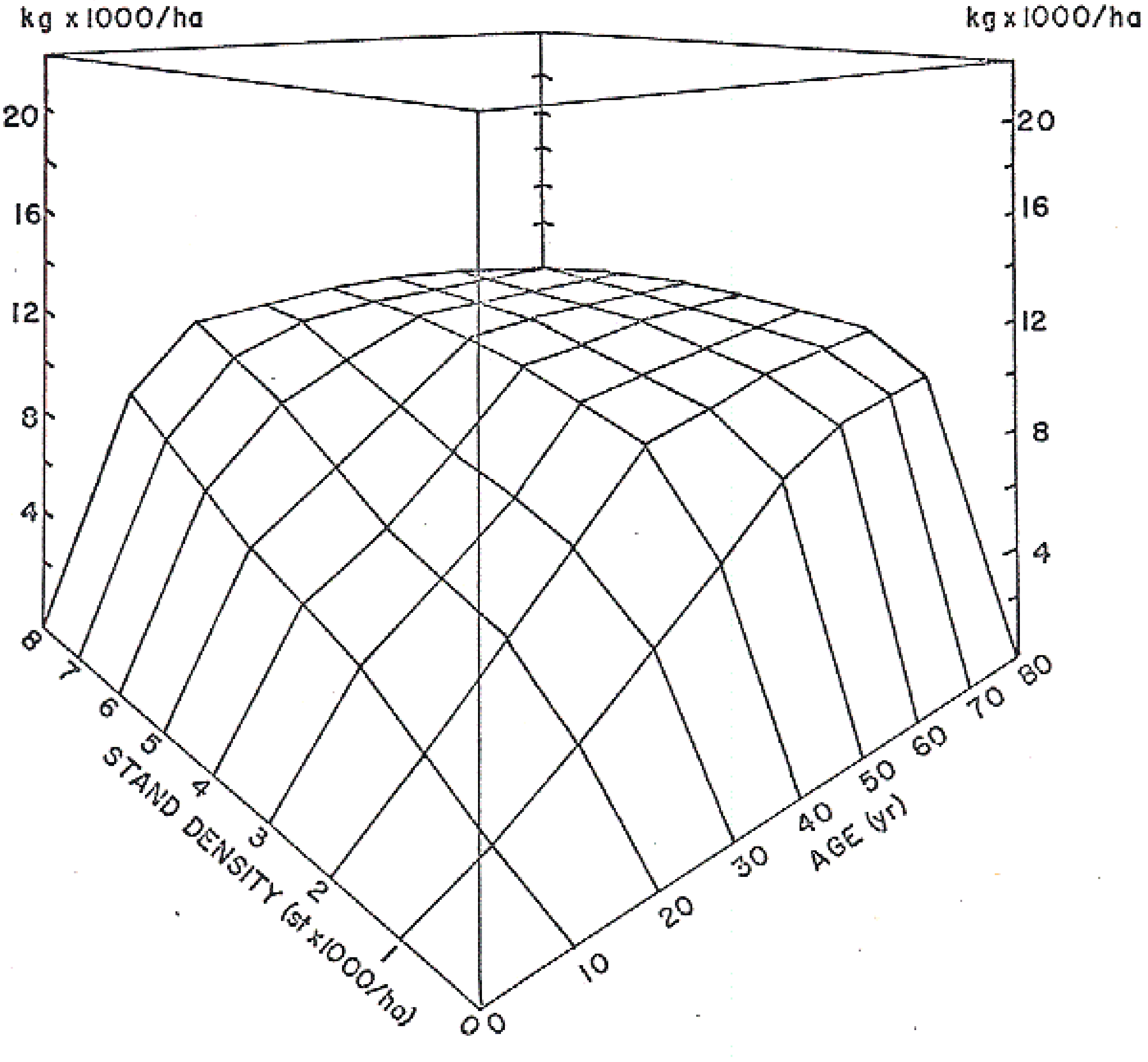


Figure 16. Three dimensional diagram showing the relationship between the foliar biomass, the stand age, and the stems per hectare, of a Site Quality IV Douglas-fir Stand .

the mosses are reaching a steady-state level but further data would be needed to verify this.

As many of the components are not reaching steady-state in terms of the biomass, it is necessary at this stage to modify the original hypothesis. This is especially important, as by the method of study, the nutrient cycle is a modulation of the organic matter cycle, so that if the organic matter does not reach steady-state, then it is doubtful that the nutrients will either.

This modification to the hypothesis will be done in such a way that the definition of steady state includes not only the narrow limits characterized by a constant quantity in a component over a long period of time, but also allows for a constant increase in the component over time. Thus, it is proposed that the constant component (a horizontal line with time) will be the "true" steady-state situation, while the constant increase will define a "modified" steady-state. It is assumed that a constant accumulation or release from a compartment will have the same relative effect or role within the nutrient cycle as if the compartment were constant, *i.e.*, when the situation where the component nutrient is constant, with constant inputs and outputs, is compared to a similar situation but with constant accumulation, the only difference will be that the output will be smaller in the latter case.

(f) Tree Nutrient Distribution

The N content of the tree foliage (Figure 17) showed a definite levelling off at about 110 kg/ha after crown closure. There was some

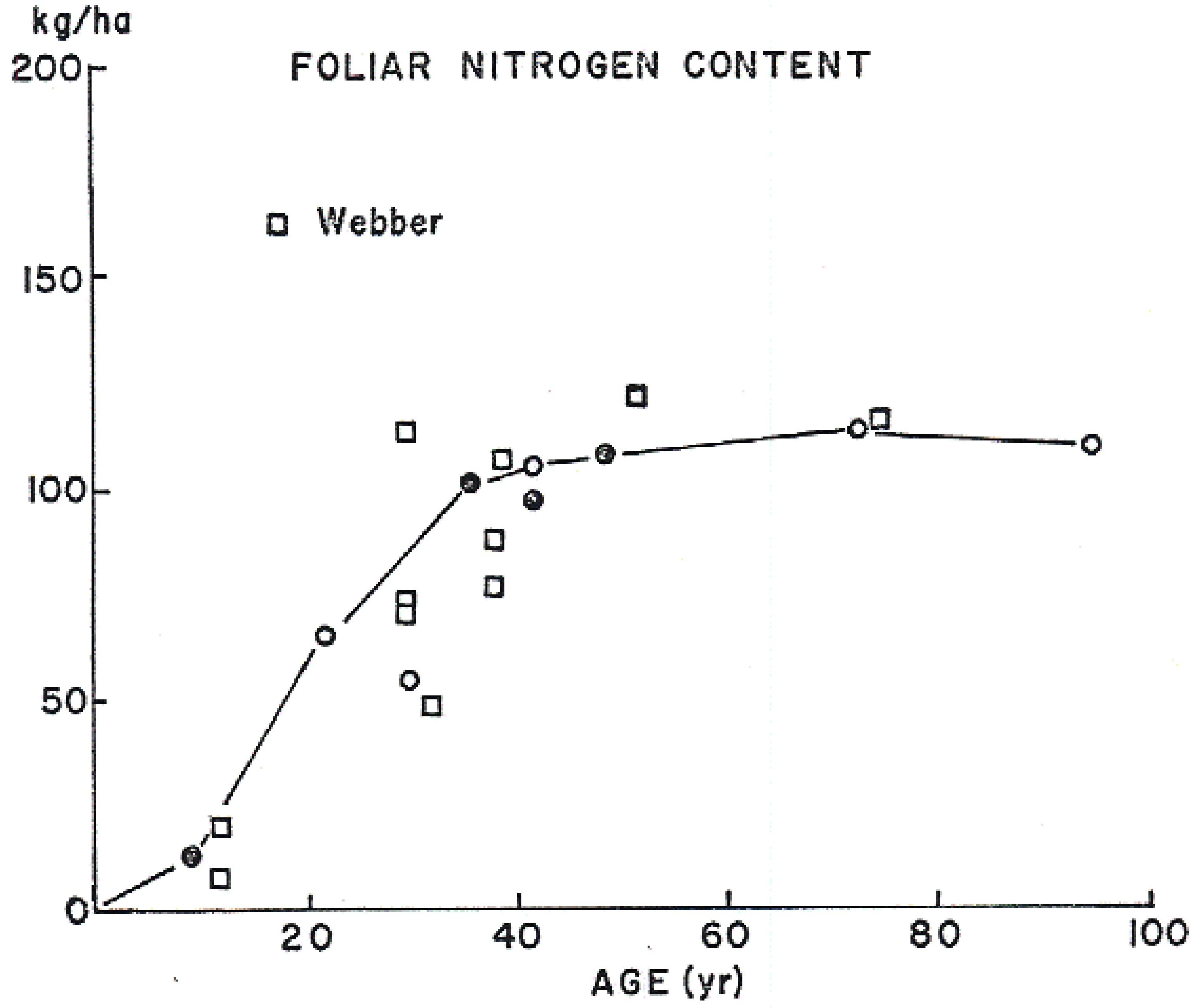


Figure 17. Nitrogen content of the foliage (kg/ha) in the age sequence of stands. The filled-in circles are the plantation data, the open circles are the data of the other Cedar River plots, and the squares are the data of Heilman (1961), Paddock (1962) and Webber (1972). Webber's (1972) data were indicated because of their obvious difference.

variation of the data in the younger stands but the pattern was similar to the organic matter distribution implying a stand density effect. Magnesium similarly appeared to be very stable, after crown closure, at about 14 kg/ha. The distribution of some of the other nutrients in the foliage (figure 18) showed much more variability than for N or Mg. Potassium had more variability but in the older stands it did become fairly stable, while P, Mn, and Ca indicated increasing quantities accumulated as the stand increased in age. For these last three nutrients this increase would imply that there were increasing concentrations of the nutrients within the foliar tissue as the stand aged, because the foliar biomass remains fiarly constant (except in the case of the 95-year-old stand). The increase in P content of the foliage of the 95-year-old stand is proportional to the increase in foliar biomass and thus may be explained by this, but this effect does not apply to Ca and Mn. The increased average concentration of these two nutrients may be related to an increase in needle retention time with progressing age of the stand, thus allowing more time for nutrient accumulation to occur. Evidence for this increase in needle retention shows up in the leaf litter/standing foliar biomass ratio which is low for the younger stands and higher for the older stands (the 22-year-old stand appears to retain needles for only two to three years while the 95-year-old stand's retention time is nearer to six years).

The nutrient content of the wood increased in all cases as the stand age increased (Figure 19), essentially paralleling the biomass changes. This indicates that, unlike the foliage, there is neither large accumulation patterns nor excessive retranslocation. The 42-year-old natural stand was higher in its concentration of N than the other stands studied

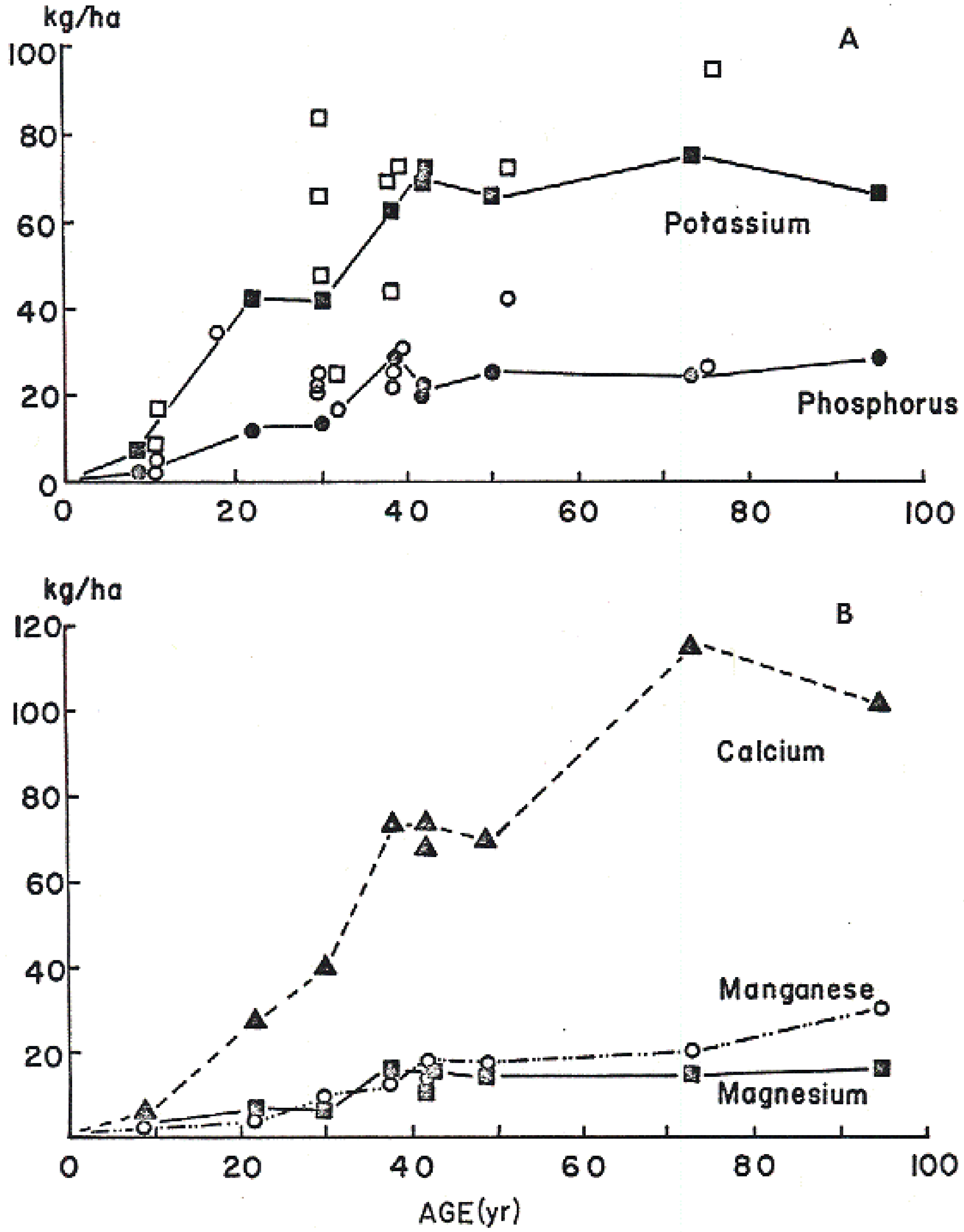


Figure 18. The P and K content of the foliage (kg/ha) are indicated in part A. This includes the Cedar River Data plus that of Heilman (1961) and Paddock (1962). Part B shows the Ca, Mg, and Mn contents of the foliage (kg/ha) for Cedar River. No other data were available for these nutrients.

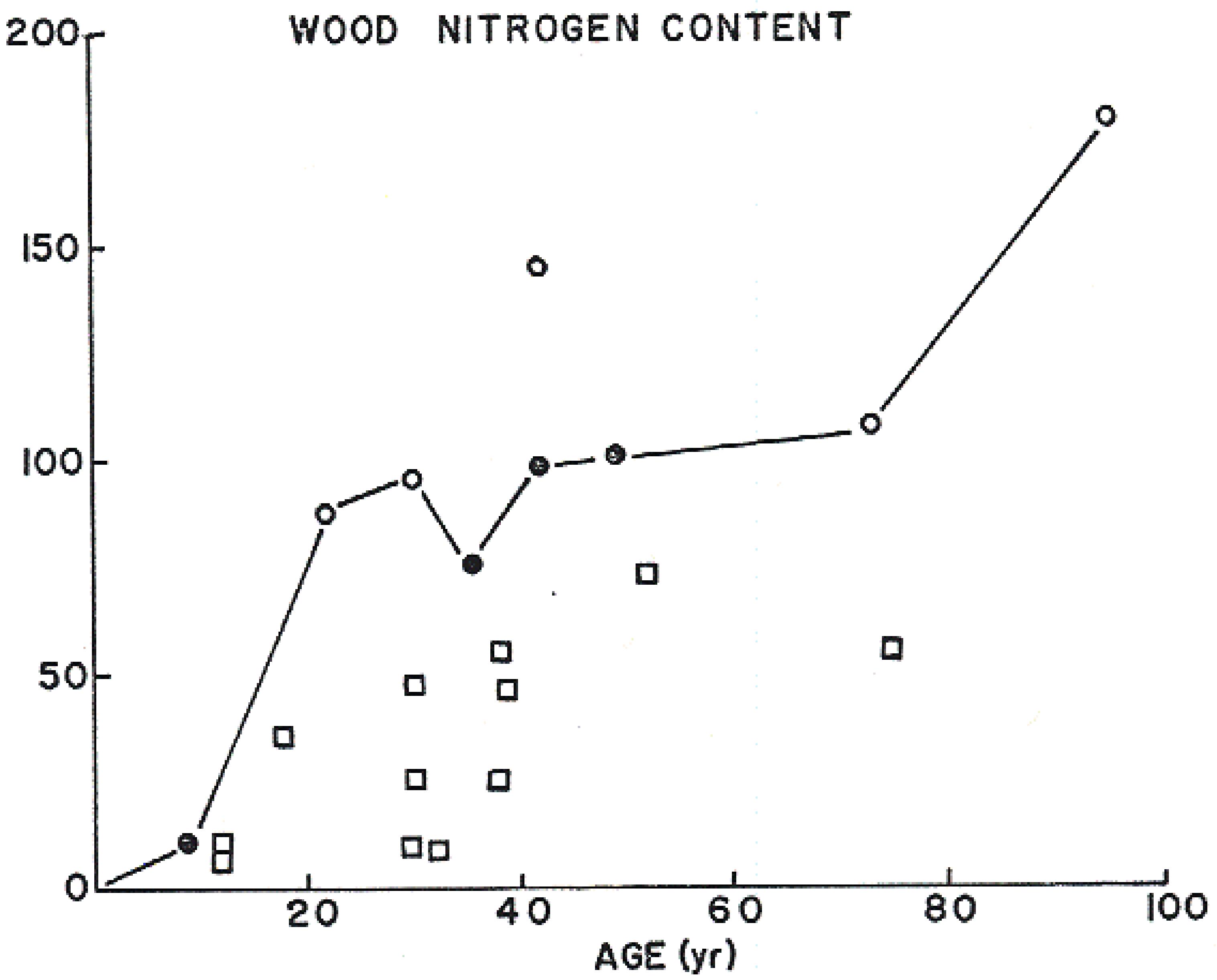


Figure 19. Nitrogen content of the wood (kg/ha) in the age sequence of stands at Cedar River (circles). The data of Heilman (1961) and Paddock (1962) (squares) are also included.

but there was no obvious reason for this. While Mn was accumulating in the foliage, it remained constant, or was retranslocated in the wood and branches indicating that, not only do the nutrients differ from each other in the cycling and accumulation patterns, but the pattern of an individual nutrient within the different tissues of the tree also varies.

(g) Forest Floor Nutrient Distribution

The total forest floor nutrient contents were plotted in Figure 20 and the results indicated continuous N accumulation with increasing stand age. This was probably related to the slow organic matter decomposition rate. A regression describing the accumulation of N was calculated, and for the humus component yielded;

$Y = 3.68\ (\text{Age}) - 2.13$, ($r^2 = 0.96$, S.E. = 13.8%), while for the total forest floor N, $Y = 5.66\ (\text{Age}) - 10.43$, ($r^2 = 0.7$, S.E. = 35%. This gave annual accumulation rates of 3.7 and 5.7 kg $ha^{-1}yr^{-1}$ for the organic matter in the humus and total forest floor respectively. This may be partly explained that if the organic matter input has a fairly high C/N ratio, as the N already in the forest floor becomes mobilized it may be re-utilized by the micro-organisms for further organic matter decomposition. If there is only a small amount of N available there will be a lag period before decomposition of organic matter and this will show up as a net annual accumulation of organic matter and the related nutrients requiring decomposition for mobilization. Because of the close relationship between the organic matter and N there will be a parallel accumulation

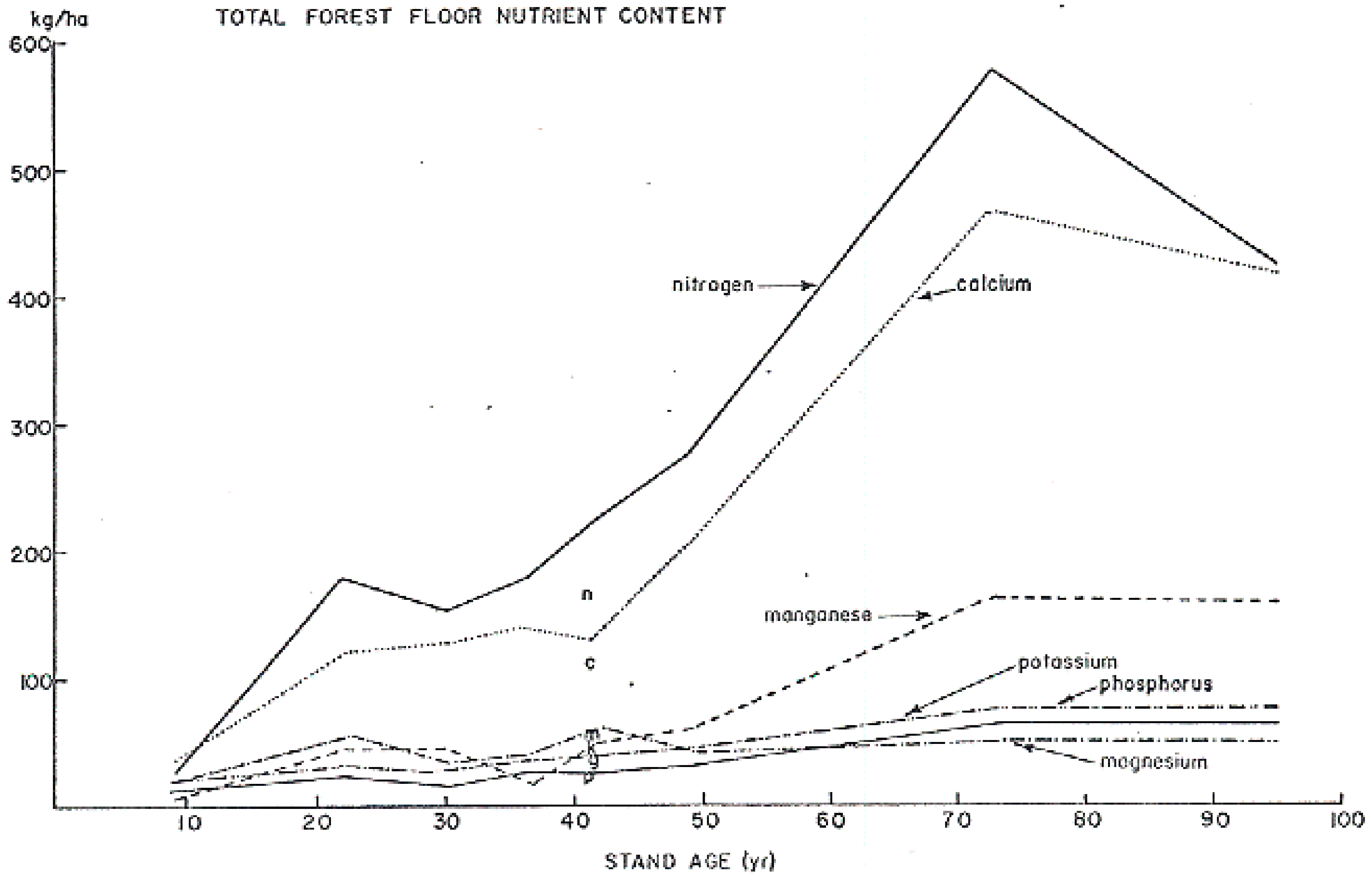


Figure 20. Quantities of N, P, K, Ca, Mg, and Mn (kg/ha) in the total forest floor of the stands at Cedar River. The letters n, p, k, c, g, and m are the quantities of N, P, K, Ca, Mg, and Mn respectively in the 42-year-old sparsely stocked stand.

of N in the forest floor. Similarly, there is a continuous accumulation of Ca and Mn, but K, Mg, and P are fairly constant over time. This aspect was not studied in any further detail, but whether a nutrient is accumulated or released may be related to the form in which it occurs within the litter and whether it is fairly independent of, partially dependent upon, or almost totally dependent upon microbial decomposition for release from the forest floor organic matter. Thus Ca and Mn are in a form within the plant material which requires considerable decomposition before mobilization, whereas K would require little if any, microbial decomposition before it is available for utilization. Tables 31 to 41 in Appendix I indicate that humus followed a similar trend to the total forest floor but with less fluctuation. Because of the similarity it was not plotted.

All nutrients accumulated in the forest floor in the early part of the stand's life, but after a certain point some cease to accumulate (P, K, Mg) while others continue to do so (Ca, Mn, and N). Part of the reason for this shift in cycling patterns may be due to the changes occurring in the return of nutrients as the result of the change in the understory from broadleaf which is relatively high in N to the moss return which is low in N and high in Ca and Mn. Simultaneously there is a change in the tree component from the younger stands with lower needle retention time, relatively high N and low Ca and Mn to the older stands which return more woody material, and leaf material which is lower in N but higher in such nutrients as Ca and Mn. The surface configuration and characteristics of the organic matter also differs and this may affect the rate of decomposition.

(h) Understory Nutrient Contents.

The understory nutrient contents (Figure 21) follow the biomass trends fairly closely in the case of N, Ca, and Mg. Phosphorus, K, and Mn vary significantly and this is mainly because of the changes in the accumulation patterns of the understory species as the stand increases in age. In the young stands the understory is dominated by salal and bracken fern. These species are generally high in the macro-nutrients and lower in the micro-nutrients (for example Mn). Bracken fern is relatively high in K and appears to specifically accumulate this nutrient. The older stands are dominated by mosses lower in N, K, Ca, and Mg but higher in P and Mn. Thus, while their trends appear to closely follow that of the biomass, each nutrient is different as a result of various accumulation patterns by the individual species. This emphasizes the importance of the changing trends of the understory nutrient accumulation patterns in the overall nutrient cycle. If steady-state is occurring in this component of the ecosystem it is only in the very oldest (73- and 95-years-old) and is appearing as a slowing down in the rate of change.

(i) Nutrient Returns to the Forest Floor.

The total return of nutrients to the forest floor are plotted in Figure 22 and this shows that there was a peak of return in the 22-year-old stand. This is mainly the result of very high litter return, especially by the understory. There is a further peak of return for Mg and Mn in the 73-year-old stand resulting from wood return and higher concentrations of these nutrients in the litter. In the case of the 36-year-old stand (Cole *et al.*, 1968) the returns by the understory were ignored resulting in a significant underestimation.

As most past studies have not accounted for the understory returns further detail is given (Figure 23) to indicate the nutrients and organic matter returned by the understory as a proportion of the total return. In the early stages of the stand's lfie, there are very high proportions of the returns originating from the understory and it could be assumed that in stands near time zero 100% of the return would originate from the understory. The proportion of the return is lower in the 42- and 49-year-old stands, especially for the organic matter, arising from higher stem wood return by the trees. Manganese is the lowest of the nutrients returned in the 9-year-old stand, but it has one of the highest proportional returns in the older stands, mainly as a result of the mosses concentrating this nutrient. Manganese is accumulated in the older leaves of salal, but the leaves appear to have a shorter retention time in younger stands, leading to less accumulation. The understory does play an important role in the return of nutrients to the forest floor but this role declines with increasing age of the stand. However, even in the 95-year-old stand, it may return up to 20% of some nutrients.

(j) Nutrient Uptake.

The nutrient uptake by trees and the total stand (trees plus understory) are plotted against age in Figures 24 and 25. The data indicate that there is a peak of uptake for most nutrients at about 22 years of

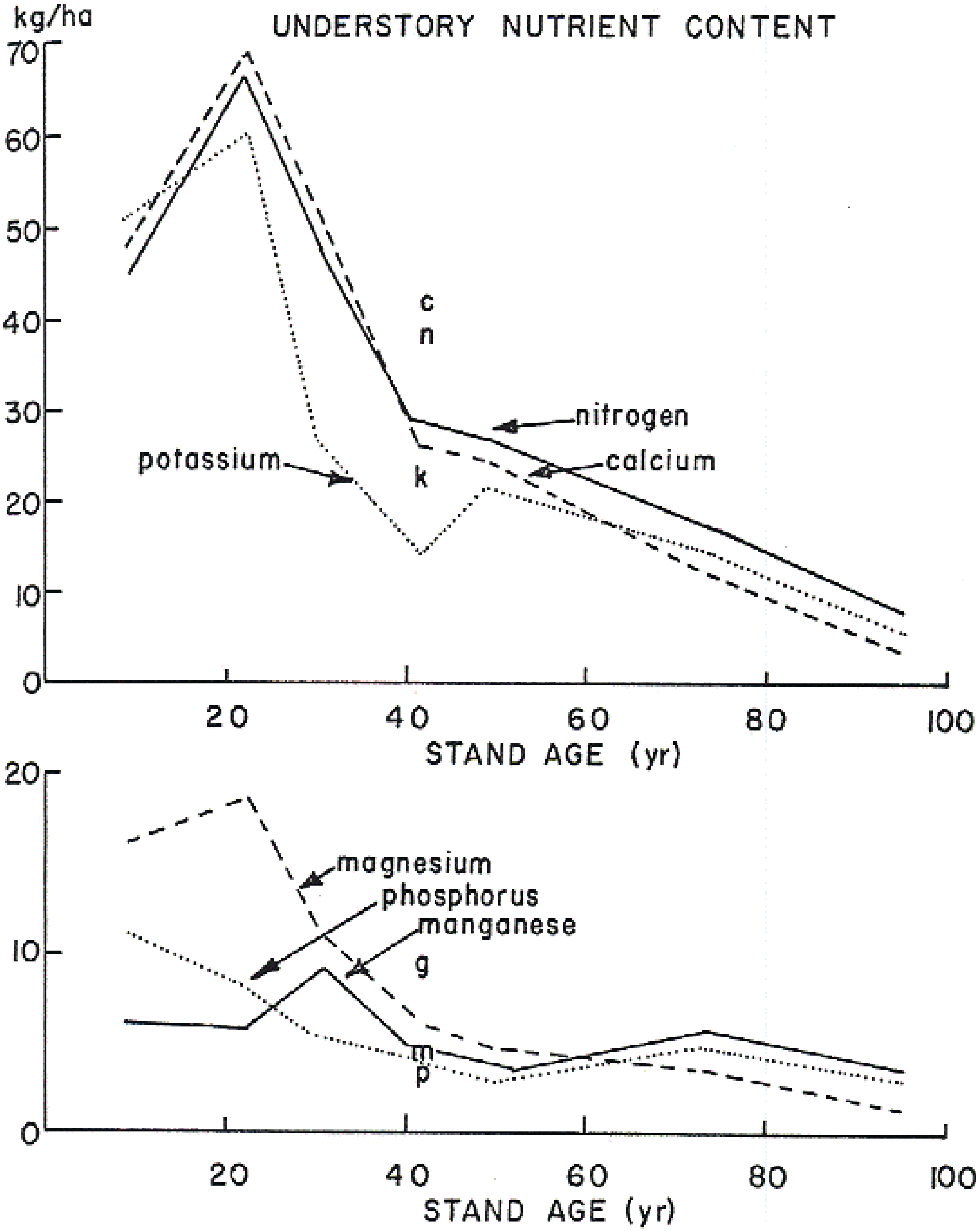


Figure 21. The quantities of N, P, K, Ca, Mg, and Mn (kg/ha) in the understory of the stands at Cedar River. The letters n, p, k, c, g, and m indicate the quantities of N, P, K, Ca, Mg, and Mn respectively in the sparse 42-year-old stand. Note difference in scale.

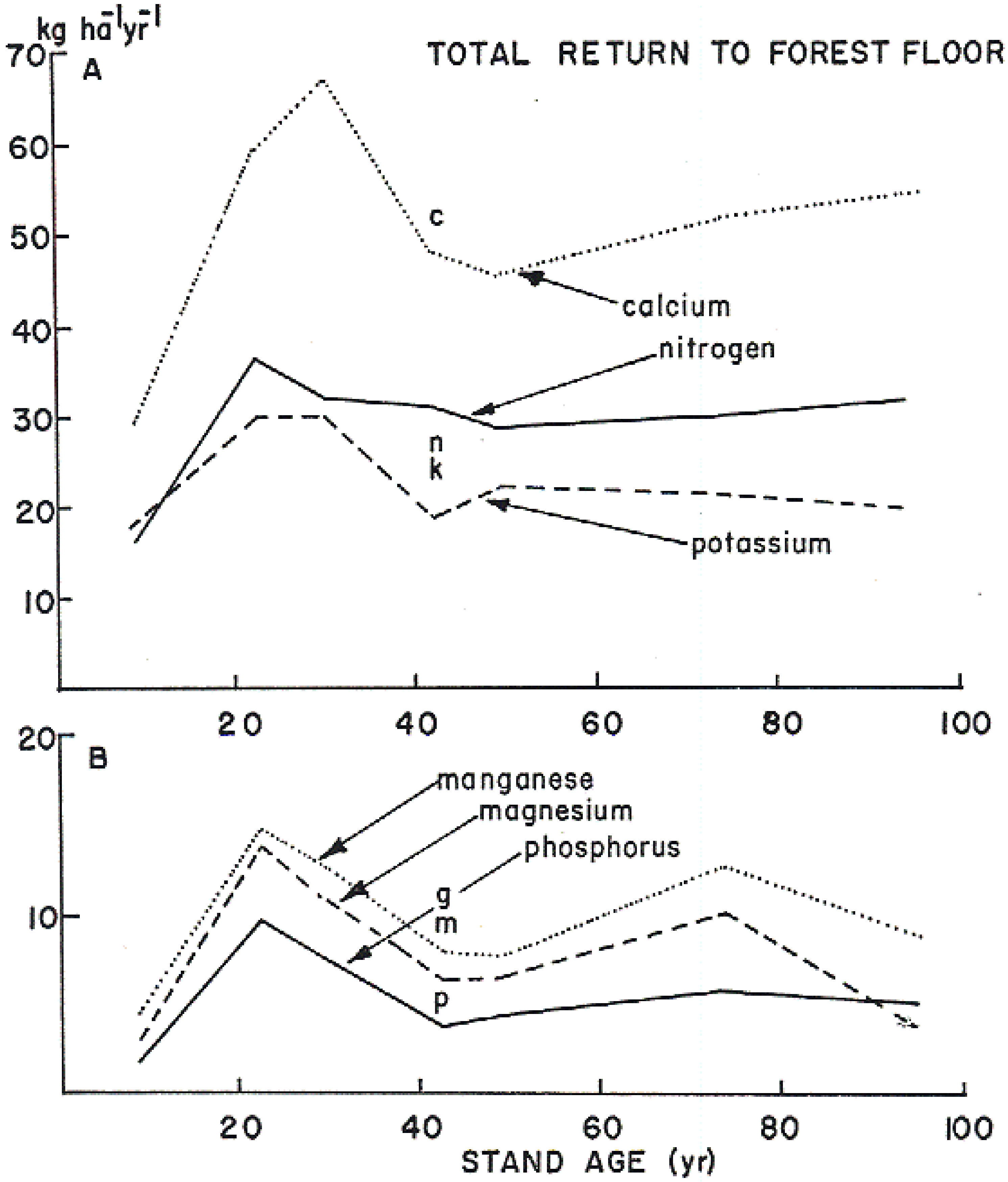


Figure 22. The total quantities of N, P, K, Ca, Mg, and Mn returned to the forest floor at Cedar River (kg ha^{-1} yr^{-1}). The returns by the 42-year-old natural stand are indicated by n, p, k, c, g, and m for N, P, K, Ca, Mg, and Mn respectively. Note difference in scale.

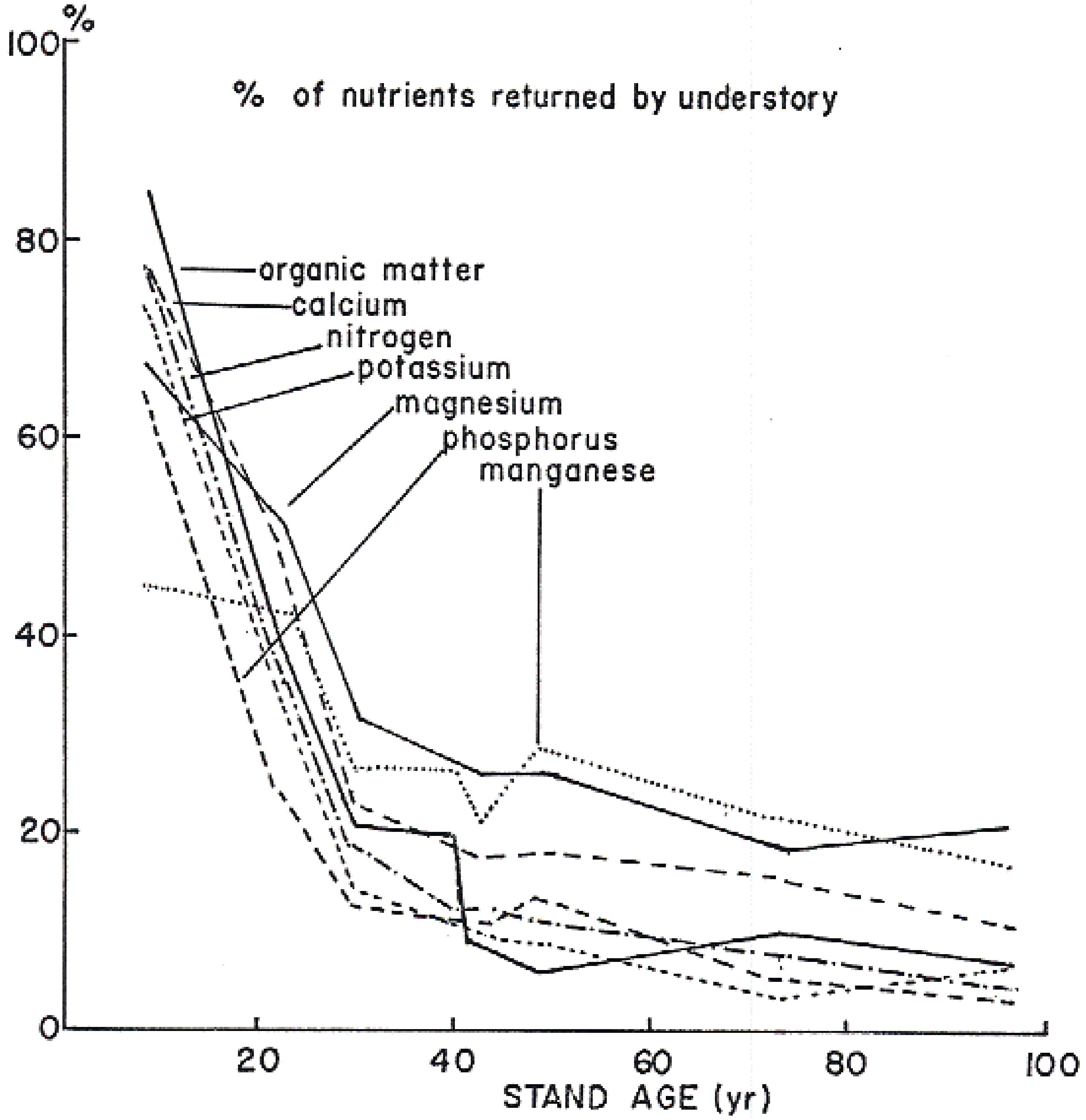


Figure 23. Percentage of total organic matter, nitrogen, phosphorus, potassium, calcium, magnesium, and manganese returned to the forest floor by the understory. The 42-year-old stand was not included.

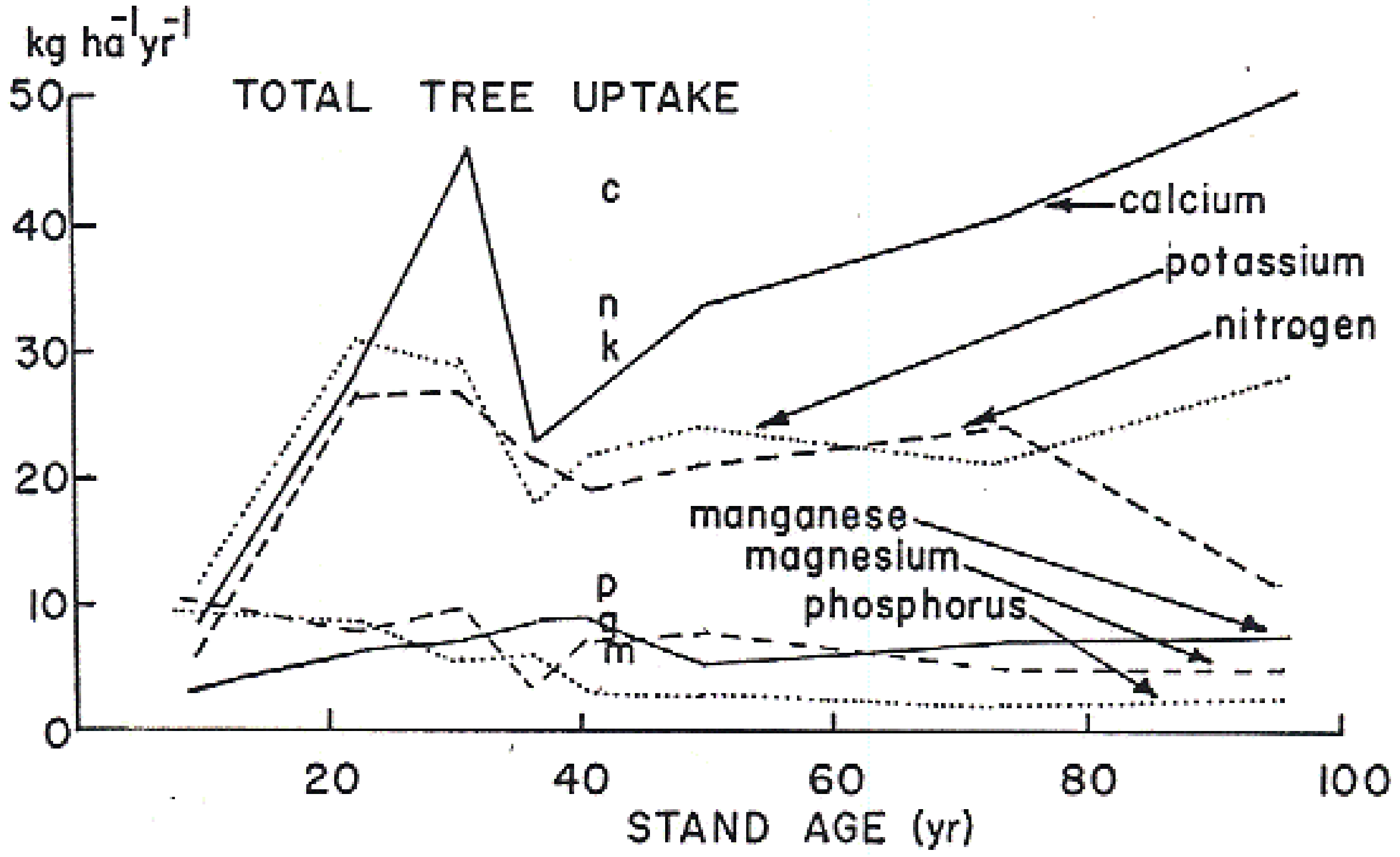


Figure 24. Uptake of nutrients by the tree component of the ecosystem (kg ha^{-1} yr^{-1}) at Cedar River. The n, p, k, c, g, and m are the uptake of N, P, K, Ca, Mg, and Mn respectively of the sparse 42-year-old natural stand.

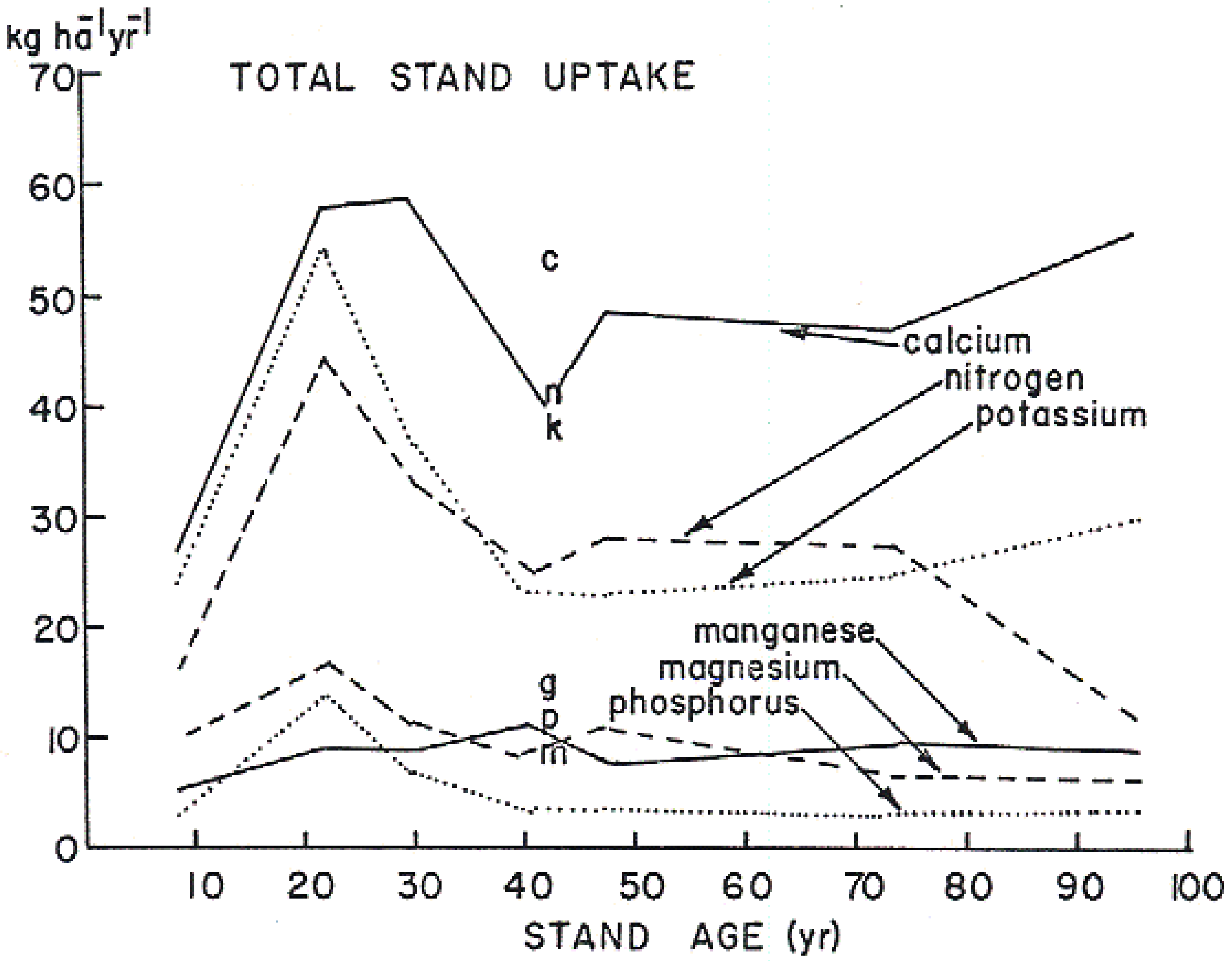


Figure 25. Total uptake by the stands (tree plus understory) (kg ha^{-1} yr^{-1}) at Cedar River. The n, p, k, c, g, and m are the uptake of N, P, K, Ca, Mg, and Mn by the sparse 42-year-old natural stand.

age, and thereafter there is either a decrease towards steady-state, or in the case of Ca, a steady increase. The sparsely stocked (naturally regenerated) 42-year-old stand was similar to the younger stands (especially the 22-year-old stand) in regard to its nutrient transfers, probably indicating that the actual age of the stand in years is of less significance than the stage of stand development. The changing role the understory was playing in nutrient uptake as the stand increased in age could be assessed by comparing the 22- and 95-year-old stands. The trees of the 95-year-old stand, for example, were taking up just over half as much N as the 22-year-old stand and approximately 20% of the P. When the understory was taken into account it was found that the vegetation of the 22-year-old stand was taking up more than three times more N than that of the 95-year-old stand but approximately the same proportion of P. This indicates the importance of the understory in the utilization of marginally available nutrients, in this case N.

When the uptake of nutrients was compared to the requirement for nutrients, (Figure 26) the relative roles of the accumulating versus mobile nutrients can be observed. Whereas Ca had the highest uptake, its requirement was very much less than that of N or K. The P uptake and requirement are fairly similar indicating neither gross accumulation nor excessive mobility. This aspect can be better understood by plotting the uptake as a percent of the requirement (% uptake/requirement) which is the previously discussed efficiency of utilization ratio. This is plotted in Figure 27 for the tree component (the total stand was not plotted as it shows a very similar trend). The nutrient which is deficient, N, shows a decreasing trend for this ratio as the stand increases in age,

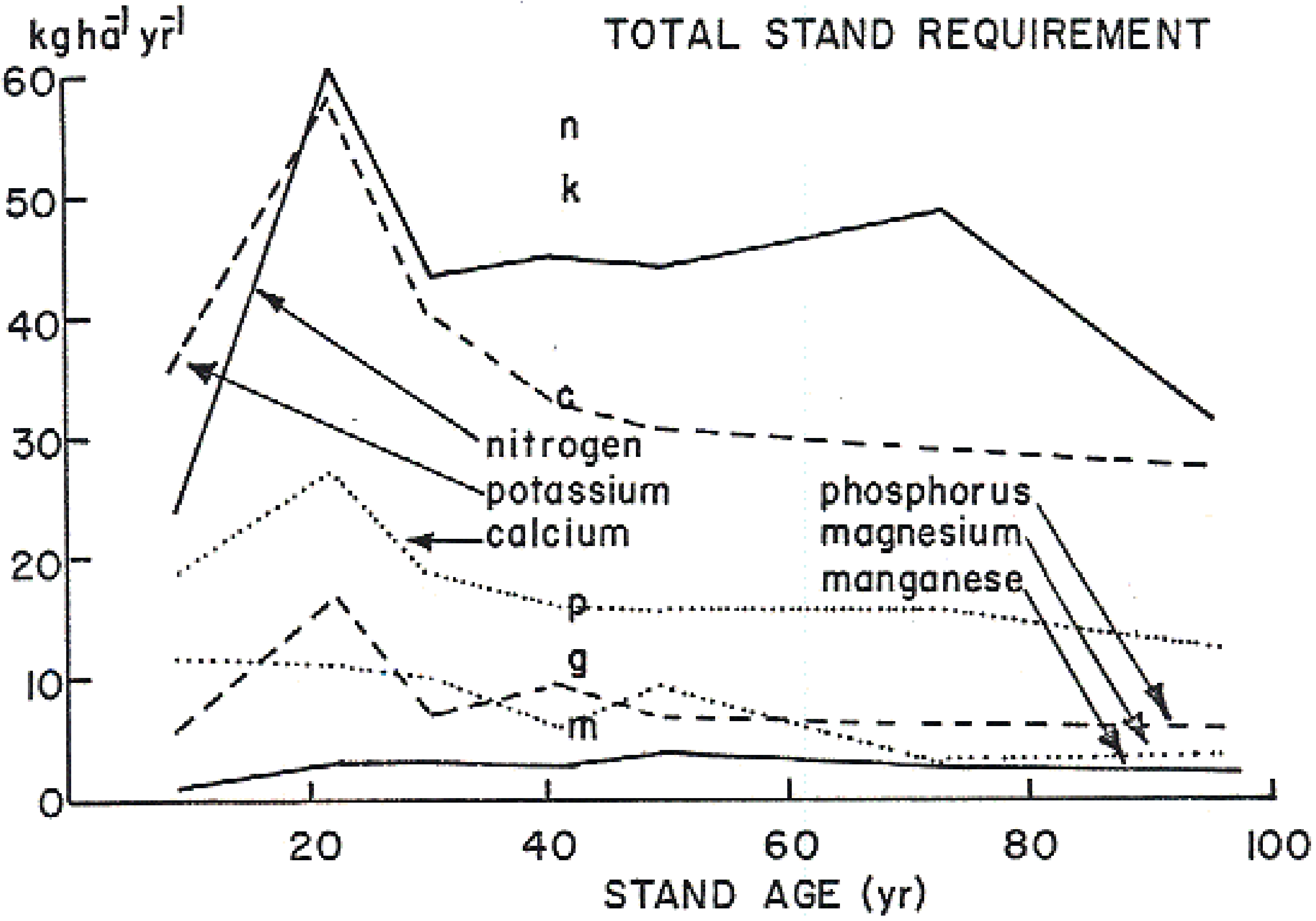


Figure 26. The total requirement for nutrients by the stand (kg ha^{-1} yr^{-1}). The n, k, c, p, g, and m are the N, K, Ca, P, Mg, and Mn requirements of the 42-year-old sparse natural stand.

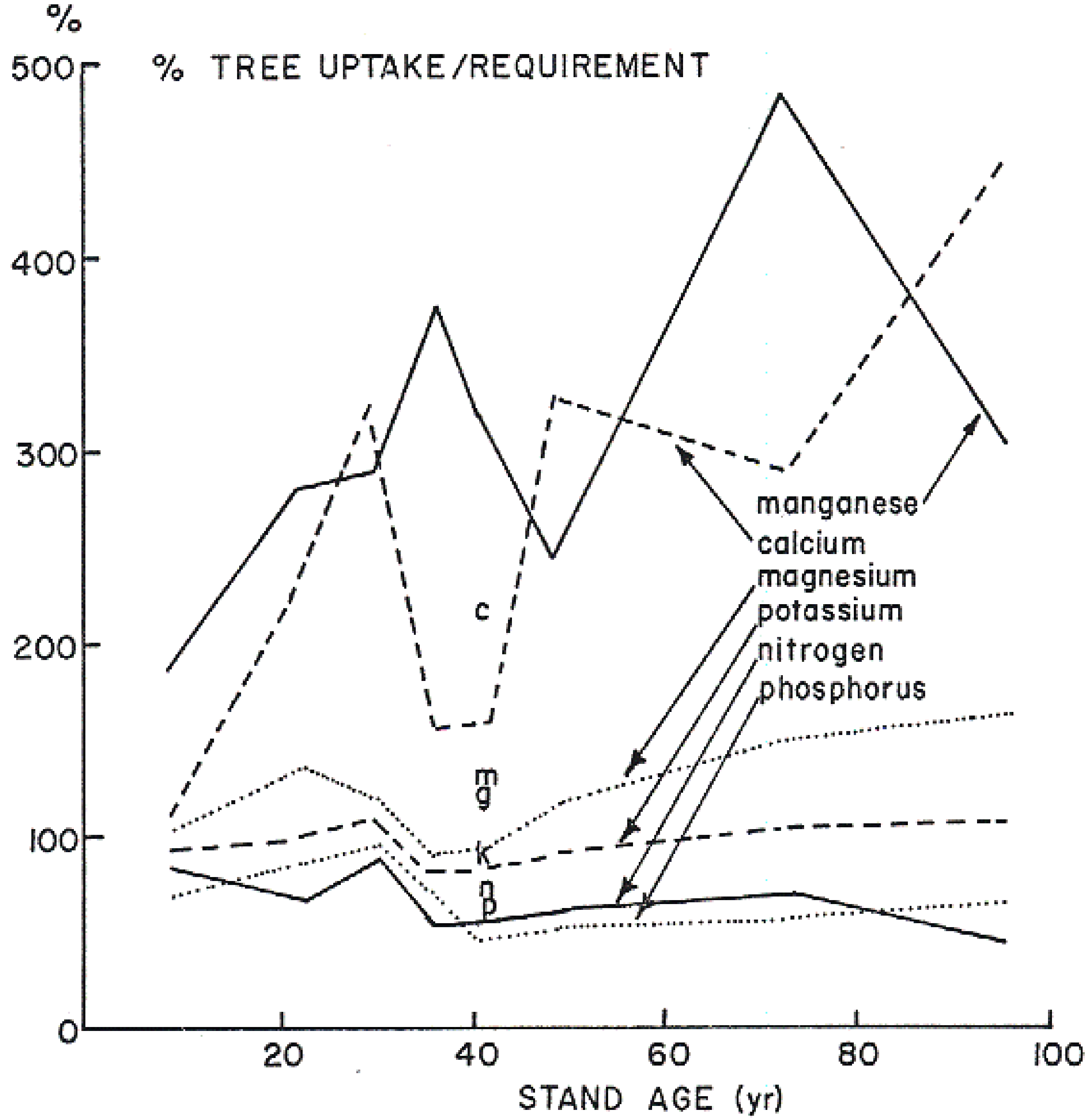


Figure 27. The % uptake/requirement of the tree component of the ecosystem as it matures. The n, p, k, c, g, and m are the % uptake/ requirement of the sparse 42-year-old natural stand.

indicating that the stand is becoming more efficient at redistributing nutrients to fulfill its requirements. This is partly a result of reduced tree requirement. If the soil-humus complex and the tree are considered as two distinct sources of nutrients, and, it is assumed that to remove nutrients from either of these sources for utilization energy is required, then, in a simplistic way, it could be said that the tree would utilize the source requiring the least amount of energy. Earlier on in the stand's life, where there is high requirement and no accumulation within the tree, there may be very little option from where the tree acquires nutrients. In the older stands with two definite sources (internal and external) and reduced requirements, the tree may utilize the nutrient sources demanding the least energy. Probably in a general statement the strategy will be to conserve limiting nutrient and so we see, with age, the tree becoming more efficient in its conservation of N while it accumulates or remains constant for other nutrients in the uptake/requirement ratio.

(k) Forest Floor Inputs and Outputs.

By measuring the inputs, outputs, and accumulation of nutrients within the forest floor and assuming the remainder to be plant uptake, an estimate of what percentage of the uptake was removed from the forest floor was made and is shown in Figure 28. This is the same calculation as performed for the plantation and shown in Table 32. This could be done for N, P, and Ca as there was continuous accumulation. For the other nutrients there was no accumulation after crown closure so that the inputs approximately equalled the outputs. The accumulation rate within the forest floor was based upon a regression line which will over-estimate for some stands and under-estimate for others. This calculated estimate of percentage uptake from the forest floor serves only to give some idea of the probable trends. The trend (Figure 28) indicates that a higher proportion of the uptake is being taken from the forest floor as the stand matures. There was some variation in the 30-year-old stand possibly because of its lower site quality. This trend means that the stands are becoming less and less dependent upon the mineral soil for their nutrient supply, changing in the extreme cases form 100% to less than 20% of the requirement supplied from the mineral soil.

(1) General Conclusions.

These results all indicate that after crown closure steady-state does occur in the cycling of some nutrients. This is dependent upon the nutrient in question, but N, P, and K appear the most likely, while Ca, Mn, and Mg appear less likely to achieve steady-state, possibly because of the tendency to accumulate in excessive quantities within organic matter.

The greatest efficiency of utilization occurs with N probably because of deficiency. In the younger stand the available soil pool and understory are of prime importance while in the older stand the mobile tree and forest floor components become more important. The transfers dominant in the younger stands are soil to plant, plant returns and leaching, and the available soil pool is constantly being replenished from the total pool. In the older stands tree internal redistribution, forest floor to tree,

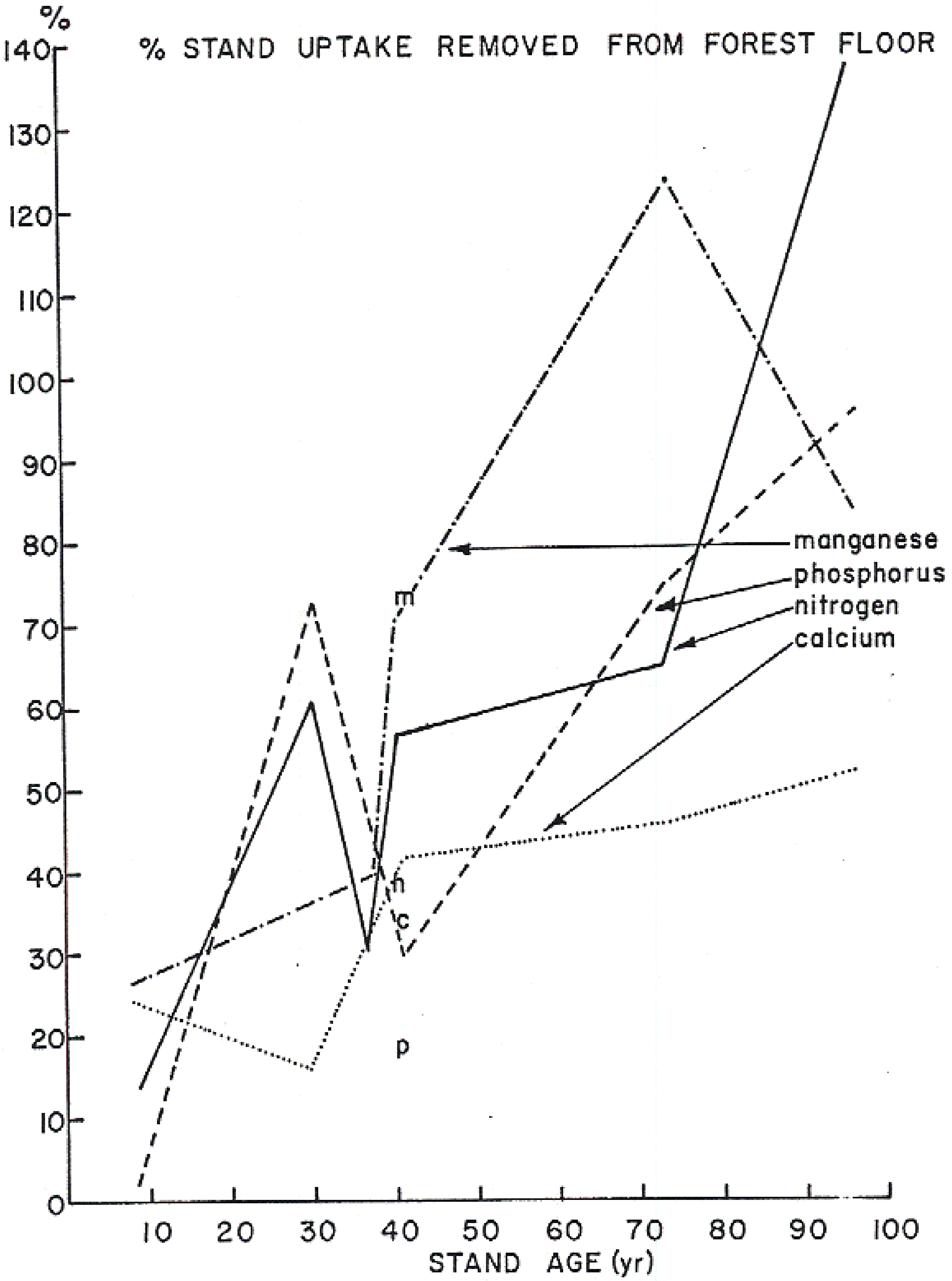


Figure 28. The percentage of the stand uptake removed from the forest floor. The letters n, p, c, and m are the estimates of the N, P, Ca, and Mn for the sparsely stocked 42-year-old natural stand.

and tree return are of greater importance. While the wood (included in the unavailable tree) is large it is not active in cycling. Thus we are now dealing, in a mature stand, with a cycle of forest floor to tree, within tree, and return to forest floor.

5. Manipulation of the Forest Stand...N Availability.

(a) Experimental Background.

Use of the age sequence of Douglas-fir stands indicated some trends in regard to the uptake and utilization of nutrients as the ecosystem matured. This assumed that by selection of uniform site quality stands, considered to be limited by N, it would be possible to analyze a time dimension of an ecosystem. The age sequence study of the Douglas-fir stands indicated that two important components of the nutrient supply were (i) internal redistribution, and (ii) uptake from the forest floor. Internal redistribution was the ermoval of readily retranslocatable nutrients from one part of the tree to another. By having this internal source the tree has a "back-up" supply of nutrients thus allowing some flexibility of supply during periods of nutrient stress. If the external supply is limited, it is hypothesized that more nutrients will be translocated, thus maintaining regular growth. The internal supply may be utilized to overcome seasonal inadequacies but only the net annual result will be studied here.

To add a further dimension to the study the controlling factor of site quality, *i.e.*, N availability, could be altered and the changes analyzed. This type of short term manipulation of the N availability will differ from the situation where the stands are permanently at either a higher or lower level of N, as there would be more or less flexibility respectively in the reserves within the tree.

To further study the redistribution patterns within the tree, a fertilization experiment was established, the plot layout of which was shown in the methods section. The experimental design involved changing (or attempting to change) the level of available N of the forest ecosystem, so that theoretically, four levels were established. A fifth treatment was aimed at unbalancing the N within the tree on the assumption that the unbalancing of the ratio of the macro-nutrients would induce further N stress (Raupach *et al.*, 1969).

One plot was maintained as a control, the second plot had 220 kg/ha N applied as urea to create an adequate level of N, and a third plot had 880 kg/ha N applied to try and create a luxury supply. It is hypothesized that these two urea treatments would increase the uptake of N into the tree and that, even though the requirement may also be higher, redistribution would be lower. If the older age classes of needles increased in N concentration, there could be negative redistribution, or accumulation, as was found for Ca and Mn in the previous section of the study.

The final two treatments were aimed at reducing the N availability to the tree. In one plot, carbohydrate, in the form of sugar and sawdust, was applied, widening the C/N ratio from approximately 40 to 110 and thus reducing the available N as the micro-organisms immobilized the N to enable them to utilize the enregy supply. The final treatment was a repeat of the previous treatment with the addition of P, K, S, and Ca, to internally "unbalance" any N taken up into the tree. These treatments, if successful, would test two aspects of the N cycling. The first would be the sensitivity of the tree uptake to the forest floor nutrient supply. This would indicate the importance of the forest floor in supplying N to the tree. The other aspect would involve reduced uptake of N "forcing" the tree to redistribute more N, and thus enabling observations on the flexibility of the internal nutrient supply, as hypothesized, to be made.

Thus, three hypothesized situations for N could be summarized as below. These figures are not meant to be absolute but only to give relative importance to the various components.

1. Control
   a) Uptake supply--50% mineral soil + 50% forest floor,
   b) Requirement--50% uptake + 50% redistribution,
   c) Litter loss approximates uptake by the tree.
2. Carbohydrate applied (reduced N availability)
   a) Uptake supply reduced--80% mineral soil + 20% forest floor,
   b) Requirements reduced--25% uptake + 75% redistribution,
   c) Litter loss from the tree greater than uptake by the tree.
3. Urea applied (increased N availability)
   a) Uptake supply--no estimate can be made of the relative importance of mineral soil and forest floor,
   b) Requirement increased--90% uptake + 10% redistribution,
   c) Litter loss much less than uptake by the tree.

A summary of the results is shown in Table 35, where, since the previous study showed that it was dominant in this aspect of nutrient cycling, the foliage has been emphasized. As only a few branch and wood samples were taken, the wood distribution and requirement were based mainly upon percentage changes in growth, which were quite small. At this stage, stem growth changes were quite minor in all treatments.

(b) Results of Carbohydrate Addition.

The results indicate that by addition of carbohydrate to the forest floor and the subsequent widening of the C/N ratio, the N uptake by the tree component is reduced by 50%. This is probably an indication of the sensitivity of the forest floor in the N supply to the tree, although if the sugar were leached into the soil a similar microbial immobilization could be expected in the soil. Thus the uptake is reduced from the forest floor supply and, to a lesser extent, from the soil. This has reduced requirement (as defined in this study), but the tree has retranslocated more N (as hypothesized) from 11.6 to 17.6 kg $ha^{-1}yr^{-1}$ N. The lower requirement was related to reduced growth in the current foliage (Figure 29). Redistribution from older tissue caused earlier senscence and thus increased leaf litter production. Both of these factors reduced, at least temporarily, the foliar biomass of the trees. With the reduction in requirements, all the other nutrients were affected in their uptake-redistribution patterns.

Table 35. Requirement, redistribution, and uptake by the trees (kg ha^{-1} yr^{-1}) on the fertilizer experimental plots. Treatments are listed in assumed order of decreasing N availability.

Treatment and Transfer	Organic matter	N	P	K	Ca	Mg	Mn
<u>880 kg/ha N as urea</u>							
current foliage (kg/ha)	2,550	37.0	4.1	12.9	5.7	2.0	0.94
total foliage (kg/ha)	10,340	136.7	19.7	45.6	72.7	9.8	19.6
leaf litter	1,290	11.2	2.7	3.5	11.0	0.4	3.1
leaf wash		0.8	0.4	10.0	6.0	0.5	0.2
Requirement							
- foliage		37.0	4.1	12.9	5.7	2.0	0.94
- branch*		4.0	0.3	2.7	1.9	0.7	0.3
- wood*		9.0	1.0	8.0	3.2	4.0	0.5
Total		50.0	5.4	21.6	10.8	6.7	1.74
Translocation							
- foliage		-21.8	0.0	4.9	-2.6	4.7	-1.83
- branch*		2.4	0.0	1.9	-0.6	0.5	0.1
- wood*		3.6	0.2	2.8	0.0	1.1	-0.2
Total		-15.8	0.2	9.6	-3.2	6.3	-1.9
Uptake		65.8	5.6	24.0	20.0	0.9	3.6
% uptake/requirement		132	104	102	185	13	206

Table 35. (continued)

		N			Ca	Mg	Mn
220 kg/ha N as urea							
current foliage(kg/ha)	2,530	32.4	3.8	15.0	6.5	2.3	1.2
total foliage(kg/ha)	9,900	111.3	17.4	54.1	71.1	8.6	16.0
leaf litter	1,710	13.0	2.9	3.1	12.0	1.2	2.1
leaf wash		1.0	0.5	10.2	4.7	0.5	0.2
Requirement							
- leaf		32.4	3.8	15.0	6.5	2.3	1.2
- branch*		3.0	0.3	1.5	1.2	0.5	0.1
- wood*		8.0	0.7	6.0	3.0	3.0	0.6
Total		43.4	4.8	22.5	10.7	5.8	1.9
Translocation							
- leaf		4.2	-0.9	2.7	-11.9	4.0	-2.5
- branch*		1.2	0.1	1.0	-0.2	1.0	0.2
- wood*		4.0	0.2	3.0	-0.3	1.0	0.7
Total		9.4	1.8	6.7	-14.2	6.0	-1.6
Uptake		35.0	3.5	26.0	29.6	0.3	3.5
% uptake/requirement		81	73	116	277	5	231
Control							
current foliage(kg/ha)	2,200	22.0	4.3	14.5	14.9	3.4	2.3
total foliage(kg/ha)	9,400	94.0	21.8	54.1	93.2	15.0	18.8
leaf litter	1,880	14.1	3.6	3.6	21.1	1.5	3.1
leaf wash		0.9	0.4	9.9	5.1	0.5	0.2
Requirement							
- foliage		22.0	4.3	14.5	14.9	3.4	2.3
- branch*		2.1	0.2	1.3	1.0	0.4	0.1
- wood*		7.4	0.6	5.4	2.7	2.5	0.5
Total		31.5	5.1	21.2	18.6	6.3	2.9
Translocation							
- foliage		7.6	1.4	8.9	-22.0	2.0	-2.7
- branch*		1.0	0.1	1.2	-0.2	1.1	0.2
- wood*		3.0	0.1	2.8	-0.3	1.5	0.7
Total		11.6	1.6	12.9	-22.5	4.6	-1.8
Uptake		20.8	3.9	18.2	36.2	1.7	6.9
% uptake/requirement		66	76	86	195	181	238

Table 35. (continued)

Carbohydrate							
current foliage(kg/ha)	1,790	19.4	3.1	11.2	11.1	2.0	1.1
total foliage(kg/ha)	8,480	80.2	16.8	47.9	90.0	12.7	21.5
leaf litter	2,390	14.3	5.3	9.8	32.0	3.2	10.3
leaf wash		0.8	0.4	10.0	5.1	0.5	0.2
Requirement							
- foliage		19.4	3.1	11.2	11.1	2.0	1.1
- branch*		4.0	0.3	2.7	1.9	0.7	0.3
- wood*		3.0	0.2	2.0	0.8	1.1	0.2
Total		26.4	3.6	15.9	13.8	3.8	1.6
Translocation							
- foliage		11.6	1.0	6.0	-17.7	1.0	-7.9
- branch*		2.4	0.0	1.9	-0.6	0.5	0.1
- wood*		3.6	0.2	2.8	0.0	1.8	-0.2
Total		17.6	1.2	10.7	-18.3	3.3	-0.8
Uptake		9.6	2.8	15.2	37.2	1.0	2.6
% uptake/requirement		36	78	96	270	26	163
Carbohydrate plus P,K,S,Ca							
current foliage(kg/ha)	1,870	18.3	5.2	12.6	6.7	2.5	1.3
total foliage (kg/ha)	8,530	83.0	19.9	46.7	76.6	13.6	23.3
leaf litter	2,425	16.4	3.5	9.7	38.8	4.8	10.6
leaf wash		1.0	0.6	12.5	6.0	0.5	0.2
Requirement							
- foliage		18.3	5.2	12.6	6.7	2.5	1.3
- branch*		3.0	0.2	2.5	1.6	0.5	0.2
- wood*		2.6	0.1	1.2	0.6	0.8	0.1
Total		23.9	5.5	16.3	8.9	3.8	1.6
Translocation							
- foliage		10.1	1.3	6.3	-22.4	-1.0	-8.0
- branch*		2.0	0.0	1.7	-0.5	0.5	0.1
- wood*		3.7	0.2	2.0	0.0	2.0	-0.3
Total		14.8	1.5	10.0	-22.9	1.5	-8.2
Uptake		10.1	4.7	18.8	37.8	2.8	10.0
% uptake/requirement		42	85	115	425	74	630

* A limited number of samples only was available for this estimate.

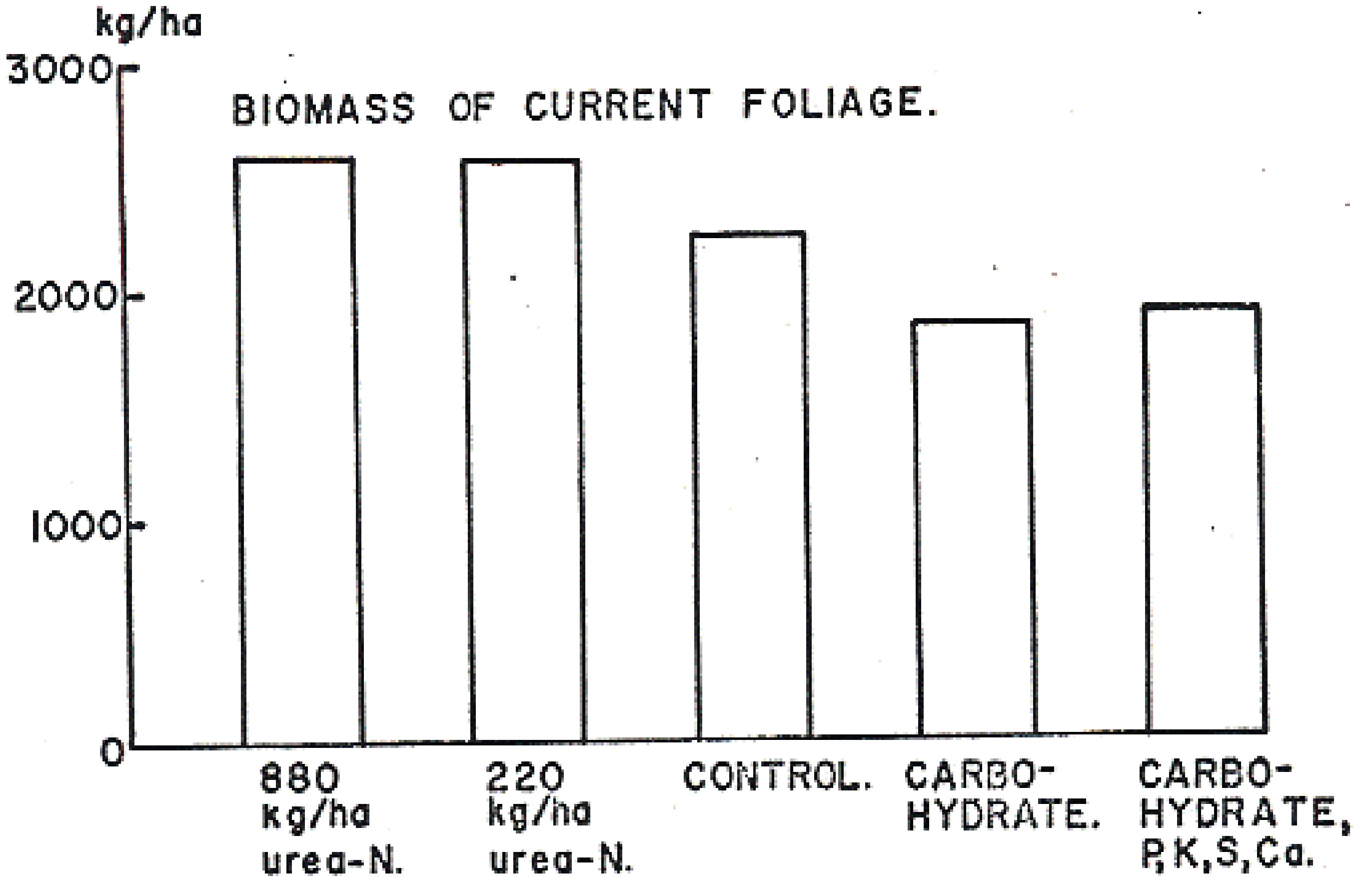


Figure 29. The biomass of the current foliage (kg/ha) for the fertilizer treatments listed according to hypothesized nitrogen availability.

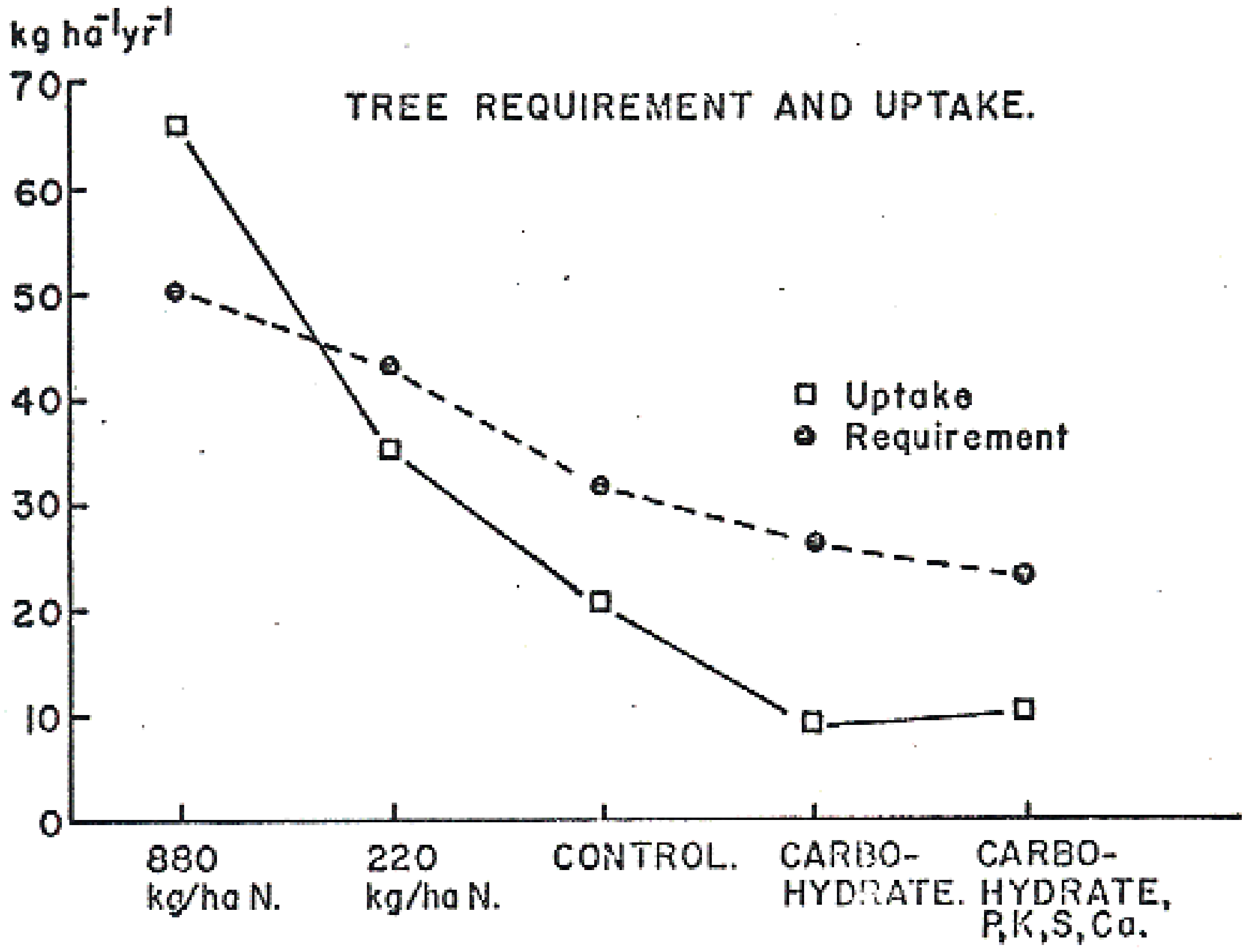


Figure 30. Nitrogen requirement and uptake by the trees on the fertilizer plots (kg ha^{-1} yr^{-1}) listed according to hypothesized nitrogen availability. The connecting of the points is to make assessment easier, and does not imply a continuous series.

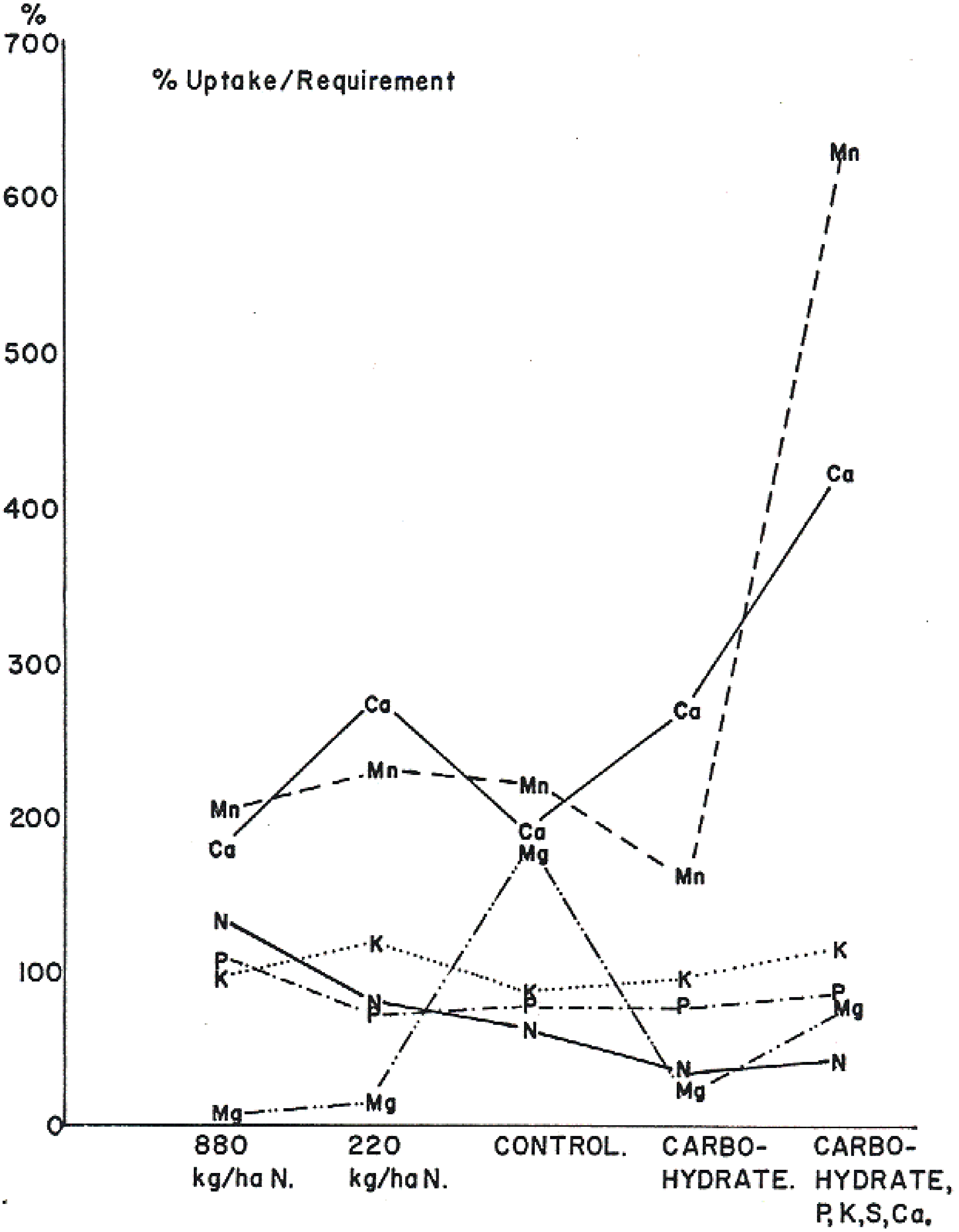


Figure 31. The percent uptake/requirement for the trees on the plots of the fertilizer experiment listed in order of assumued nitrogen availability. The connected lines do not imply a continuous series.

(c) Results of N Addition.

Fertilizing with N caused greatly increased uptake. This was evident in the increased foliar N concentrations of the nutrients shown in Table 47 of Appendix 3. The older age classes of neeldes also increased in their N concentrations which meant that only the redistribution occurring would be from the falling needles in the litter. This would be calculated as negative redistribution or accumulation. The increase in uptake was from 20.8 kg $ha^{-1}yr^{-1}$ in the control plot, to 35 kg $ha^{-1}yr^{-1}$ in the 220 kg/ha N treatment and 65.8 kg $ha^{-1}yr^{-1}$ in the 880 kg/ha N treatment. In this last treatment (880 kg/ha N) approximately one third (21.3 kg $ha^{-1}yr^{-1}$) of this uptake was utilized in accumulation in the older needles.

With the lowered redistribution in the fertilized plots, needles were retained longer, causing lower needle fall, and this, with the increased weight of the current needles, led to a greater foliar biomass (Figure 29). This was supported by Heilman (1961).

The other nutrients were affected due to the change in requirements arising from the alteration in foliar biomass. This alteration occurred as a result of changes in (i) the current foliage production, and (ii) longer retention of older foliage classes. The effect of the treatments on the concentration of the nutrients (Appendix 3) in the foliage showed interesting patterns. The increased N concentration with N fertilization has been mentioned, and was as would be expected. Potassium was fairly constant as was P. Phosphorus was higher in the treatment where P was added. Where N was added, Ca was lower in concentration in the current needles, possibly because of a dilution effect, but there did not seem to be enough additional growth to support this idea. There could also be a depression of uptake by competing cations, *e.g.*, ammonium competing with calcium.

A similar effect occurred for Mg, but in this case all age classes were affected. Possibly the urea affected Mg availability leading to more Mg translocation. This may be an indication of incipient Mg deficiency. Manganese was lower in the current foliage of the N treatments, as it was for Ca, but in the older tissue of both carbohydrate treatments there was very rapid accumulation. The mobile nutrients were taken up in higher quantities in the fertilizer treatments, for example the K increased from 18 kg $ha^{-1}yr^{-1}$ in the control treatment to 24 kg $ha^{-1}yr^{-1}$ in the 800 kg/ha N treatment, and reduced to 15 kg $ha^{-1}yr^{-1}$ in the carbohydrate treatment. On the other hand, the immobile nutrients appeared to follow a reverse trend, with Ca uptake 20 kg $ha^{-1}yr^{-1}$ in the 880 kg/ha N treatment, 36 kg $ha^{-1}yr^{-1}$ in the control, and 37 kg $ha^{-1}yr^{-1}$ in the carbohydrate treatment.

(d) Lysimeter Plate Collections

As the concentrations of N (and most other nutrients) collected from the forest floor lysimeter plates were returning to the control plot levels in all treatments (Table 36) within a year after treatment, it may be assumed that the concentrations of available N for tree uptake were also returning to pretreatment concentrations, that is, in a period of less than a year, the high concentration of available N had been immobilized. Thus, it may be assumed that treatment responses lasting a long period of time after fertilizer application may not be a result of long term

Table 36. Concentrations of nutrients in solutions (ppm) collected in forest floor lysimeter plates.

Plot	N	P	K	Ca	Mg	Mn
22 APRIL						
24	50.0	0.47	2.27	0.80	0.09	0.04
21	15.5	1.07	3.75	4.55	0.08	0.05
23	0.45	0.03	1.60	1.44	0.25	0.04
22	0.72	0.03	3.20	1.75	0.20	0.07
25	0.58	26.6	39.0	10.50	0.91	1.07
22 JULY						
24	1.84	0.02	10.3	22.0	7.73	1.92
21	0.56	0.02	2.72	2.60	0.46	0.06
23	0.43	0.03	3.89	2.00	0.45	0.06
22	0.53	0.20	6.25	1.70	0.30	0.06
25	0.80	6.27	14.2	5.10	0.57	0.41

increased soil availability levels. The increased N accumulation within a tree as a result of increased uptake may cause continued response, together with possible higher N release from the soil, arising from internal redistribution. By assuming increased growth (response) is a result of improved future foliar growth, and increased productivity of the current growth for several years to come, response would occur for at least three years in the 220 kg/ha N treatment and up to five or more years in the 880 kg/ha N treatment.

The trends in the quantities of N uptake and requirement are shown in Figure 30, while the % uptake/requirement is shown in Figure 31. These indicate that the trees will utilize the most available N source, and with internal redistribution there was flexibility in the sources of available N.

(e) General Conclusions.

The results from carbohydrate addition which led to increased N deficiency were obtained from a stand where the trees were able to draw upon an internal supply of N. The stands were only marginally deficient. different patterns may be seen where the stands have been deficient over a long period of time, as they will not have the same internal reserves. This experiment was designed to test how the trees would respond when its regular source of N was reduced rather than a study in long term N deficiency. Adding further inorganic fertilizer to induce internal stress appeared to have had little effect.

FINAL DISCUSSION

This study, originating as a project to determine if the results of an intensive study site were applicable to other locations and forest conditions, involved the analysis of the annual nutrient budgets of forest ecosystems as the stand matured.

The ecosystems being analyzed were considered N deficient and thus the nutrition aspects of this nutrient were concentrated upon and within the tree N was found to be fairly mobile. Five other nutrients were also studied, these being P, K, Ca, Mg, and Mn. It was obvious from a comparison of the cycle of these nutrients that to properly understand a nutrient cycle and nutrient accumulation patterns, the physio-chemical aspects of the respective nutrients must be considered. The aspects of particular interest for each of the nutrients were as follows. The N in the ecosystem was limiting for growth, and N together with P, and Mg appear to closely follow the organic matter cycle. Thus, while realizing there are differences in nutrient concentration in the tissues of the forest stand, any increases in organic matter are followed by a proportional increase in N, P and Mg.

Potassium, on the other hand, appeared to closely follow the hydrologic cycle within the forest stand. This nutrient is very mobile, both internal and external to the tree. Thus, changes or transfers of organic matter such as litterfall, may not be paralleled by a comparable K transfer. This led to problems in estimation of transfers of this nutrient within the tree, mainly where leaching from the tree had to be taken into account. Calcium and Mn, because of their rapid accumulation pattern within the plant tissue (especially foliage), are highly dependent upon the organic matter cycle, but did not follow that cycle closely.

The various properties of each nutrient could also be asssed in its leaching from the forest floor. Organic matter accumulated within the forest floor and with it so did the N. Nitrogen is related closely to the organic matter decomposition, thus the microbial population will immobilize N in its utilization of the organic matter as an energy source. Nutrients such as Ca and Mn need organic matter decomposition to be released and therefore an organic matter accumulation will involve an accumulation of these nutrients. Potassium is transferred mainly by water and is also easily leached from organic matter on the forest floor, thus it is almost independent of organic matter decomposition. Phosphorus and Mg appear to be intermediate between N and K in their behavior.

The study indicated that organic matter and nutrient content of the foliage of the stand increased up to a certain level and reached a steady-state level as the stand matured, except for Ca and Mn. Wood and forest floor components of the stand generally increased with age. The rate of wood increase changed with age but forest floor accumulation was fairly constant over the length of the age sequence.

The understory of the forst stands initially increased and then, as the canopy closed, it decreased. It also changed with stand age, as the understory changed from being predominantly vascular to being moss dominated. All nutrients tended to follow this trend but because of differential accumulation rates of nutrients by the different species, the rates of change were different. The rates of change of the understory appeared to be greater than any other ecosystem component.

The nutrient transfers measured within the system appeared to reach a peak in the 22-year-old stand. This involved return to the forest floor, loss from the forest floor, and transfers within the vegetation.

The critical points of this study on transfers were that the understory, while deteriorating to a relatively insignificant proportion of the stand biomass, at all stages played a very significant role in the uptake and return of nutrients within the forest ecosystem. This was because a high proportion of the understory biomass returned to the forest floor every year, and a relatively high proportion of the understory is replaced by new growth each year. The understory also had a relatively low proportion of nutrients immobilized in the nutrient pool, but it had a very high turnover rate.

The nutrient requirement by the tree and total stand reached a peak at about 22 years of age and after that point declined. Uptake also declined. Thus, as the stand matured, it fulfilled more of its requirement from internal redistribution. This efficiency was especially noticeable with N, which was a deficient nutrient. At all stages of the stand's life the accumulating nutrients, Ca and Mn, had a greater quantity of nutrients taken up than were required for current growth. For Mn % uptake/requirement was usually 300%. Of the nutrients that were taken up into the tree, there was evidence that as the stand matured, a higher proportion of the nutrients would come from the forest floor than from the mineral soil. Thus, the ecosystem was changing from an understory dominated system, obtaining the nutrients required for growth from internal redistribution and the forest floor, with a much smaller dependence upon the mineral soil. It is hypothesized that these alternative sources of nutrients, coupled with a much smaller uptake for nutrients as the stand matured, gave the ecosystem a great deal of flexibility in its nutrient supply.

When the available N supply was altered by fertilization and widening of the C/N ratio to increase and decrease available N respectively, there was an indication that the tree was able to store nutrients, specifically N, within the tree for later utilization. Thus, in the N treatments, redistribution was very small and uptake very high, in fact three times the control level. It is hypothesized that this treatment and resulting storage would lead to increased growth for several years after treatment, even though the available soil N may be reduced to the initial low level.

The reduced available N treatment indicated that the tree was able to resort to higher redistribution to maintain growth. This also demonstrated the possible sensitivity of the tree to the forest floor N supply. These experiments also indicated how closely related all components of the nutrient cycle were, so that reduction in uptake will cause greater redistribution, leading to the dropping of greater quantities of leaf litter. There may be reduced growth leading to a lower accumulation of nutrients within the tree. Larger quantities of wide C/N ratio leaf material will also affect the forest floor biomass, related decomposition and release of nutrients.

Thus, the theories that the ecosystem reaches a steady-state and that this is flexible in terms of perturbation have been shown to be valid for nutrients closely following the organic matter cycle.

CONCLUSIONS

The conclusions from this study can be summarized as follows:

1. Foliage organic matter, N, K, Mg, and P reach a constant level shortly after crown closure. Calcium and Mn continue to increase in mass.

2. Wood biomass and nutrient content increases throughout the life of the stand although the rate of increase declines with age.

3. Understory biomass and nutrient content reaches a peak in the 22-year-old stand and thereafter declines. The rate of change of the nutrient content is not the same as the organic matter, and the individual nutrients vary because of different accumulation patterns by species. Only scattered information was available previously on this component.

4. The organic matter on the surface of the soil (forest floor) increases in weight as the stand increases in age. Nitrogen, Ca, and Mn also increase in weight, while P, K, and Mg remain constant after about 42 years of age.

5. Return of organic matter and nutrients from the trees to the forest floor was fairly constant over the life of the stand. The proportion of a nutrient returned by organic matter or water depended upon the individual nutrient. No previous available study had mentioned this.

6. Return of organic matter and nutrients from the understory to the forest floor was always significant even though the actual understory biomass may be quite low. This was because of the high turnover rate of the understory compared to the tree. The proportion of nutrients returned by the understory depends upon the age of the stand. This

supports views of previous investigators.

7. Uptake by the trees and understory reaches a peak at about 22 years, i.e., the time of maximum productivity of the stand.

8. As the stand increases in age, a higher proportion of the nutrients required for current growth is taken from internal redistribution in the case of mobile nutrients. Immobile nutrients take up an excess over requirement and this is measured as accumulation. This study is the first detailed discussion on this aspect of nutrient cycling.

9. The organic matter layer over the soil plays a greater role in the supply of nutrients to the tree as the stand ages. This supports the results of previous workers.

10. These results indicate that for nitrogen the ecosystem changes from an understory dominated system, removing most nutrients from the mineral soil in the young stands, to a tree dominated system obtaining the nutrients from the forest floor and by internal redistribution.

11. The age of the stand in years is not the best measure of the stage of the mineral cycle, rather a time sequence based on stand development parameters should be used (e.g., crown closure, understory deterioration, stand deterioration, etc.).

12. Nitrogen application to a stand indicated that increased N uptake reduced redistribution and thus changed other nutrient transfers such as leaf litterfall. As current growth and needle retention were affected, all other nutrients were also affected. This has also been found by some other workers.

13. The widening of the C/N ratio of the forest floor caused a decline in N uptake which led to greater redistribution within the tree. Current growth was reduced and needle litter was increased. The other nutrients

were also affected. This is a unique study in forestry.

14. Use of a single intensive study plot for monitoring nutrient cycling is of limited value, especially if a more general application of the results is to be made. Several plots would be of more use if they represent some logical sequence or represent some other relationship (e.g., age sequence, successional sequence, different nutrient regimes, etc.).

LITERATURE CITED

Abee, A. and D. Lavender. 1972. Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands. IN: J.F. Franklin, L. J. Dempster, and R. H. Waring (eds.), Proceedings -- Research on coniferous forest ecosystems -- A symposium, p. 133-144. USDA Forest Service, Portland, Ore. 322pp.

Adams, S. N. and D. A. Dickson. 1973. Some short-term effects of lime and fertilizers on a Sitka spruce plantation. 1. Field studies on the forest litter and the uptake of nutrients by trees. Forestry 46: 31-37.

Akai, T., S. Ueda, and T. Furono. 1970. Mechanisms related to (dry) matter production in a young slash pine forest. Bull. Kyoto Univ. For. 41: 56-79.

Akai, T., S. Ueda, and T. Furono. 1971. Mechanisms related to matter production in a young white pine forest. Bull. Kyoto Univ. For. 42: 143-162.

Akai, T., S. Ueda, T. Furono, and H. Saito. 1972. Mechanisms related to dry matter production in a thrifty loblolly pine forest. Bull. Kyoto Univ. For. 43: 85-105.

Aljibury, F. K. and D. D. Evans. 1961. Soil sampling for moisture retention and bulk density measurements. Soil Sci. Soc. Amer. Proc. 25: 180-183.

Allen, S. E., A. Carlisle, E. J. White, and C. C. Evans. 1968. The plant nutrient content of rainwater. J. Ecol. 56: 497-504.

Ando, T. 1965. Estimation of dry-matter and growth of the young stand of Japanese pine (Pinus thunbergii). Adv. Front. Plant Sci. 10: 1-10.

Ando, T. 1970. Litterfall and decomposition in some evergreen coniferous forests. Jap. J. of Ecol. 20: 170-181.

Art, H. W., and P. L. Marks. 1971. A summary table of biomass and net annual production in forest ecosystems of the world. IN: H. E. Young (ed.), Forest biomass studies. p. 1-32. (16th. IUFRO Congr.), Univ. Maine Press, Orono. 205p.

Askew, H. O. 1937. The chemical composition of Pinus radiata needles. N. Z. J. Sci. Tech. 18: 651-655.

Assman, E. 1970. The principles of forest yield study: studies in the organic production, structure, increment and yield of forest stands. Pergamon, Oxford. 506p.

Attiwill, P. M. 1966. The chemical composition of rainwater in relation to cycling of nutrients in mature Eucalyptus forest. Plant and Soil, 24: 390-406.

Balci, N. 1964. Physical, chemical and hydrological properties of certain forest floor types. Ph. D. thesis, U. of W., Seattle. 192p.

Baskerville, G. L. 1965a. Dry matter production in immature forest stands. For. Sci. Monog. 9: 1-42.

Baskerville, G. L. 1965b. Estimation of dry weight of tree components and total standing crop in conifer stands. Ecol. 46: 867-869.

Baskerville, G. L. 1966. Dry matter production in immature balsam fir stands: Roots, lesser vegetation and total stand. For. Sci. 12: 49-53.

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2: 49-53.

Baule, H. and C. Fricker. 1970. The fertilizer treatment of forest trees. B. L. V. Munich. 259p. (Transl. by C. C. Whittles).

Beaton, J. D., A. Moss, I. Macrae, J. W. Konkin, W. P. T. McGhee and R. Kosick. 1965. Observations on foliage nutrient content of several coniferous tree species in British Columbia. For. Chron. 41: 222-236.

Beaton, J. D., G. Brown, R. C. Speer, I. MacRae, W. P. T. McGhee, A. Moss and R. Kosick. 1965. Concentration of micronutrients in foliage of three coniferous tree species in British Columbia. Soil Sci. Soc. Am. Proc. 29: 299-302.

Bengtson, G.W. (ed.) 1968. Forest fertilization - theory and practice. T.V.A. National Fertilizer Development Center, Muscle Shoals, Ala. 306p.

Bormann, F. H., G. E. Likens, T. G. Siccama, R. S. Pierce, and J. S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol. Monog. 44: 255-277.

Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. IN: H. E. Young (ed.), Primary productivity and mineral cycling in natural ecosystems. p. 186-196. (AAAS. Symp.), Univ. of Maine, Orono. 245p.

Bowen, C. W. 1972. Progressive acid dissolution as a technique for determining the potassium supply of forest soils. M. S. thesis. U. of Montana, Missoula. 49p.

Brackett, M. H. 1964. Patterns of elemental distribution and response of Douglas-fir foliage to nitrogen fertilizer. M. F. thesis, U. of W., Seattle. 92p.

Bray, J. R. and E. Gorham. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2: 101-157.

Buckman, H. O. and N. C. Brady. 1969. The nature and properties of soils. Collier-MacMillan Ltd., London, 7th ed. 653p.

Burger, H. 1929. Holz, Blattmenge und Zuwachs. I. Die Weymouthsföhre Mitt. Schweiz. Centralanst. Forstl. Versuchswes. 15: 243-292.

Burger, H. 1935. Holz, Blattmenge und Zuwachs. II. Die Douglasie. Mitt. Schweiz. Centralanst. Forstl. Versuchswes. 19: 21-72.

Burger, H. 1940. Holz, Blattmenge und Zuwachs. IV. Ein 80 jähriger Buchenbestand. Mitt. Schweiz. Centralanst. Forstl. Versuchswes. 21: 307-348.

Carlisle, A., A. H. F. Brown and E. J. White. 1966. The organic matter and nutrient elements in the precipitation beneath a sessile oak (Quercus petraea) canopy. J. Ecol. 54: 87-98.

Cole, D. W. and S. P. Gessel. 1965. Movement of elements through a forest soil as influenced by tree removal and fertilizer additions. IN: C. T. Youngberg (ed.), Forest-soil relationships in North America. p. 95-104. Oregon State Univ. Press, Corvallis, Ore.

Cole, D. W. and S. P. Gessel. 1968. Cedar River Research - A program for studying pathways, rates and processes of elemental cycling in a forest ecosystem. For. Resources. Monog. #4, U. of W., Seattle. 53p.

Cole, D. W. and P. S. Machno. 1969. Factors affecting percolation in a forest soil. p. 101-109. Proceedings on "Water balance in North America". Banff. American Water Resources Ass. Proc. series. #7.

Cole, D.W., S. P. Gessel and S. F. Dice. 1968. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir ecosystem. IN: H. E. Young (ed.), Primary productivity and mineral cycling in natural ecosystems. p. 197-213. (AAAS Symp.), Univ. of Maine Press, Orono. 245p.

Cole, D. W., S. P. Gessel and J. Turner. 1973. Elemental cycling and even-age forest management. IN: R. K. Hermann and D. P. Lavender (ed.), Even-Age Management, O. S. U., Corvallis, Ore. 250p.

Coppenet, M. 1969. [Results of twelve years of lysimetric observations at Quimper (1954 - 65).] Annals Agron. 20: 111-143. (in French)

Crane, W. J. B. 1972. Urea nitrogen transformation, soil reactions, and elemental movement via leaching and volatilization in coniferous forest ecosystems following fertilization. Ph. D. thesis, U. of W., Seattle. 284p.

Curlin, J. W. 1970. Nutrient cycling as a factor in site productivity and forest fertilization. IN: C. T. Youngberg and C. R. Davey (ed.), Tree growth and forest soils. p. 313-326. 3rd. Nth. Amer. Soil Conf. 527p.

Dice, S. F. 1970. The biomass and nutrient flux in a second-growth Douglas-fir ecosystem (a study in quantitative ecology). Ph. D. thesis, U. of W., Seattle. 105p.

Dimock, E. J. 1958. Litter fall in a young stand of Douglas-fir. Northwest Science. 32: 19-29.

Driessche, Van Den. 1969. Tissue nutrient concentration of Douglas-fir and Sitka Spruce in sand culture and value of nutrient concentration levels for interpretting foliar analysis. British Columbia For. Serv. Res. Div. Res. Note No. 47. 42p.

Driessche, Van Den. 1973. Foliar nutrient concentration between provenances of Douglas-fir and their significance to foliar analysis interpretation. Can. J. For. Res. 3: 323-328.

Duvigneaud, P. and S. Denaeyer-De Smet. 1970. Biological cycling of minerals in temperate deciduous forests. IN: D. E. Reichle (ed.), Analysis of temperate forest ecosystems. p. 199-225. Springer Verlag, N. Y. 304p.

Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the Western Cascades of Oregon. Ecology. 54: 57-69.

Epstein, E. 1972. Mineral Nutrition of Plants: principles and perspectives. Wiley and Sons, N. Y. 412p.

Evers, F. H. 1972. Annual fluctuations of nutrient concentrations in Spruce needles and their importance for the interpretation of the results of foliar analysis. Allg. Forst-u. Jaydztg. 143(3/4): 68-74.

Forrest, W. G. and J. D. Ovington. 1970. Organic matter changes in an age series of Pinus radiata plantations. J. Appl. Ecol. 7: 177-186.

Fortescue, J. A. C. 1973. The use of branches as a basis for the estimation of the copper, zinc, lead and nickel status of a forest stand. Can. J. of For. Res. 3: 27-33.

Frankland, J. C., J. D. Ovington and C. Macree. 1963. Spatial and seasonal variations in soil, litter, and ground vegetation in some Lake District woodlands. J. Ecol. 51: 97-112.

Fredriksen, R. L. 1972. Nutrient budget of a Douglas-fir forest on an experimental watershed in western Oregon. IN: J. F. Franklin, L. J. Dempster, and R. H. Waring (eds.), Proceedings -- Research on coniferous forest ecosystems -- A symposium, p. 115-131. USDA Forest Service, Portland, Ore. 322p.

Fujimori, T. 1971a. Analysis of forest canopy on the basis of a Tsuga heterophylla forest. Jap. J. of Ecol. 21: 134-139.

Fujimori, T. 1971b. Primary productivity of a young Tsuga heterophylla stand and some speculations about biomass of forest communities on the Oregon coast. USDA For. Serv. Res. Pap. PNW-123. 11p.

Fujimori, T. 1972. Discussion about the large forest biomasses of the Pacific Northwest in U. S. A. J. Jap. For. Soc. 54: 230-233.

Gagnon, J. D. 1964. Relationships between site index and foliage nitrogen at two crown levels for mature black spruce. For. Chron. 40: 169-174.

Gambell, A. W. and D. W. Fisher. 1966. Chemical composition of rainfall, eastern North Carolina and Southeastern Virginia. Geol. Survey Water

Supply Paper 1535K: 1-41.

Gentle, S. W. and F. R. Humphreys. 1967. Experience with phosphatic fertilizers in man made forests of Pinus radiata in N.S.W. For. Commission of N.S.W. 37p.

Gerloff, G. C., D. G. Moore and J. T. Curtis. 1966. Selective absorption of mineral elements by native plants in Wisconsin. Plant and Soil, 25: 393-405.

Gersper, P. L. and N. Holwaychuk. 1971. Some effects of stemflow from forest canopy trees on chemical properties of soils. Ecology, 52: 691-702.

Gessel, S. P. 1962. Progress and problems in mineral nutrition of forest trees. IN: T. T. Kowlowski (ed.), Tree Growth. Ronald Press Co., N.Y. p. 221-235.

Gessel, S. P., T. N. Stoate, and K. J. Turnbull. 1965. The growth behavior of Douglas-fir with nitrogenous fertilizer in Western Washington. Coll. of Forestry, U. of W., Res. Bull. #1, 204p.

Grier, C. C., D. W. Cole, C. T. Dyrness, and R. C. Fredriksen. 1974. Nutrient cycling in 37- and 450-year-old Pseudotsuga menziesii (Mirb.) Franco ecosystems. IN: R. H. Waring (ed.), Integrated Research in the Coniferous Forest Biome. p. 28-47. U.S.I.B.P., Coniferous For. Biome Bull. #5. 146p.

Hall, M. J. and M. Raupach. 1963. Foliage analyses and growth responses in Pinus radiata (D. Don) showing potassium deficiencies in Eastern Victoria. Appita 17: 76-84.

Hammond, L. E., W. L. Pritchett and V. Chew. 1958. Soil sampling in relation to soil heterogeneity. Soil Sci. Soc. Amer. Proc. 22: 548-552.

Harada, H. and H. Sata. 1966. On the dry matter and nutrient contents of the stem of mature Cryptomeria trees and their distribution to the bark, sapwood and heartwood. J. Jap. For. Soc. 48: 315-324.

Harada, H., H. Sata, I. Hotta, and Y. Tadaki. 1969. On the amount of nutrient contained in 28-year-old Cryptomeria forest (C. japonica D. Don) and Chamaecyparis forest (C. obtusa Sieb. et Zucc.). J. Jap. For. Soc. 51: 125-133.

Harada, H., H. Sata, I. Hotta, K. Hatiya, and Y. Tadaki. 1972. Study on the nutrient contents of mature Cryptomeria forest. Bull. Gov. For. Expt. Sta., Tokyo. 249: 17-74.

Heiberg, S. O. and D. P. White. 1950. Potassium deficiency of reforested Pine and Spruce stands in northern New York. Abst. of Papers, 7th. Int. Bot. Congr. Stockholm. 2p.

Heilman, P. E. 1961. Effects of nitrogen fertilization on the growth and nitrogen nutrition of low-site Douglas-fir stands. Ph. D. thesis, U. of W., Seattle. 214p.

Heilman, P. E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes of interior Alaska. Ecol. 47: 825-834.

Heilman, P. E. and S. P. Gessel. 1963. Nitrogen requirement and the biological cycling of nitrogen in Douglas-fir stands in relationship to the effects of nitrogen fertilization. Plant and Soil, 18: 386-402.

Henderson, J. A. 1970. Biomass and composition of the understory vegetation of some Alnus rubra stands in Western Oregon. M. S. thesis, Oregon State U. 64p.

Höhne, H. 1963. Foliar analysis studies in young spruce. Arch. Forstw., 12(4): 341-360.

Höhne, H. 1967. The influence of tree age and site unit on formation and nutrient content of pine needles. Arch. Forstw. 16: 609-616.

Hitchcock, C. L. and A. Conquist. 1973. Flora of the Pacific Northwest. U. of W. Press. 730p.

Humphreys, F. R. and J. Kelly. 1962. The variation of phosphorus content in Pinus elliottii foliage. Aust. For. 26: 77-86.

Humphreys, F. R., J. Turner and A. J. Watt. 1971. Annual nutrient variation in Pinus radiata (D. Don) over a period of nine years. Aust. For. Nut. Conf. Aug., 1971. Canberra, Australia.

Irby, F. 1967. A study of the sampling variability of bulk density, gravel content and total nitrogen in two forest soils. M. F. thesis, U. of W., Seattle.

Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall, Englewood-Cliffs, N. J. 498p.

Jenny, H., S. P. Gessel and F. T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68: 419-432.

Johnson, N. M., G. E. Likens, F. H. Bormann, D. W. Fisher, and R. S. Pierce. 1969. A working model for the variation in stream water chemistry at the Hubbard Brook Experimental Forest, New Hampshire. Water Resources Res. 5: 1353-1363.

Johnson, P. L. and W. T. Swank. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. Ecol. 54: 70-80.

Johnstone, W. D. 1971. Total standing crop and tree component distributions in three stands of 100-year-old lodgepole pine. IN: H. E. Young (ed.), Forest Biomass Studies. p. 81-92. (16th. IUFRO Congr.), Univ. Maine

Press, Orono. 205p.

Jordan, C. F. and J. R. Kline. 1972. Mineral cycling: some basic concepts and their application in a tropical rainforest. Ann. Rev. of Ecol. and Syst. 3: 33-50.

Keay, J. and A. G. Turton. 1970. Distribution of biomass and major nutrients in a maritime pine plantation. Aust. For. 34: 39-48.

Khashes, T. S. M. 1972. Diurnal and seasonal variation of the potassium content of leaves of woody species under irrigation. Lesovedenie 5: 53-61. (F. A. 33: 3798).

Kelly, J. M. 1973. Dynamics of litter decomposition, microbiota populations, and nutrient movement following nitrogen and phosphorus additions to a deciduous forest stand. Oak Ridge National Laboratory, ORNL-4893. 194p.

King, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser For. Paper 8. 49p.

Kittredge, J. 1944. Estimation of the amount of foliage of trees and stands. J. For. 42: 905-912.

Knutsen, S. K. 1965. Hydrologic processes in 30-35 year old Douglas-fir and alder stands in Western Washington. M. F. thesis, U. of W., Seattle. 131p.

Lavender, D. P. 1970. Foliar analysis and how it is used - a review. School of For., Oregon State, Res. Note 52. 5p.

Lavender, D.P. and R. L. Carmichael. 1966. Effect of three variables on mineral concentrations in Douglas-fir needles. For. Sci. 12: 441-446.

Leaf, A. L., J. V. Berglund and R. E. Leonard. 1970. Annual variation in foliage of fertilized and/or irrigated red pine plantations. Soil Sci. Soc. Amer. Proc. 34: 677-682.

Likens, G. E. and F. H. Bormann. 1970. Chemical analyses of plant tissues from the Hubbard Brook Ecosystem in New Hampshire. Yale University, School of Forestry. Bull. 79. 25p.

Likens, G. E., F. H. Bormann, N. M. Johnson and R. S. Pierce. 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. Ecol. 48: 772-785.

Long, J. N. 1973. Initial stages of secondary plant succession in a series of <u>Pseudotsuga menziesii</u> / <u>Gaultheria shallon</u> stands in western Washington. M. S. thesis, U. of W., Seattle. 77p.

Long, J. N. and J. Turner. 1974. Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. J. Appl. Ecol. (In press).

Lowry, G. L. and P. M. Avard. 1965. Nutrient contents of black spruce needles. 1. Variations due to crown position and needle age. Pulp and Paper Res. Inst., Canada Tech. Rep. Ser. 425. Woodl. Res. Inst., Mont., Canada.

Lull, H. W. and J. H. Axley. 1958. Forest soil-moisture relations in the coastal plain sands of southern New Jersey. For. Sci. 4: 2-19.

Mader, D. L. 1963. Soil variability - a serious problem in soil site studies in the Northeast. Soil Sci. Soc. Amer. Proc. 27: 707-709.

Madgwick, H. A. I. 1965. The weights and nutrient compositions of understory species in an ashwood. J. of Ecol. 53: 335-341.

Madgwick, H. A. I. 1970. Biomass and productivity models of forest canopies. IN: D. E. Reichle (ed.), Analysis of temperate forest ecosystems. p. 47-54. Springer Verlag, New York, Heidelberg, Berlin. 304p.

Mahendrappa, M. K. and E. D. Ogden. 1973. Effects of fertilization of a Black Spruce stand on nitrogen contents of stemflow, throughfall and litterfall. Can. J. For. Res. 3: 54-60.

Mayer, R. and B. Ulrich. 1974. Conclusions on the filtering action of forest from ecosystem analysis. Oecol. Plant. 9: 157-168.

McColl, J. G. 1972. Dynamics of ion transport during moisture flow from a Douglas-fir forest floor. Soil Sci. Soc. Amer. Proc., 36: 668-674.

McColl, J. G. 1973. Environmental factors influencing ion transport in a Douglas-fir forest soil in western Washington. J. Ecol. 61: 71-84.

McColl, J. G. 1973. A model of ion transport during moisture flow from a Douglas-fir forest floor. Ecol. 54: 181-187.

Mead, D. J. 1971. Movement of added nitrogen and phosphorus in a pine forest ecosystem. Ph. D. thesis, Univ. of Florida. 246p.

Metz, L. J., C. G. Wells and B. F. Swindel. 1966. Sampling soil and foliage in a pine plantation. Soil Sci. Soc. Amer. Proc. 30: 397-399.

Miller, H. G. 1966. Current research into the nitrogen nutrition of Corsican Pine. Supplement to "Forestry", Physiology in Forestry, Report of sixth discussion meeting, Edinburgh.

Miller, R. B. 1963. Plant nutrients in hard beech. I. The immobilization of nutrients. II. Seasonal variation in leaf composition. III. The cycle of nutrients. N. Z. J. Sci. 6: 365-413.

Mina, J. N. 1955. Cycle of N and ash elements in mixed oakwoods of the forest-steppes. Pochvovedenie. 6: 32-44.

Minderman, G. 1968. Addition, decomposition and accumulation of organic matter in forests. J. Ecol. 56: 355-362.

O'Carroll, N. and R. McCarthy. 1973. Potassium supplied by precipitation and its possible role in forest nutrition. Irish Forestry. 30: 88-93.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, 44: 322-331.

Ovington, J. D. 1955. Studies of the development of woodland conditions under different trees III. J. of Ecol. 43: 1-21.

Ovington, J. D. 1956. The form, weights and productivity of tree species grown in close stands. New Phytol. 55: 289-304.

Ovington, J. D. 1957. Dry-matter production by *Pinus sylvestris* L. Ann. Bot. n.s. 21: 287-314.

Ovington, J. D. 1962. Qualitative ecology and the woodland ecosystem concept. Advan. Ecol. Res. 2: 103-192.

Ovington, J. D. and H. A. I. Madgwick. 1959. Distribution of organic matter and plant nutrients in a plantation of Scots Pine. For. Sci. 5: 344-355.

Ovington, J. D., W. G. Forrest and J. S. Armstrong. 1967. Tree biomass estimation. IN: H. E. Young (ed.), Primary productivity and mineral cycling in natural ecosystems. p. 4-32. AAAS Symp. Univ. Maine Press, Orono. 245p.

Paddock, R. W. 1962. Certain quantitative nutrient descriptions for different stages of plant succession of the Fern Lake Watershed. M. F. thesis, U. of W., Seattle. 102p.

Peterson, P. J. 1961. Variations in the mineral content of Kauri (*Agathis australis* Salisb.) leaves with respect to leaf age, leaf position and tree age. N. Z. J. Sci. 4: 669-678.

Piper, C. S. 1944. Soil and plant analysis. Interscience Pub., Inc., New York. 368p.

Rahman, A. H. M. M. 1964. A study of the movement of elements from tree crown by natural litterfall, stemflow and leaf wash. M. F. thesis,

U. of W., Seattle. 117p.

Rapp, M. 1971. Cycle de la matière organique et des éléments minéraux dans quelques écosystèmes méditerranéens. Recherche cooperative sur programme du C.N.R.S. #40. Éditions du centre national de la recherche scientifique. 184p.

Raupach, M., R. Boardman, and A. R. P. Clarke. 1969. Growth rates of Pinus radiata (D. Don) in relation to foliar levels of nitrogen and phosphorus for plantations in S.E. of South Australia. C.S.I.R.O. Pub. 26. 28p.

Raupach, M., A. R. P. Clarke and M. P. C. de Vries. 1971. An investigation at four forest sites in South Australia on the optimum tree position and time of sampling for analysis. p. 326-332. Aust. For. Tree Nutrition Conf. Proc. For. and Timber Bur. Canberra. 392p.

Rennerfelt, E. and C. O. Tamm. 1962. The contents of major plant nutrients in Spruce and Pine attacked by Fomes annosus (Fr.) Cke. Phytopath. Z. 43(4): 371-382.

Rennie, P. J. 1955. Uptake of nutrients by mature forest growth. Plant and Soil 7: 49-95.

Reynolds, E. R. C. 1966. The percolation of rainwater through soil demonstrated by fluorescent dyes. J. of Soil Sci. 17: 127-132.

Riekerk, H. 1967. The movement of phosphorus, potassium, and calcium in a Douglas-fir forest ecosystem. Ph. D. thesis, U. of W., Seattle. 142p.

Rodin, L. E. and N. I. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edin. and London. 288p. (Translated by G. E. Fogg).

Safford, L. O. and H. E. Young. 1968. Nutrient content of the current foliage of Red Spruce growing on three soils in Maine. Research in the Life Sciences. 27-31.

Satoo, T. 1967. Primary production relations in woodlands of *Pinus densiflora*. IN: H. E. Young (ed.), Primary productivity and mineral cycling in natural ecosystems. p. 52-80. (AAAS Symp.) Univ. Maine Press, Orono. 245p.

Satoo, T. 1968. Materials for the study of growth in stands. 7. Primary production and distribution of produced dry matter in a plantation of *Cinnamomum camphora*. Bull. Tokyo Univ. For. 64: 241-275.

Schlichte, A. K. 1968. The mineralogy of the Everett series soil on the Cedar River watershed. M. S. thesis, U. of W., Seattle. 105p.

Scott, D. R. M. 1954. Amount and chemical composition of the organic matter contributed by overstory and understory vegetation to the forest soil. Yale University School of Forestry, Bull. 62. 72p.

Shiozaki, M. and T. Nakaoko. 1971. Study of humus layer decomposition (1). Effect of calcium and urea fertilizer application on the decomposition of humus layer and the infiltrated soil water in the Yezo Spruce (*Picea jezoensis*) stand. Bull. Gov. For. Exp. Sta. 242: 1-19.

Silver, G. T. 1962. The distribution of Douglas-fir foliage by age. For. Chron. 38: 433-438.

Smirnova, K. M. and G. A. Gorodentseva. 1958. The consumption and rotation of nutritive elements in birch woods. Bull. Soc. Nat. Moscou (biol). 62: 135-147.

Smith, J. H. G. 1972. Persistence, size, and weight of needles on Douglas-fir and western hemlock branches. Canad. J. of For. Res. 2: 173-178.

Sonn, S. W. 1960. Der einfluss des Waldes auf die Böden. Gustav Fischer, Verlag, Jena. 166p.

Sukachev, V. N. 1944. On the principles of genetical classification in biocoenology. J. ge. Biol., Moscow. 5: 213-277. (Russian).

Swank, W. T. and J. W. Elwood. 1971. Seasonal and annual flux of cations for forested ecosystems in the Appalachian Highlands. Unpublished paper, Second National Biological Congress, Miami, Florida. p. 23-26.

Switzer, G. L. and L. E. Nelson. 1972. Nutrient accumulation and cycling in Loblolly Pine (Pinus taeda L.) plantation ecosystems: the first twenty years. Soil Sci. Soc. Amer. Proc. 36: 143-147.

Switzer, G. L., L. E. Nelson and W. H. Smith. 1966. The characterization of dry matter and nitrogen accumulation by loblolly pine (Pinus taeda L.). Soil Sci. Soc. Amer. Proc. 30: 114-119.

Tadaki, Y. 1966. Some discussion on the leaf biomass of forest stands and trees. Bull. Gov. For. Expt. Sta., Tokyo. 184: 135-161.

Tadaki, Y. and Y. Kawasaki. 1966. Studies on the production structure of forest 9. Primary productivity of a young Cryptomeria plantation with excessively high stand density. J. Jap. For. Sci. 48: 55-61.

Tadaki, Y., K. Hatiya, and H. Miyauchi. 1967a. Studies on the production structure of forest 12. Primary productivity of Abies veitchii in the natural forest at Mt. Fuji. J. Jap. For. Sci. 49: 421-428.

Tadaki, Y., N. Ogata, and Y. Nagatomo. 1963. Studies on the production structure of forest 5. Some analyses on productivities of artificial stands of Acacia mollissima. J. Jap. For. Soc. 45: 293-301.

Tadaki, Y., N. Ogata, and Y. Nagatomo. 1967b. Studies on the production structure of forest 11. Primary productivities of 28-year-old plantations of Cryptomeria of cuttings and of seedlings origin. Bull. Gov. For. Expt. Sta., Tokyo. 199: 47-66.

Tadaki, Y., K. Hatiya, K. Tochiaki, H. Miyauchi, and U. Matsuda. 1970. Studies on the production structure of forest 16. Primary productivity of Abies veitchii forest in the subalpine zone of Mt. Fuji. Bull. Gov.

For. Expt. Sta., Tokyo. 229: 1-20.

Tamm, C. O., C. Carbonnier, and N. Hagberg. 1960. Recent results of fertilizer experiments in Swedish forests. Proc. 5th. Wld. For. Congr. Seattle. 1: 558-561.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16: 289-307.

Turner, J. and J. Kelly. 1973. Foliar chloride levels in some Eastern Australian Plantation forests. Soil Sci. Soc. Amer. Proc. 37: 443-445.

Turner, J. and M. J. Singer. Nutrient distribution and cycling in a subalpine coniferous forest ecosystem. J. Appl. Ecol. (submitted).

Van Cleve, K., L. A. Viereck, and R. L. Schlenfeld. 1971. Accumulation of nitrogen in alder (Alnus) ecosystems near Fairbanks, Alaska. Arc. Alp. Res. 3: 101-114.

Viro, P. J. 1953. Loss of nutrients and the natural nutrient balance of the soil in Finland. Comm. Inst. Forest. Fenn. 42: 1-50.

Viro, P. 1967. Forest manuring on mineral soils. Meddr. norske Skogsfors Ves. 23: 113-136.

Webber, B. D. 1973. Plant biomass and nutrient distribution in a young Pseudotsuga menziesii forest ecosystem. Ph. D. thesis, O.S.U., Corvallis. 163p.

Weetman, G. F. 1962. Nitrogen relations in a Black Spruce (Picea mariana Mill.) stand to various fertilizer and soil treatments. Woodlands Res. Index 129. 112p.

White, D. P. 1954. Variation in the nitrogen, phosphorus and potassium contents of pine needles with season, crown position and sample treatment. Soil Sci. Soc. Amer. Proc. 18: 326-330.

Will, G. M. 1957. Variations in the mineral content of radiata pine needles with age and position in tree crown. N. Z. J. Sci. Tech. 38: 699-706.

Will, G. M. 1959. Nutrients return in litter and rainfall under some exotic conifer stands in New Zealand. N. Z. J. Agric. Res. 2: 719-734.

Williams, B. L. 1972. Nitrogen mineralization and organic matter decomposition in Scots Pine humus. Forestry 45: 177-188.

Wright, T. W. and G. M. Will. 1958. The nutrient content of Scots and Corsican pines growing on sand dunes. Forestry 31: 13-25.

Xydias, G. K. 1964. Dry matter and nutrient element relations in _Pinus resinosa_ Ait. plantations. M. S. thesis, Syracuse, Univ. 57p.

Yamamoto, T. and E. Sanada. 1970. Nutrients uptake by planted Todo Fir (_Abies sachalinensis_ Mast.) nutrient circulation and a change in soil on forest land. Bull. Gov. For. Expt. Sta., Tokyo. 229: 89-121.

Young, H. E. and P. M. Carpenter. 1967. Weight, nutrient element and productivity of seedlings and saplings of eight tree species in natural ecosystems. Maine Agric. Exp. Sta. Tech. Bull. 28. 39p.

Youngberg, C. T. 1966. Forest floors in Douglas-fir forests: 1. Dry weight and chemical properties. Soil Sci. Soc. Amer. Proc. 30: 406-409.

Zavitkovski, J. and M. Newton. 1971. Litterfall and litter accumulation in red alder stands in western Oregon. Plant and Soil 35: 276-268.

Zinke, P. J. 1969. Nitrogen storage of several California forest-soil-vegetation systems. IN: Biology and Ecology of Nitrogen. U.S. National Committee for the International Biological Program. p. 40-53.

APPENDIX 1

Distribution of nutrients in the naturally regenerated Douglas-fir stands.

Table 37. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 22-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage-current	2,100	29.8	4.6	21.4	7.0	2.9	1.8
-total	4,995	65.1	12.5	42.6	27.0	5.8	5.0
Branch-current	540	2.2	0.5	3.0	3.4	0.6	0.4
-total	8,162	17.6	7.1	40.3	34.7	7.9	4.7
Wood -current	6,130	9.8	0.8	6.6	2.9	3.3	0.3
-total	99,435	87.5	82.6	19.2	71.5	8.6	4.0
Bark	13,903	57.1	10.0	28.8	69.1	6.7	6.5
Total aboveground	126,500	227.4	112.3	130.1	202.2	29.0	20.2
SUBORDINATE VEGETATION							
Vascular	6,432	47.2	5.5	41.4	60.8	15.5	6.3
Fern	1,176	19.2	3.1	17.8	7.8	3.0	0.1
Moss	30	0.2	0.1	0.2	0.1	0.0	0.0
Total	7,638	66.6	8.7	59.4	68.7	18.5	6.4
FOREST FLOOR							
Wood	613	4.0	0.4	0.5	2.9	0.7	1.1
Litter	11,406	73.5	14.4	21.3	50.6	30.5	20.8
Humus	8,520	100.3	10.8	15.9	60.5	22.8	20.8
Total	20,540	177.7	25.6	37.8	118.1	54.0	41.7

Table 38. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 30-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage-current	3,142	25.0	5.6	22.7	10.2	3.1	2.1
-total	6,211	54.2	13.5	42.4	39.8	6.7	9.2
Branch-current	527	1.6	0.6	1.0	1.8	0.9	0.3
-total	9,396	23.8	5.4	19.6	54.2	5.1	3.9
Wood -current	4,763	6.2	0.2	3.8	2.4	3.5	0.4
total	121,265	95.6	6.1	78.4	58.4	16.3	7.4
Bark	16,120	47.2	13.7	47.6	95.4	9.7	9.4
Total aboveground	152,990	220.8	38.7	187.9	247.8	37.8	29.9
SUBORDINATE VEGETATION							
Vascular	4,152	39.9	4.0	18.0	47.1	9.6	8.7
Fern	340	5.4	0.9	5.4	2.1	0.8	0.1
Moss	563	2.5	0.9	3.3	2.8	0.7	0.3
Total	5,055	47.8	5.8	26.7	52.0	11.1	9.1
FOREST FLOOR							
Wood	1,396	10.9	0.9	1.4	7.0	1.1	1.2
Litter	5,850	45.9	7.2	9.6	47.1	10.2	16.4
Humus	9,437	97.4	11.6	15.5	75.9	16.4	26.4
Total	16,683	154.2	19.6	26.5	129.9	27.6	44.0

Table 39. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 42-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage-current	2,230	30.6	5.4	25.0	8.3	3.2	2.1
-total	8,274	105.5	22.3	73.4	68.1	9.9	13.9
Branch-current	673	2.7	0.8	3.2	4.2	0.8	0.5
-total	11,252	24.2	10.5	39.2	45.8	11.8	6.2
Wood -current	6,392	11.5	9.0	13.4	14.7	6.4	3.1
-total	157,516	147.5	9.6	64.5	61.2	12.7	6.2
Bark	19,532	78.3	15.6	45.3	98.1	10.2	11.1
Total aboveground	196,574	355.5	58.0	222.4	273.2	44.6	37.5
SUBORDINATE VEGETATION							
Vascular	3,667	32.2	3.1	9.1	37.9	8.5	4.7
Fern	252	4.4	0.5	3.6	1.8	0.7	0.1
Moss	323	2.0	0.5	2.0	1.8	0.6	0.1
Total	4,242	38.6	4.1	14.7	41.5	9.8	4.9
FOREST FLOOR							
Wood	nil						
Litter	2,410	20.3	2.9	3.8	15.1	3.5	6.3
Humus	14,726	142.4	20.9	27.0	104.5	25.6	47.3
Total	17,136	162.7	23.8	30.8	119.6	29.0	53.7

Table 40. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 73-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage-current	2,280	27.8	3.9	19.8	11.6	2.2	1.1
-total	10,745	113.7	24.2	75.7	114.9	14.0	19.7
Branch -current	330	2.6	0.2	1.7	1.3	0.4	0.2
-total	15,448	62.2	5.8	60.7	71.9	7.4	5.8
Wood -current	2,500	4.3	0.3	3.0	1.2	1.2	0.2
-total	236,892	107.4	12.0	153.0	97.3	24.6	11.9
Bark	30,440	67.0	12.5	63.9	149.2	12.2	18.3
Total aboveground	293,525	350.3	54.5	353.3	433.2	58.2	55.7
SUBORDINATE VEGETATION							
Vascular	1,169	8.5	1.2	7.9	10.5	2.7	3.4
Fern	2	-	-	-	-	-	-
Moss	1,575	9.3	3.5	7.2	4.2	1.4	1.9
Total	2,746	17.8	4.7	15.1	14.7	4.1	5.3
FOREST FLOOR							
Wood	56,372	219.3	21.7	35.0	233.1	19.2	47.6
Litter	10,991	42.8	13.2	6.8	45.4	3.7	9.3
Humus	28,372	312.0	34.2	34.8	185.1	43.8	103.8
Total	95,735	574.1	69.1	76.6	463.6	66.7	160.7

Table 41. Distribution of N, P, K, Ca, Mg, Mn, and organic matter (kg/ha) in a 95-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
TREE							
Foliage-current	2,147	19.8	3.2	17.2	7.5	2.0	1.9
-total	12,884	108.6	28.4	66.3	100.7	14.9	29.4
Branch -current	410	3.8	0.3	2.4	1.9	0.7	0.3
-total	15,293	59.0	12.1	32.2	92.8	8.4	6.4
Wood -current	2,715	5.1	0.8	6.3	2.5	0.6	0.3
-total	292,803	179.2	19.0	105.4	128.8	28.1	11.7
Bark	27,138	98.5	20.4	49.7	111.0	6.2	9.2
Total aboveground	348,118	445.3	79.9	253.6	333.3	57.7	56.7
SUBORDINATE VEGETATION							
Vascular	199	1.9	0.2	1.4	1.4	0.5	0.5
Fern	-	-	-	-	-	-	-
Moss	1,002	6.7	1.7	5.4	3.1	1.2	1.7
Total	1,201	8.6	1.9	6.8	4.5	1.7	2.2
FOREST FLOOR							
Wood	37,262	124.1	14.9	12.7	107.3	10.1	9.7
Litter	9,210	87.1	9.3	12.8	65.3	10.3	30.6
Humus	34,216	323.8	34.4	47.5	242.8	38.3	113.9
Total	80,688	423.3	58.6	73.0	415.4	58.7	154.2

APPENDIX 2

Transfer of nutrients in the naturally regenerated Douglas-fir stands.

Table 42. Transfer of N, P, K, Ca, Mg, Mn, and organic matter (kg ha^{-1} yr^{-1}) in a 22-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree - leaf	2,680	18.8	3.2	9.7	22.9	4.4	6.9
- branch	156						
- stem							
Understory							
- vascular	1,892	14.1	2.1	10.9	29.1	7.0	6.2
- moss	8	0.03	0.01	0.03	0.12	0.02	0.04
- total	1,990	14.2	2.1	10.9	29.3	7.0	6.3
Total litter	4,826	33.0	5.4	20.6	52.2	11.4	13.2
Solution							
- leaf wash		2.9	1.8	7.0	5.2	1.5	1.7
- stem flow		nd	nd	nd	nd	nd	nd
Total with precipitation		4.6	4.1	9.2	7.4	2.0	1.8
Total return to forest floor		37.6	9.5	29.8	59.6	13.3	15.0
Loss from forest floor		nd	nd	nd	nd	nd	nd
Within Plants							
Foliage - requirement	2,100	29.8	4.6	21.4	7.0	2.9	1.8
- translocation		13.6	0.6	2.1	-13.6	-1.9	-2.4
- uptake		19.15	5.8	26.3	25.8	5.3	5.9
Branch - requirement	540	2.2	0.5	3.0	3.4	0.6	0.4
- translocation		0.7	0.03	0.9	1.2	0.05	0.05
- uptake		1.49	0.5	2.1	2.2	0.5	0.3
Wood - requirement	6,130	9.8	0.8	6.6	2.9	3.2	0.3
- translocation		2.9	0.3	4.8	1.4	0.2	0.4
- uptake		6.9	4.9	1.7	1.3	3.4	0.7
Total requirement	8,770	41.9	13.1	30.9	13.2	6.7	2.5
Total uptake		27.6	11.2	30.2	29.3	9.2	7.0
% uptake/requirement		66	85	98	221	137	280
Understory - requirement	2,074	28.6	4.6	27.7	14.0	5.1	0.6
- translocation		11.9	1.8	7.8	-6.0	0.2	-1.0
- uptake		16.7	2.8	19.9	20.0	4.9	1.6
Total uptake		44.1	13.9	55.1	58.4	17.7	10.3
Uptake - return		6.5	4.5	25.4	1.3	4.4	-4.7

nd - not determined. Some totals may be off due to rounding errors.

Table 43. Transfer of N, P, K, Ca, Mg, Mn, and organic matter (kg ha^{-1} yr^{-1}) in a 30-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree - leaf	2,919	18.5	4.1	6.1	31.7	3.7	7.1
- branch	719	2.9	0.7	0.7	7.0	0.0	1.1
- stem							
Understory							
- vascular	796	5.6	0.8	4.2	12.6	2.9	2.6
- moss	151	0.6	0.1	0.6	2.3	0.4	0.7
- total	947	6.2	0.9	4.7	14.9	3.3	3.3
Total litter	4,585	27.5	6.8	11.5	55.6	7.0	11.4
Solution							
- leaf wash		2.9	1.5	17.5	12.6	2.9	0.5
- stem flow		0.02	0.01	0.4	0.2	0.1	0.02
Total with precipitation		4.7	1.8	20.1	15.0	3.4	0.7
Total return to forest floor		32.2	7.5	31.7	70.5	10.5	12.1
Loss from forest floor		6.6	1.9	25.8	42.1	10.8	0.2
Within Plants							
Foliage - requirement	3,142	25.0	5.6	22.7	10.2	3.1	2.1
- translocation		5.4	1.2	-3.1	-31.2	-4.8	-5.7
- uptake		22.5	5.8	25.8	41.4	7.9	7.8
Branch - requirement	527	1.6	0.6	1.0	1.8	0.9	0.3
- translocation		0.3	0.3	-0.1	-1.3	0.7	0.1
- uptake		1.3	0.3	1.1	3.1	0.3	0.2
Wood - requirement	4,763	6.2	0.2	3.8	2.4	3.5	0.4
- translocation		2.6	0.0	0.8	0.1	3.0	0.1
- uptake		3.6	0.2	3.1	2.3	0.5	0.3
Total requirement	6,811	32.8	6.4	27.6	14.5	7.5	2.8
Total uptake		27.4	6.4	30.0	46.7	8.7	8.3
% uptake/requirement		84	99	109	323	116	294
Understory - requirement	952	11.0	1.5	12.4	5.8	2.3	0.6
- translocation		4.4	1.0	4.1	-6.7	-0.5	-1.4
- uptake		6.6	0.5	8.3	12.5	2.8	2.0
Total stand uptake		34.0	6.9	38.3	59.2	11.5	10.4
Stand uptake - return		1.8	0.7	6.6	-11.3	1.0	-1.7
Return - forest floor loss		25.6	5.6	5.9	13.4	-0.3	11.9

Table 44. Transfer of N, P, K, Ca, Mg, Mn, and organic matter (kg $ha^{-1}yr^{-1}$) in a 42-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree - leaf	1,713	21.1	2.3	6.6	35.7	6.3	5.3
- branch	856						
- stem							
Understory							
- vascular	560	3.9	0.5	2.5	8.3	2.0	1.8
- moss	83	0.3	0.1	0.3	1.3	0.2	0.4
- total	633	4.2	0.5	2.9	9.6	2.2	2.2
Total litter	3,202	25.3	2.8	9.4	45.3	5.5	7.4
Solution							
- leaf wash		3.7	1.3	7.5	5.4	1.0	0.5
- stem flow							
Total with precipitation		5.4	1.6	9.7	7.6	1.5	0.6
Total return to forest floor		30.7	4.4	19.1	52.9	10.1	8.0
Loss from forest floor		9.9	1.7	26.7	30.2	9.1	0.9
Loss from rooting zone		4.0	1.2	4.9	7.1	4.7	0.1
Loss from system		2.4	0.4	2.4	3.9	1.9	0.1
Within Plants							
Foliage - requirement	2,230	30.6	5.4	25.0	8.3	3.2	2.1
- translocation		7.3	-0.3	8.2	-22.9	-0.8	-2.4
- uptake		26.9	5.7	24.3	31.2	4.0	4.5
Branch - requirement	673	2.7	0.8	3.2	4.2	0.8	0.5
- translocation		1.4	0.2	1.0	1.7	0.2	0.1
- uptake		1.3	0.6	2.2	2.5	0.7	0.3
Wood - requirement	6,392	11.5	9.0	13.4	14.7	6.4	3.1
- translocation		5.8	5.1	7.0	6.4	1.3	0.6
- uptake		5.8	3.8	6.4	8.3	5.1	2.5
Total requirement	9,295	44.8	15.1	41.6	27.2	10.4	5.7
Total uptake		34.0	10.1	32.9	42.0	9.8	7.3
% uptake/requirement		76	67	79	155	94	129
Understory - requirement	850	11.8	1.4	10.0	5.8	1.8	0.5
- translocation		4.5	0.9	1.9	-7.0	-0.5	-1.3
- uptake		7.3	0.5	8.0	12.8	2.3	1.8
Total stand uptake		41.3	10.6	40.9	54.8	12.1	9.1
Stand uptake - return		10.6	6.2	21.8	1.9	2.0	1.1
Return - forest floor loss		20.8	2.7	-7.5	22.7	0.9	7.1

Table 45. Transfer of N, P, K, Ca, Mg, Mn, and organic matter (kg $ha^{-1}yr^{-1}$) in a 73-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree - leaf	2,278	17.1	2.3	6.1	34.5	4.3	7.8
- branch	649						
- stem	2,440	4.9	0.2	0.5	0.2	0.2	1.0
Understory							
- vascular	100	0.7	0.1	0.5	0.2	0.2	1.0
- moss	467	1.9	0.3	1.8	7.2	1.3	2.2
- total	567	2.6	0.4	2.2	9.0	1.7	2.6
Total litter	5,934	24.6	3.0	8.9	43.7	6.3	11.5
Solution							
- leaf wash		3.6	2.1	9.8	5.8	3.1	0.9
- stem flow		0.04	0.01	0.32	0.23	0.03	0.01
Total with precipitation		5.3	2.4	12.4	8.2	3.6	1.0
Total return to forest floor		29.9	5.4	21.2	51.9	9.9	12.4
Loss from forest floor		6.6	1.8	15.6	26.0	7.2	0.5
Within Plants							
Foliage - requirement	2,280	27.8	3.9	19.8	11.6	2.2	1.1
- translocation		9.8	1.7	4.6	-26.8	0.3	-5.1
- uptake		21.6	2.2	21.7	38.5	5.0	7.1
Branch - requirement	330	2.6	0.2	1.7	1.3	0.4	0.2
- translocation		1.3	0.1	0.4	-0.2	0.2	0.1
- uptake		1.3	0.1	1.3	1.5	0.2	0.1
Wood - requirement	2,500	4.3	0.3	3.0	1.2	1.2	0.2
- translocation		3.3	0.2	1.4	0.2	0.9	0.1
- uptake		1.1	0.1	1.6	1.0	0.3	0.1
Total requirement	3,110	34.7	4.4	24.5	14.1	3.8	1.5
Total uptake		24.0	2.4	24.6	41.0	5.4	7.3
% uptake/requirement		69	56	100	290	144	487
Understory - requirement	567	4.9	1.8	4.4	1.8	0.8	0.5
- translocation		1.2	0.3	1.8	-4.3	0.5	-1.3
- uptake		3.7	1.5	2.6	6.1	0.3	1.8
Total stand uptake		27.8	3.9	27.2	47.1	5.7	9.2
Stand uptake - return		-2.1	-4.5	5.9	-4.8	-4.2	3.3
Return - forest floor loss		23.3	3.6	5.6	25.9	2.7	11.9

Table 46. Transfer of N, P, K, Ca, Mg, Mn, and organic matter (kg ha^{-1} yr^{-1}) in a 95-year-old naturally regenerated Douglas-fir ecosystem.

Component	Organic matter	N	P	K	Ca	Mg	Mn
Litterfall							
Tree - leaf	2,358	27.2	3.1	5.2	38.1	3.2	6.7
- branch	2,474						
- stem							
Understory							
- vascular	51	0.3	0.04	0.2	0.8	0.2	0.2
- moss	297	1.2	0.2	1.1	4.6	0.8	1.4
- total	348	1.6	0.3	1.3	5.4	1.0	1.6
Total litter	5,180	28.8	3.4	6.5	43.5	4.2	8.3
Solution							
- leaf wash		1.2	1.11	11.1	8.6	0.1	0.5
- stem flow		0.05	0.02	0.5	0.3	0.05	0.01
Total with precipitation		2.95	1.4	13.8	11.1	0.6	0.6
Total return to forest floor		31.7	4.8	20.3	54.6	4.9	8.9
Loss from forest floor		17.4	1.8	23.3	22.2	3.4	0.5
Loss from rooting zone		1.9	0.6	2.6	4.7	1.5	0.1
Within Plants							
Foliage - requirement	2,147	19.8	3.2	17.2	7.5	2.0	1.9
- translocation		12.1	1.1	4.0	-38.6	-1.1	-5.0
- uptake		8.9	2.1	24.2	46.1	3.1	6.9
Branch - requirement	410	3.8	0.3	2.4	1.9	0.7	0.3
translocation		2.3	-0.1	1.6	-0.7	0.5	0.1
- uptake		1.6	0.4	0.9	2.5	1.1	0.4
Wood - requirement	2,715	5.1	0.8	6.3	2.5	0.6	0.3
- translocation		3.4	0.6	3.7	1.3	0.3	0.2
- uptake		1.7	0.2	2.6	3.8	0.9	0.6
Total requirement	5,272	28.7	4.3	25.9	11.9	3.2	2.5
Total uptake		12.1	2.7	27.7	52.4	5.1	7.8
% uptake/requirement		42	62	107	442	159	314
Understory - requirement	310	3.1	0.9	2.8	1.1	0.6	0.6
- translocation		0.8	0.2	1.1	-2.4	-0.3	-0.8
- uptake		2.3	0.7	1.7	3.5	0.9	1.4
Total stand uptake		12.4	3.3	29.4	55.9	6.7	9.2
Total uptake - return		-17.4	-1.5	9.1	1.4	1.1	0.3
Total return - forest floor loss		19.3	3.0	-3.0	32.4	1.5	8.4

APPENDIX 3

Mean nutrient concentration (%) of age classes of foliage on the fertilizer plots. Samples were collected in late summer (July, 1974).

Table 47. Mean nutrient concentration (%) of age classes of foliage on the fertilizer plots. Samples were collected in late summer (July, 1974).

Plot number and treatment	Needle age	N	P	K	Ca	Mg	Mn
Plot 24 (880 kg/ha N)	current	1.45	0.162	0.504	0.222	0.079	0.037
	1 year	1.50	0.189	0.447	0.751	0.152	0.210
	2 year	1.42	0.220	0.470	0.836	0.112	0.260
	3 year	1.17	0.173	0.347	0.994	0.088	0.230
	4 year	1.01	0.213	0.413	0.855	0.046	0.240
	5 year	0.866	0.220	0.274	1.218	0.033	0.216
Plot 21 (220 kg/ha N)	current	1.28	0.149	0.593	0.256	0.090	0.046
	1 year	1.26	0.174	0.618	0.649	0.099	0.158
	2 year	1.11	0.178	0.568	0.785	0.090	0.202
	3 year	1.00	0.185	0.515	0.856	0.080	0.218
	4 year	0.912	0.200	0.424	1.213	0.071	0.227
Plot 23 (Control)	current	0.98	0.195	0.659	0.678	0.153	0.105
	1 year	1.11	0.233	0.608	0.937	0.189	0.204
	2 year	1.00	0.236	0.528	1.177	0.170	0.235
	3 year	0.90	0.261	0.508	1.149	0.123	0.247
	4 year	0.80	0.270	0.460	1.230	0.101	0.250
Plot 22 (Carbohydrate)	current	1.09	0.174	0.627	0.622	0.112	0.164
	1 year	1.00	0.185	0.598	0.757	0.176	0.219
	2 year	0.97	0.214	0.556	1.071	0.186	0.282
	3 year	0.76	0.216	0.493	1.307	0.117	0.290
	4 year	0.72	0.240	0.409	1.340	0.132	0.431
Plot 25 (Carbohydrate +P+K+S+Ca)	current	0.98	0.277	0.675	0.358	0.132	0.070
	1 year	1.03	0.287	0.576	0.850	0.194	0.239
	2 year	1.05	0.257	0.563	1.093	0.195	0.300
	3 year	0.93	0.182	0.507	1.143	0.136	0.423
	4 year	0.87	0.144	0.402	1.107	0.146	0.436

APPENDIX 4

Definition of some terms used in the dissertation.

Definition of some terms used in the dissertation.

Accumulation (nutrient). This term has been reserved for nutrients whose concentration increases in the tissue as the age of the tissue increases, and is the opposite of redistribution. This is different from the concept in the literature of any quantity of nutrient within a tissue being considered accumulation e.g., the accumulation of nutrients in the foliage.

Forest floor. Organic matter layer on the top of the mineral soil originating from dead plant material. In this study it was divided into "humus" (see below) and "other" (mainly wood and material readily identifiable to source).

Humus. Component of the forest floor comprising organic matter which is fairly uniform in composition and non-distinguishable as to source of origin.

Immobile nutrients. Nutrients not readily translocated in the plant tissue and they therefore tend to accumulate in the plant tissue as it increases in age. This is a relative term and is quite variable as a nutrient immobile in one tissue may be quite mobile in another.

Mobile nutrients. Readily translocateable nutrients.

Redistribution (translocation). These two terms are used synonymously in this study to indicate the quantities of nutrients removed from older tissue to younger tissue in the plants. This was measured by mass balance and is therefore the net result, i.e., unless there was a net difference at the end of a year no redistribution or accumulation occurred.

<u>Requirement</u>. The nutrient content of the current tissue is assumed, in this study, to be the quantity of that nutrient needed by the plant to put on current growth, hence "requirement".

<u>Stemflow</u>. Water running down the stem of the tree, also including the nutrients it carries.

<u>Throughfall</u>. Water passing through the crown of the trees in the stand. This water originates from the rainfall. It is also applied to the nutrients that it carries. In some studies, this has been termed crownwash.

<u>Understory</u>. Vascular and non-vascular plants found as a secondary layer in the forest stands. In some studies, this is termed a ground layer.

<u>Uptake</u>. Removal of nutrients by plants from the soil-organic complex, and its transport into plant tissue for utilization.

VITA

Name: John Turner

Born: May 1st., 1947; Barnsley, Yorkshire, England.

Parents: Ernest and Edna Turner

Family: Married December 12th., 1970, to Suzanne Margaret Tunney, in Canberra, A.C.T., Australia.

Education: 1964: Graduated from Caringbah High School, N.S.W., Aust.

1969: Batchelor of Science in Forestry, Australian National University, Canberra, Australia.

1975: Doctor of Philosophy
University of Washington, Seattle, Washington, USA.

Professional: 1970-71: Forester at the Division of Wood Technology, Forestry Commission of N.S.W., Sydney, Australia.

1972-75: Granted leave to complete Doctoral program at the University of Washington.

6/1975: Returning to Sydney, N.S.W., to resume working for the Forestry Commission.

Address: N.S.W. Forestry Commission,
Division of Wood Technology,
P.O. Box 100,
Beecroft. N.S.W. 2119. Australia.