# THE ROLE OF UNDERSTORY VEGETATION IN THE NUTRIENT CYCLE OF FORESTED ECOSYSTEMS IN THE MOUNTAIN HEMLOCK BIOGEOCLIMATIC ZONE

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## ABSTRACT

A study was carried out to ascertain the biogeochemical role of understory vegetation in three representative sites characteristic of the Mountain Hemlock Biogeoclimatic Zone. The three sites were selected to represent a typical topographic sequence of plant associations and were classified as members of the Vaccinio (membranacei) - Tsugetum mertensianae, Abieto (amabilis) - Tsugetum mertensianae and Streptopo (rosei) - Abietetum amabilis plant associations (xeric, mesic, and hygric site types, respectively).

The overstory layer was found to be typical of old growth, high elevation forests of southwestern coastal British Columbia. Overstory biomass on the three sites was estimated to be 60.88, 55.68, and 34.05 $kg \cdot m^{-2}$ for the hygric, mesic, and xeric site types, respectively. Understory aboveground biomass was found to be less than one percent of the aboveground overstory biomass. Average values for the three sites were: 44.1, 66.1, and 399.3 $g \cdot m^{-2}$ for the hygric, mesic, and xeric site types, respectively.

Understory aboveground production (UAP) was found to represent a greater proportion of overstory aboveground production, as indicated by the mean annual increment (MAI), than the biomass figures might suggest. UAP values of 25.95, 14.19, and 63.12 $g \cdot m^{-2} \cdot yr^{-1}$ for the hygric, mesic, and xeric site types, respectively, were equivalent to 11.28 percent, 6.06 percent, and 48.55 percent of the estimated aboveground overstory production.

Only a small percentage of the total aboveground nutrient standing crop was found in the understory. This is in agreement with comparable published values for old growth forest ecosystems. However, the understory was found to cycle a much greater proportion of its total standing crop annually compared to overstory. Approximately 80 percent of the macronutrients present in the understory standing crop are found in the understory annual production on the Streptopo - Abietetum amabilis site (hygric site type).

Estimates of 17.6, 8.3, and 20.6 $g \cdot m^{-2} \cdot yr^{-1}$ of understory aboveground litterfall (exclusive of the moss layer) were obtained for the hygric, mesic, and xeric sites, respectively. These values are substantially less than for overstory litterfall, but the biomass of different litterfall components (e.g. understory or overstory) was shown to be a poor indicator of the proportional contribution of the components to the quantity of nutrients in aboveground litterfall. Understory was shown to return a significant proportion of the litterfall nutrients on a yearly basis, the bulk of which was returned as a single pulse during the first autumn snowfall.

Understory vegetation above the moss layer was shown to have a significant effect on the quantity of nutrients present in throughfall precipitation reaching the ground. The effect was seasonal in nature with $PO_4$-P, $NO_3$-N, and $NH_4$-N being removed in the spring and Ca, Mg, and K being added to overstory throughfall in the autumn. It was concluded that modifications of water chemistry previously attributed to the forest floor may in some cases reflect unmeasured influences of understory vegetation.

The understory aboveground nutrient cycles follow two basic patterns. The first pattern, a conservative cycle, is exemplified by nitrogen and phosphorus and has the following characteristics: (1) removal of nitrogen and phosphorus from overstory throughfall by the non-bryophyte understory, (2) estimated annual nitrogen and phosphorus uptake up bryophyte production in excess of the remaining throughfall nitrogen and phosphorus content and (3) a large proportion of the annual requirement was accounted for by internal redistribution within the understory plants. The second cycling pattern, an open cycle, is characteristic of calcium and magnesium and displays characteristics opposite to those of the "conservative cycle". The potassium, manganese, zinc, and copper cycles are intermediate between the "conservative" and "open" nutrient cycles. The results are discussed with respect to a proposed model of ecosystem function and it is hypothesized that understory plays a major role in maintaining ecosystem stability by promoting nutrient cycling.

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# CHAPTER 1

## Introduction

Once upon a time, man had a minor influence on the way ecosystems functioned; his utilization of various natural resources resulted in relatively minor perturbations of his environment. As human populations grew, their demands on their environment increased and it became necessary to manage various ecosystems in order to ensure adequate supplies of desired resources. Early environmental management generally was restricted to the enhancement of commercially useful portions of ecosystems. Very little consideration was given to noncommercial components, and this frequently led to undesirable alterations in ecosystem structure and function, and sometimes to the total destruction of ecosystems. The practical importance of managing all parts of an ecosystem in order to sustain production of a derived component has been recognized only recently.

Within ecosystems, complex and interrelated groups of organisms have evolved, whose functional processes determine the characteristics of the community. The degree of integration between the biotic components of the ecosystem is such that relatively diminutive components, such as microorganisms, often play a key role in the functioning of the entire system. The role of minor vegetation in forest ecosystems is another example. Within these ecosystems minor vegetation or understory plays a role, the significance of which has been investigated only in a few isolated cases, but which appears to be far greater than might be concluded from the frequently diminutive size of this ecosystem component. This thesis examines an aspect of this role in the subalpine forests of coastal British Columbia: the contribution of the minor vegetation to the biogeochemistry of the forest ecosystem. Throughout the thesis, the terms understory vegetation and minor vegetation are used synonymously to refer to all vegetation below the level of the overstory exclusive of tree regeneration and epiphytes. This exclusion results in only minor underestimates of vegetation in the lower strata because of the scarcity of tree regeneration on the study sites.

Recognition of the importance of investigating the functional role of understory vegetation has occurred only recently. The topic has attracted attention for several decades in Scandinavia (Mikola, 1954), where it is felt that a deciduous or herbaceous understory improves litter decomposition and the general soil environment. It has been known for about 25 years that different species decompose at different rates (Melin, 1930) and recently it has been shown that pine litter decomposition is improved when a subcanopy of hazel (*Corylus cornuta* Marsh.) is present (Tappeiner and Alm, 1975).

Investigations of understory vegetation in other countries have tended to be more recent. For example, Ovington (1962, 1968) noted the polycyclic biogeochemistry of forest ecosystems and drew attention to the contribution of minor vegetation in nutrient cycling. Day and McGinty (1975) described nutrient cycles in a southern Appalachian watershed. They found that *Cornus florida* L. was important in an annual cycle, *Rhododendron maximum* L. was important in a cycle of seven years length, and *Quercus prinus* L. was important in both an annual cycle and a long term (100-200 years) cycle. Marks (1971) investigated the importance of early successional species (i.e. minor vegetation) in the maintainance of ecosystem stability after disturbance. He demonstrated the maintainance of site nutrient capital by noncommercial species; capital that will be available for subsequent growth of commercially important tree species. It has also been shown that certain species of understory vegetation actually improve height growth while causing no additional mortality to planted commercial tree species (Plass, 1977).

In addition to investigations of the role of understory vegetation in general, specific biogeochemical roles have been ascribed to individual understory species. For example, *Cornus florida* was shown to be an efficient calcium "pump" (Thomas, 1969). *Erythronium americanum* Ker. has been considered to be a short term sink for nitrogen and potassium during the period of spring runoff, thus preventing excessive leaching of those elements (Muller, 1975).

In recent years, the increasing scarcity of mature timber at lower elevations has forced logging companies to move to higher elevations to find merchantable timber. High elevation forests are associated with a variety of management problems, such as difficulties with regeneration. However, little is known about such forests, both locally in coastal British Columbia and elsewhere in the world. The recently terminated International Biological Program stimulated research both in high elevation forested ecosystems and in ecosystems found at high latitudes, but extrapolation of the results of these studies is often difficult and none were conducted in British Columbia. Because of this lack of knowledge it was decided to carry out a study of ecosystem biochemistry within the Mt. Hemlock Biogeoclimatic Zone (Krajina, 1965) of coastal British Columbia. This thesis, which formed a point of this broader study, had as its objective the determination of the biogeochemical role of understory vegetation on typical examples of the three most common ecosystem types (Brooke et al., 1970) within the Mt. Hemlock Zone. Studies of overstory biomass, nutrient cycling, of litter decomposition, of roots, and of soil were carried out concurrently by other researchers.

The structure of the thesis is as follows. Chapter two describes the location and characteristics of the three sites. Chapter three describes the study of biomass, production and nutrient content of the understory, while Chapter four presents an analysis of two major recycling pathways: litterfall and throughfall leaching. Finally, in Chapter five the overall nutrient cycle in minor vegetation is described. The biogeochemical significance of the understory is then discussed on the basis of a hypothesized model of ecosystem functioning. Due to time constraints it was possible to quantify only the aboveground portion of the minor vegetation nutrient cycle.

# CHAPTER 2

## Location and Description of the Study Site

### 2.1 Location

The study area was located in Garibaldi Provincial Park approximately 10 km northeast of Squamish, British Columbia (49°35' N 123°10' N) (Figure 2.1). All plots had a north aspect and were located between 1290 m and 1370 m above sea level (Table 2.1). Two hygrothermographs were located in the study area. Station 1 was located near the Streptopo - Abietetum amabilis site at 1290 m above sea level. Station 2 was located in the Vaccinio - Tsugetum mertensianae site at 1340 m above sea level. A recording rain gauge was located in a nearby clearcut at 1060 m above sea level.

### 2.2 Vegetation

The study area was located within the Mt. Hemlock Biogeoclimatic Zone (Krajina, 1965). Three plots were chosen to represent typical plant associations of a topographic sequence. According to Brooke, et al. (1970) and Krajina (1965) the three associations selected for study represent typical xeric, mesic and hygric ecosystem types.

The overstory layer consisted of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), mt. hemlock (*Tsuga mertensiana* (Bong.) Carr) and a few Alaska yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach). The three plant associations are briefly described below:

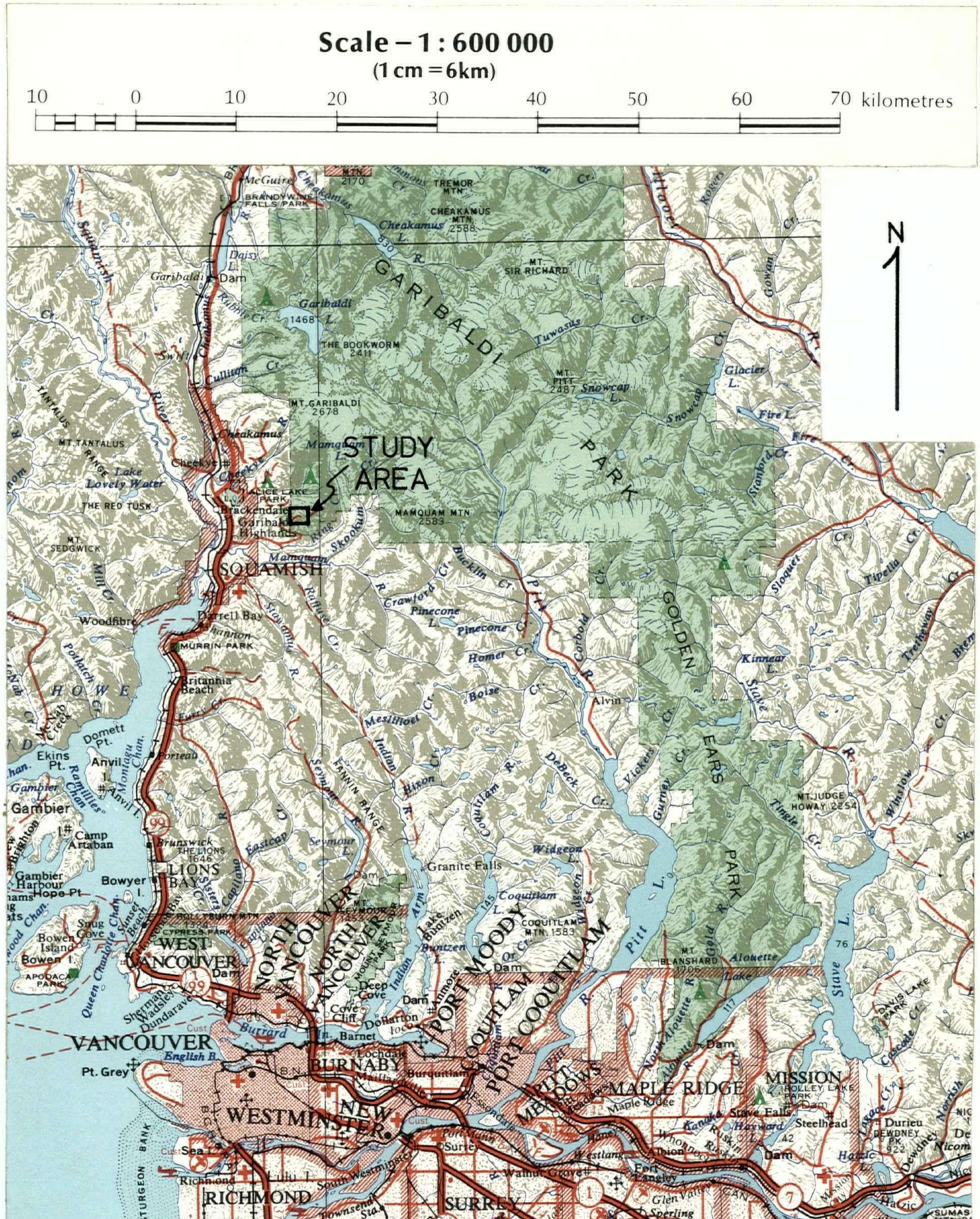



Figure 2.1 Location of the study area

TABLE 2.1

Physical Site Factors of the Three Study Sites

| Item | Plant Association: Streptopo - Abietetum amabilis | Plant Association: Abieto - Tsugetum mertensianae | Plant Association: Vaccinio - Tsugetum mertensianae |
|---|---|---|---|
| Hygrotope | Hygric | Mesic | Xeric |
| Aspect | N | N | N |
| % Slope | 24 | 58 | 15 |
| Elevation | 1290 m (4220') | 1320 m (4320') | 1370 m (4500') |
| Soil Subgroup | Orthic ferro-humic podzol | Lithic ferro-humic podzol | Lithic ferro-humic podzol |

1) Vaccinio (membranacei) - Tsugetum mertensianae plant association (Figures 2.2 and 2.3)

This association occurred on a broad ridge top. The overstory was relatively open with most of the trees growing in clumps. The understory included the shrubs *Vaccinium alaskaense* Howell, *V. membranaceum* Dougl., *Rhododendron albiflorum* Hook. and the moss *Dicranum pallidisetum* (Bailey) Irel.

2) Abieto (amabilis) - Tsugetum mertensianae plant association (Figure 2.4)

This association occurred at a midslope position. The overstory canopy was closed and relatively uniform in height and composition. Understory species included the shrubs *Vaccinium alaskaense, V. ovalifolium* Smith, *Rubus pedatus* J.E. Smith and the herb *Streptopus streptopoides* (Ledeb.) Frye and Rigg.

3) Streptopo (rosei) - Abietetum amabilis plant association (Figure 2.5)

This association, which occurred on a bench directly below the Abieto - Tsugetum mertensianae site, had a slightly more open overstory canopy. Understory species included *Streptopus roseus* Michx, *S. amplexifolius* (L.) D.C.,*Rubus pedatus, Veratrum viride* Ait. in the herbaceous strata and the moss *Rhizomnium nudum* (Williams) Koponen.

A more detailed description of the overstory layer follows, and a complete list of understory species sampled is included in Appendix 1. Throughout the remainder of the thesis the terms hygric, mesic, and xeric will be used to refer to the three plant associations; Streptopo

Figure 2.2. Looking into the Vaccinio - Tsugetum mertensianae Plant Association

Figure 2.3. The Vaccinio - Tsugetum mertensianae Plant Association

Figure 2.4. The Abieto - Tsugetum mertensianae Plant Association

Figure 2.5. The Streptopo - Abietetum amabilis Plant Association

- Abietetum amabilis, Abieto - Tsugetum mertensianae and Vaccinio - Tsugetum mertensianae, respectively.

## 2.3 Climate

The climate of the study area has been classified according to Koppen (1936) as Dfc (Krajina, 1965; Brooke et al., 1970). It can be described as a microthermal, subcontinental, humid climate with heavy snow cover (Krajina, 1965). Temperature and precipitation data for the study period are presented in Appendix 2. The year 1976 was characterized by relatively late snowmelt, and below normal temperatures and precipitation. Snow-course measurements for nearby mountains in April show a larger than average snow pack in the winter of 1975/1976, followed by an extremely low snowpack in 1976/1977 (Appendix 2). Krajina (1965) gives a mean annual temperature of 3-7°C for the study area. During 1976 the mean annual temperature was estimated as 2.8°C for Station 1 and 2.6°C for Station 2.

## 2.4 Soils

The parent material of the study site is principally glacial till, composed mainly of Garibaldi volcanics (Danner, pers. comm.; Krumlik, 1978). Two soil pits were dug per site and the soil was classified to subgroup (Table 2.1). An Orthic Ferro-humic Podzol approximately 75 cm deep was found on the hygric site. The forest floor layer averaged 4 cm in depth with a range of 2 to 7 cm. On the mesic and xeric sites three of the four soils sampled were classified as Lithic Ferro-humic Podzols, approximately 25 cm deep. On the mesic site the humus layer averaged 17 cm in depth with a range of 10 to 25 cm. The humus layer on the xeric site was approximately 3 cm deep. The fourth soil sampled, found on the xeric site, was classified as a Folisol and was approximately 75 cm deep. It was estimated that this soil type underlies approximately 15 percent of the xeric site. Brief soil descriptions are included in Appendix 3.

## 2.5 Overstory Description

The primary objective of the thesis was to quantify the nutrient cycle in the understory vegetation of the three study sites; overstory vegetation received relatively little attention since it was the subject of another study (Krumlik,1978). However, understory vegetation reflects crown closure and stand structure and the thesis is concerned with the role of understory relative to that of the overstory. Consequently, a summary description of the overstory on the three sites is presented.

### 2.5.1 Overstory Biomass

#### 2.5.1.1 Methods

In each plant association an overstory biomass plot was established to include all possible understory sampling sites. The boundaries were surveyed with a staff compass and chain. The plot area was calculated using the DMD-method (Brinker, 1969).

Diameter at breast height and crown length were determined for all trees with a diameter at breast height greater than 1.25 cm. These parameters were then used in regression equations to determine individual tree biomass for the following components:

1) wood and bark
2) big branches (> 2.54 cm)
3) twigs (< 0.63 cm), foliage and small branches (0.64-2.53 cm)
4) volume in cubic meters (whole stem, outside bark)

The equations used are listed in Table 2.2. The correction factor suggested by Finney (1941) and Baskerville (1972) was used on the biomass equations. The total estimates were then converted into $kg/m^2$ units.

A random sample of 15 dominant or codominant trees was selected to determine the average age of the overstory in each plant association. The mean annual increment for the overstory in each plant association was determined by dividing the plot biomass by the average stand age. This mean annual increment was considered as an approximate value for the current annual production in these old growth forests.

The percent overstory cover was estimated with a spherical densiometer at 70 randomly located sampling points.

2.5.1.2 Results

The range in overstory age for each of the three plots was: hygric, 124 to 605 years; mesic, 108 to 323 years; and xeric, 45 to 513 years, with average ages of 270, 238, and 260 years, respectively (Table 2.3). Stands of this age can be considered mature and are assumed to be

Table 2.2. Individual Tree Regression Equations.

| Species | Dependent Variable | Equation | Ref |
|---|---|---|---|
| *Abies amabilis* | Log wood biomass | $y = 2.047 + 0.953 \text{ Log } D^2.H$* | |
| | Log bark biomass | $y = 3.096 + 1.327 \text{ Log } BA$ | |
| trees greater than 15 cm DBH | Log big branch biomass | $y = 2.665 + 2.493 \text{ Log } D$ | 1 |
| | Log small branch biomass | $y = 0.681 + 0.760 \text{ Log } D.CL$ | |
| | Log twigs & foliage biomass | $y = 0.879 + 1.038 \text{ Log } D.CL$ | |
| trees less than 15 cm DBH | **Ln stem biomass | $y = 1.5589 + 1.88 \text{ Ln } D+0.9332 \text{ Ln } H$ | |
| | Ln total branch biomass | $y = 2.2870 + 3.216 \text{ Ln } D-1.0895 \text{ Ln } H$ | 2 |
| | Ln twig & foliage biomass | $y = 1.9971 + 2.7950 \text{ Ln } D-0.8048 \text{ Ln } H$ | |
| *Tsuga mertensiana* | Log wood biomass | $y = 2.319 + 0.746 \text{ Log } D^2.H$ | |
| | Log bark biomass | $y = 3.109 + 1.039 \text{ Log } BA$ | |
| trees greater than 15 cm DBH | Log big branch biomass | $y = 2.800 + 3.074 \text{ Log } D$ | 1 |
| | Log small branch biomass | $y = 0.936 + 1.007 \text{ Log } D.CL$ | |
| | Log twig & foliage biomass | $y = 0.567 + 1.297 \text{ Log } D.CL$ | |
| trees less than 15 cm DBH | Ln stem biomass | $y = -1.5128 + 1.8801 \text{ Ln } D + 0.9332 \text{ Ln } H$ | |
| | Ln total branch biomass | $y = 2.1610 + 2.8863 \text{ Ln } D -0.8043 \text{ Ln } H$ | 2 |
| | Ln twig & foliage biomass | $y = 1.7234 + 2.3289 \text{ Ln } D -0.4612 \text{ Ln } H$ | |
| *Abies amabilis* | Log cubic meter volume | $y = -4.266202 + 1.78296 \text{ Log } D + 1.10382 \text{ Log } H$ | |
| *Tsuga mertensianae* | Log cubic meter volume | $y = -4.337451 + 1.7835 \text{ Log } D + 1.12023 \text{ Log } H$ | 3 |
| *Chamaecyparis nootkatensis* | Log cubic meter volume | $y = -4.187127 + 1.77736 \text{ Log } D + 1.03299 \text{ Log } H$ | |

References: 1) Krumlik and Kimmins (1973); 2) Young, Strand, and Altenburger (1964); 3) B.C. Forest Service (1976).

* Variable abbreviations are as follows: Y - dependent variable (Kg or $m^3$); D - diameter (m); BA - basal area ($m^2$); CL - crown length (m); H - height (m).

** Log - means logarithm to the base 10
Ln - means logarithm to the base e.

Table 2.3.

Overstory Characteristics for Three Plant Associations of the Mountain Hemlock Biogeoclimatic Zone.

| Item | Plant Association Hygric | Mesic | Xeric |
|---|---|---|---|
| Plot area (ha) | 0.1841 | 0.2046 | 0.1940 |
| Age (years) | 270 | 238 | 260 |
| Density (trees/ha) | 283 | 415 | 768 |
| Percent overstory cover | 89.0 | 92.3 | 76.8 |
| Percent composition (number of trees) | | | |
| *Abies amabilis* | 87.1 | 89.4 | 64.1 |
| *Tsuga mertensiana* | 12.9 | 10.6 | 29.3 |
| *Chamaecyparis nootkatensis* | ---- | ---- | 6.6 |
| BIOMASS ($kg \cdot m^{-2}$)* | | | |
| *Abies amabilis* | 58.10 | 51.63 | 8.10 |
| *Tsuga mertensiana* | 2.78 | 4.05 | 23.13 |
| *Chamaecyparis nootkatensis* | ----- | ----- | 2.82 |
| Total | 60.88 | 55.68 | 34.05 |
| MAI ($kg \cdot m^{-2} \cdot yr^{-1}$) | 0.230 | 0.234 | 0.130 |
| MEAN TREE DIMENSIONS | | | |
| mean height (m) | 25.0 | 24.2 | 10.9 |
| mean dbh (m) | 0.495 | 0.432 | 0.262 |
| crown length (m) | 16.3 | 15.1 | 6.96 |
| vol. of mean tree ($m^3$) | 4.69 | 2.94 | 0.61 |
| VOLUME ($m^3$/ha) | | | |
| *Abies amabilis* | 1289.4 | 1163.7 | 135.4 |
| *Tsuga mertensiana* | 32.1 | 58.2 | 303.6 |
| *Chamaecyparis nootkatensis* | ------ | ------ | 29.1 |
| Total | 1321.5 | 1221.9 | 468.1 |

* A breakdown by component is included in Appendix 4.

relatively stable.

The percent composition and percent cover of the overstory are typical for these three ecosystems (Table 2.3; Krumlik, 1978; Brooke et al., 1970). The total aboveground biomass (Table 2.3), although relatively high compared to similar high elevation or high altitude (Rodin and Bazilevich, 1965), is typical for high elevation forests in south coastal British Columbia (Krumlik, 1978; Krumlik and Kimmins, 1976, 1973; Yoda, 1968).

### 2.5.2 Overstory Nutrient Standing Crop

The overstory nutrient standing crop was calculated by multiplying the estimated component biomass (Appendix 4) by chemical concentration data obtained in a study conducted at a site (called the Mamquam site) approximately 12 km away from the thesis study sites. These concentrations may underestimate the true concentrations for the study sites because of the nutrient-poor parent materials present at the Mamquam site. The results which are summarized in Table 2.4 and presented by component in Appendix 4 are therefore probably conservative estimates for the present study sites.

The calculated values for overstory nutrient standing crop are higher than those reported by Krumlik and Kimmins (1976) for the Mamquam site; this is the result of the higher biomass values estimated for the sites in the present study (Table 2.3; Krumlik, 1978). The estimates of aboveground nutrient standing crop are within the range reported by Rodin and Bazilevich (1965) for coniferous and mixed forests, and are

TABLE 2.4.

Aboveground Nutrient Standing Crop ($g \cdot m^{-2}$) for the Overstory of Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone.

| Element | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensiaeae |
|---|---|---|---|
| Nitrogen | 80.86 | 73.71 | 50.68 |
| Phosphorus | 13.81 | 12.79 | 11.20 |
| Calcium | 101.55 | 91.41 | 58.69 |
| Magnesium | 10.82 | 10.02 | 7.89 |
| Potassium | 56.16 | 51.31 | 34.36 |

in close agreement with estimates given by Krumlik (1978) for three similar adjacent sites.

Between-site differences present in Table 2.4 are the result of two factors; one, the between-site differences in total biomass and species composition and; two, the differences in chemical concentrations between species. For example, because there is very little difference in phosphorus concentrations among the three species, the site differences follow the biomass values. In contrast, calcium concentrations show a great deal of variability among species, so site differences represent not only biomass patterns but also the influence of differing chemical concentrations.

# CHAPTER 3

## Understory Biomass and Productivity

### 3.1 Introduction and Literature Review

At the heart of any nutrient cycling study is the determination of the biomass, its nutrient content and the annual change of both. This involves the measurement of standing biomass, net primary production, standing nutrient crop, and nutrients accumulated in net primary production. The objective of this part of the study was to estimate for three plant associations of the Mt. Hemlock Biogeoclimatic Zone: (1) understory aboveground biomass, (2) the nutrients contained in this aboveground biomass, (3) understory net primary production and (4) the quantity of nutrients accumulated in this net primary production.

#### 3.1.1 Literature Review - Understory Biomass

Understory biomass values as reported in the literature are quite variable (Appendix 5), ranging from 5.8 $g \cdot m^{-2}$ for an oak-hickory forest (Whittaker, 1966) to 2425.9 $g \cdot m^{-2}$ in a chestnut oak heath (Whittaker, 1963; 1966). In relation to overstory biomass, understory had its greatest reported development in the latter location at 60.6 percent of the overstory biomass (Whittaker 1963, 1966). The least developed understory was reported for a *Sequoia sempervirens* (D. Don) Endl. forest where the understory biomass (45.0 $g \cdot m^{-2}$) was only 0.01 percent of the overstory biomass (Westman and Whittaker, 1975). Actually, the lowest value possible approaches 0 $g \cdot m^{-2}$ although it has never been reported.

Considering the wide variation in the published biomass data (Appendix 5), understory vegetation represents a relatively constant average percentage of overstory biomass (Table 3.1). If the mean for the closed, mainly evergreen conifer forest with rounded crowns (IA9B) is recalculated omitting the immature stands, the average drops from 5.9 percent to 3.3 percent. Thus, understory biomass averages from three to four percent of the overstory biomass in mature coniferous forests. Ovington (1965) presents an average of two to three percent while Whittaker and Niering (1975) reported a relatively consistent percentage (less than 1 percent) along an elevational gradient in the Santa Catalina Mountains of Arizona. Long and Turner (1975) reported a range of 11.8 percent to 1.3 percent for an age series of four Douglas-fir (*Pseudotsuga menzesii* (Mirb.) Franco) stands in the Cedar River watershed. Turner and Singer (1976) reported a value of 0.8 percent in a subalpine coniferous forest ecosystem in the Cedar River watershed, Washington. However, if the dead tree wood is omitted from their

TABLE 3.1.

Summary of Aboveground Understory Biomass and Productivity by Physiognomic - Ecological Class†

| Forest Type | Biomass | | Net Primary Production | | |
|---|---|---|---|---|---|
| | Biomass $g \cdot m^{-2}$ | Percent of Overstory Biomass | NPP $g \cdot m^{-2} \cdot yr^{-1}$ | Percent of Understory Biomass | Percent of Overstory Production |
| IA9a* | | | | | |
| mean | 344.3 | 3.3 | 31.2 | 69.3 | 2.5 |
| range | 15.3- 764.0 | 0.0-11.8 | + | + | + |
| IA9b | | | | | |
| mean | 304.92 | 5.9 | 78.6 | 55.0 | 13.0 |
| range | 7.0-1492.0 | 0.0-27.1 | 4.8-183.0 | 12.3-100.0 | 0.9-36.3 |
| IA9c | | | | | |
| mean | 583.49 | 3.8 | 8.5 | 13.3 | 1.0 |
| range | 16.5-2315.4 | 0.1-15.5 | + | + | + |
| IA9d | | | | | |
| mean | 375.55 | 2.2 | | | |
| range | 163.5- 518.0 | 0.8- 4.7 | | | |
| IB1a | | | | | |
| mean | 141.0 | 0.8 | 30.0 | 21.3 | 2.4 |
| range | + | + | + | + | + |
| IB2c | | | | | |
| mean | 258.83 | 8.8 | 16.4 | 36.2 | |
| range | 5.8-2425.0 | 0.1-60.6 | 0.2- 29.1 | 20.0- 53.9 | |
| IB3a | | | | | |
| mean | 148.12 | 3.3 | 68.4 | 68.2 | 2.9 |
| range | 18.0-435.0 | 0.1- 7.0 | 7.0-160.1 | 11.2- 95.4 | + |
| IB3b | | | | | |
| mean | 1236.43 | 10.5 | 247.1 | 21.5 | 52.7 |
| range | 238.7-1760.0 | 1.8-19.9 | 163.4-379.0 | + | 44.1-63.2 |

† Summary of data from the literature which are presented in full in Appendix 5.

\+ Only one value reported.

* Physiognomic - Ecological Classification from Muller-Dombois and Ellenberg (1974).

- I - Closed forests
  - A - Mainly evergreen forests
    - 9 - Temperate and subpolar evergreen coniferous forests
      - a - Evergreen giant conifer forest
      - b - Evergreen conifer forest with rounded crowns
      - c - Evergreen conifer forest with conical crowns
      - d - Evergreen conifer forest with cylindrical crowns
  - B - Mainly deciduous forests
    - 1 - Drought deciduous forests
      - a - Lowland and submontane forest
    - 2 - Cold deciduous forests with evergreen trees admixed
      - c - Cold deciduous forests with evergreen needle-leaved trees
    - 3 - Cold deciduous forests without evergreen trees
      - a - Temperate lowland and submontane forests
      - b - Montane or boreal forests

calculation, then understory biomass represents 1.1 percent of the living overstory biomass.

The standing biomass of minor vegetation in a forest ecosystem is a function not only of the macroclimate (e.g. light, wind, temperature, etc.) but also of the effect that the overstory has on the macroclimate, the time of year that sampling occurred and the growth habit of the plant (annual vs. perennial).

The abundance of understory vegetation has been related to both light (Shirley, 1945a; McConnell and Smith, 1970; Long and Turner, 1975) and moisture (Toumey, 1929; Anderson et al., 1969). Many of the earlier studies emphasized only one environmental parameter. However, these two parameters (light and moisture) are both functions of overstory cover. Shirley (1945b) and Clements and Long (1935) were among the first to demonstrate an interaction between light and moisture.

The time of sampling can influence estimates of understory biomass. Both total biomass and the proportion of above to belowground biomass changes through the growing season (Simonovic, 1973). Different species within a community attain maximum biomass levels at different times throughout the growing season (Hughes, 1971). For example, *Erythronium americanum* Kerr., a spring herb, completes most of its aboveground life cycle between snow melt and leafing out of the overstory in northeastern deciduous forests (Muller, 1975). Maximum biomass of fall-flowering species has been shown to occur at different times throughout the growing season (Hughes, 1971; Kubicek and Brechtl, 1970). Seasonal changes have also been shown to occur within various components of five tall shrub species (Grigal et al., 1976).

Structurally, understory vegetation can be composed of many species, but the majority of the biomass will usually be accounted for by very few species. Moszynska (1970) found that two of fourteen species present in the herb layer of a bog pinewood accounted for 88 percent of the biomass. Similar results were also reported for a dry pine forest (Wojcik, 1970), for four deciduous plant associations (Traczyk, 1971) and in an age sequence of four Douglas-fir stands in the Cedar River watershed (Long and Turner, 1975).

### 3.1.2 Literature Review - Understory Net Primary Production

Understory net primary production values in the literature are variable (Appendix 5) and only contribute a small proportion of overstory production[1] (Table 3.1). When expressed as a percentage of overstory production, a minimum value of 0.87 percent was reported for a 140-year-old ponderosa pine (*Pinus ponderosa* Laws.) stand (Whittaker and Niering, 1975), although the actual minimum value approaches zero $g \cdot m^{-2} \cdot yr$ or 0.0 percent. A maximum value of 159 percent was reported for a chestnut oak heath in the Great Smoky Mountains (Whittaker, 1963, 1966).

[1] Production and net primary production are used synomously.

The factors that affect estimates of standing biomass will also affect estimates of net primary production. Bradbury and Hofstra (1976) have emphasized the importance of measuring vegetation mortality in certain grassland and herbaceous communities. They found that production would be significantly underestimated if the portion of the vegetation which died before sampling were ignored. Problems related to the measurement of production were reviewed by Whittaker and Marks (1975).

An important consideration when analyzing production is the distribution of the total production among the various plant components. Average proportions of annual production in each of seven tree and shrub components summarized from the literature are presented below:

| Component | Tree (Overstory) | Shrub (Understory) |
| --- | --- | --- |
| | % | |
| Roots | 18.0 | 58.0 |
| Stemwood | 15.0 | 3.0 |
| Stembark | 2.5 | 1.3 |
| Branchwood and Branchbark | 21.0 | 10.0 |
| Twigs | 6.0 | 6.0 |
| Leaves | 38.0 | 21.0 |
| Fruit | 1.5 | 1.3 |

(Source of data: Whittaker, 1962, 1966; Art, 1971; Young and Carpentar, 1967; Whittaker and Woodwell, 1969; Fujimori, 1971.)

Below ground production in shrubs is much greater than in trees. As a result, a smaller percentage of total production is found in shrub leaves, stemwood and branchwood plus branchbark. The similarity in the relative proportions in different components may increase when more data and improved data collection techniques are available for both trees and shrubs.

### 3.1.3 Literature Review - Understory Nutrient Standing Crop

The nutrient standing crop is a function of both the standing biomass and the concentration of each element in the various biomass components. Although the nutrient concentrations of individual species grown in one area can be highly variable (Scott, 1955; Klinka, 1976), a few consistent patterns have appeared in the literature. In general, understory species tend to have higher nutrient concentrations than overstory species (Woodwell et al., 1975; Klinka, 1976). Leaves, flowers, and fruits contain the highest concentrations, heartwood the lowest, and twigs, bark, branches, roots, and sapwood are intermediate in concentration (Woodwell et al., 1975).

It has been suggested that variation in chemical concentrations is an indication of niche differentiation between species occurring on a particular site (Muller, 1975; Woodwell et al., 1975). Based on foliar concentrations of Ca, K, Fe, and Al, Klinka (1976) was able to classify three plant species characteristic of xeric, mesic and hygric site types with the use of discriminant analysis. He then concluded that "differences in the chemical composition provided a highly significant basis on which to distinguish between taxonomically and ecologically different plant species".

The relationship of understory nutrient standing crop to overstory nutrient standing crop follows, by necessity, the same basic pattern as the relationship of understory biomass to overstory biomass. The understory/overstory nutrient ratio values are slightly higher than the biomass ratio values however, due to the higher nutrient concentrations of the understory species. Data presented by Ovington (1962) indicate that the average percentage of the total aboveground nutrient pool held by the understory is 12.3 percent, 10.7 percent, 18.2 percent, 6.8 percent, and 10.3 percent for nitrogen, phosphorus, potassium, calcium and magnesium, respectively. The ranges were 0.6 percent to 34.5 percent for nitrogen; 3.2 percent to 26.5 percent for phosphorus; 0.4 percent to 52.5 percent for potassium; 0.7 percent to 20.5 percent for calcium and 3.3 percent to 27.9 percent for magnesium. Data from four additional studies are presented in Table 3.2. The quantities of nutrients held in the understory are highly variable, but in some ecosystems a significant proportion can be found in understory vegetation (Mälkönen, 1974, 1977).

### 3.1.4 Literature Review - Nutrients Accumulated in Understory Production

The literature on this aspect of understory nutrient cycling is almost nonexistent, but two points have been made. First, minor vegetation, at least in early successional stages, can attain maximum production within a year or two of establishment (Marks, 1971). As a result of this high production minor vegetation becomes a large sink for any nutrients which might otherwise be leached from a recently disturbed site, and as such it represents an efficient nutrient conservation mechanism (Marks, 1971).

Second, Mälkönen (1974) has reported the quantity of nutrients used by understory to produce the equivalent of one kilogram dry matter in three Scots pine stands. He found that ground vegetation and shrubs

TABLE 3.2.

Percentage of Nutrients Contained in the Understory of Various Forest Ecosystems

| Stand Type | Age | Nutrient (% of aboveground total) | | | | | | | Reference |
|---|---|---|---|---|---|---|---|---|---|
| | | N | P | Ca | Mg | K | Mn | Fe | |
| *Abies amabilis* | 175 | 7.4 | 5.5 | 3.2 | 1.7 | 2.4 | 0.5 | | A |
| *Abies amabilis** | 175 | 8.0 | 6.9 | 3.2 | 2.0 | 2.8 | 0.5 | | A |
| *Pinus banksiana* | 30 | 3.5 | 6.7 | 1.8 | 5.3 | 8.6 | | | B |
| *Pinus banksiana* | 70 | 15.0 | 19.0 | 21.0 | 6.0 | 18.0 | 22.0 | 9.0 | C |
| *Pinus sylvestris* | 28 | 34.9 | 30.4 | 21.5 | | 33.4 | | | D |
| *Pinus sylvestris* | 47 | 20.0 | 18.7 | 18.5 | | 21.4 | | | D |
| *Pinus sylvestris* | 45 | 22.4 | 23.1 | 13.3 | | 25.5 | | | D |

* Values recalculated not using the large dead tree component.

References: A, Turner and Singer, 1976; B, Foster and Morrison, 1976; C, Tappeiner II and John, 1973; D, Mälkönen, 1974.

utilized from 38 percent to 166 percent (depending on the nutrient) more nutrients than the overstory in the production of one kilogram of dry matter. He then concluded that "ground vegetation plays a much greater role as a consumer of nutrients than as a producer of biomass in a stand".

## 3.2 Methods

### 3.2.1 1975 Herbaceous and Shrub Biomass

Ten randomly selected 16 $m^2$ plots were located within each plant association. This size was selected after consideration of a species area curve determined from a preliminary sample. A plot of that size should contain 95 percent of all observed species. A total of 40 subplots were then randomly selected and sampled according to a two-stage procedure in each plant association: a subsample of four (second stage) 1 $m^2$ subplots was randomly selected from within each plot (first stage).

The vegetation on each of the subplots was clipped at ground level, segregated into species, dried at 70°C until a constant weight was obtained and then weighed to the nearest 0.001 gram. Leaf and stem material were dried and weighed separately for the shrubs. The mean and standard error of the mean were calculated using methods outlined by Cochran (1963).

A maximum of five shrub stems per species were selected when possible from each of a randomly selected subsample of 20 subplots per plant association (i.e. maximum of 100 stems per species). The diameter at ground level was measured to the nearest 0.05 mm. The leaves were removed from the stem and separate dry weights were obtained for both components. Nonlinear regressions were then calculated relating stem basal diameter to leaf and stem dry weight according to a nonlinear least squares technique (Draper and Smith, 1966), using a University of California (Los Angeles) Biomedical nonlinear least squares program. All data for shrub species were analyzed using a dummy variable method outlined by Cunia (1973). This method was chosen to facilitate a subsequent covariance analysis between species to test for similarity of regression coefficients.

The covariance analysis (Cunia, 1973) was set up to test for differences in the component equations (leaf and stem) for the following species:

1) *Rhododendron albiflorum*
2) *Rubus spectabilis* Pursh
3) *Vaccinium alaskaense*
4) *V. membranaceum*
5) *V. ovalifolium*

No significant differences were found among the three *Vaccinium* species. The final regressions were then calculated using data collected in both 1975 and 1976.

3.2.2 1976 Understory Biomass Sample

Methods used to estimate shrub and herbaceous biomass were changed during the 1976 field season in order to save time. A total of 70 sampling points were located randomly within each of the three sites and a sample plot of the design shown in Figure 3.1 was established at each point.

Moss biomass was estimated by clipping a randomly selected subsample (30 of the 70 plots). Moss clipping plots were 625 $cm^2$ in area and their relative position within each shrub plot is indicated in Figure 3.1.

Herbaceous biomass was estimated using a double sampling technique (Cochran, 1963). The first phase consisted of estimating the percent cover of each species present on all 70, 0.25 $m^2$ herb plots. The second phase consisted of clipping a randomly selected subsample of 20 plots plus between two to eight additional plots per site to ensure that the range of species cover values was adequately sampled. The vegetation from the clipped plots was dried at 70° C until constant weight was obtained and weighed to the nearest 0.001 grams. A regression relating % cover to aboveground biomass was then calculated to estimate the biomass of each species on each of the seventy herbaceous plots.

Shrub biomass was estimated by regression from basal diameter measurements. Every stem rooted inside a randomly selected subsample of 30 plots was measured at ground level to the nearest 0.05 mm. A 1 $m^2$ plot was used on the hygric and mesic sites. Due to the density of shrubs on the xeric site a 0.25 $m^2$ shrub plot was used (Figure 3.1).

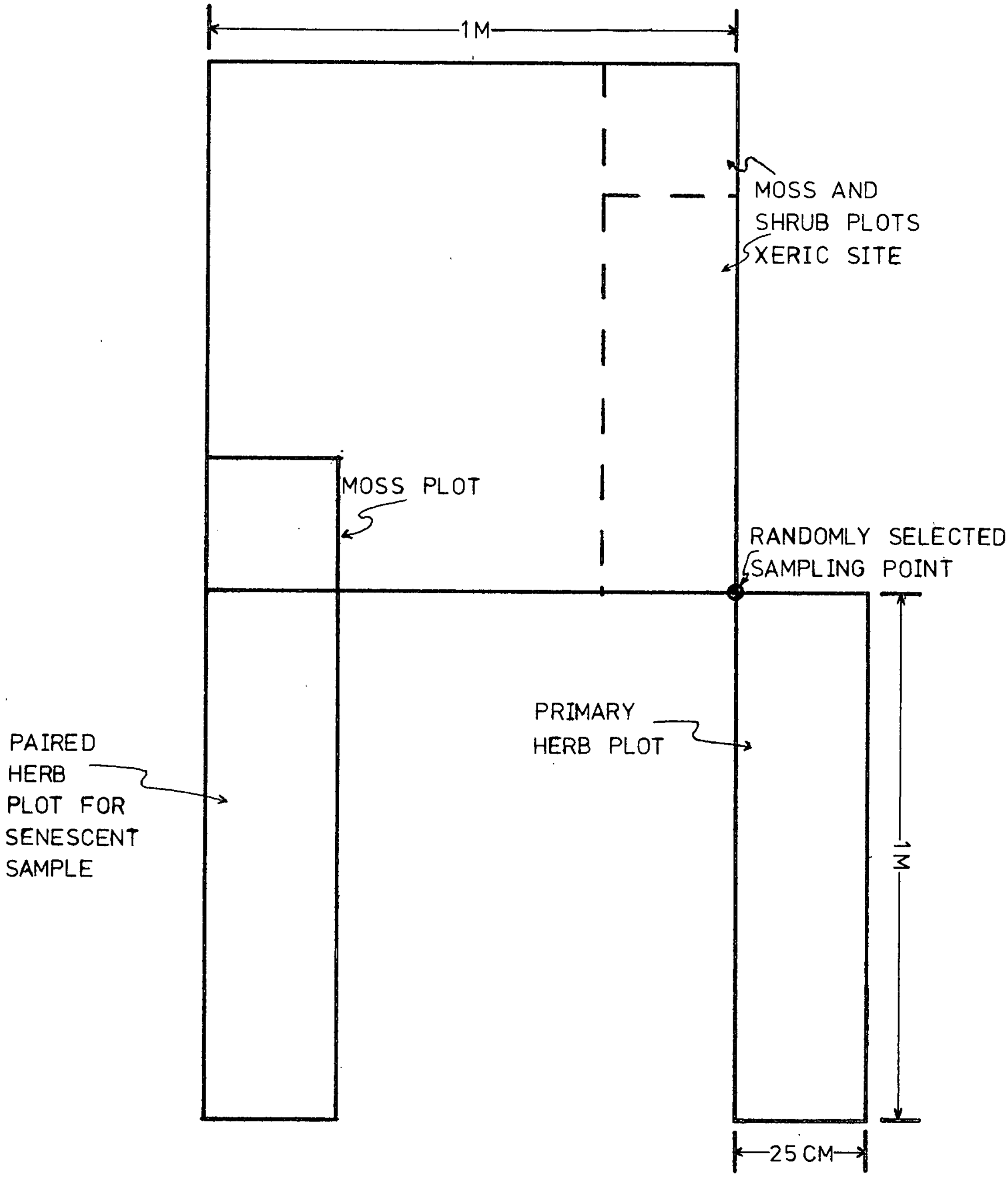



Figure 3.1. Design of the 1976 understory sampling plot.

To ensure that a reasonable approximation of peak standing biomass was obtained, phenological observations were taken weekly during the snow-free period from a randomly selected subsample of ten plots per site.

### 3.2.3 Herbaceous and Shrub Productivity

Aboveground herbaceous productivity was assumed to be equal to the peak standing biomass.

Shrub productivity was defined as the sum of three components which were estimated by regression on stem basal diameter: leaf biomass, current twig biomass and annual increment of the perennial stem. Maximum leaf biomass was used as the value for leaf production (all shrubs were deciduous). Current twig biomass was estimated by clipping the current year's new stem growth from 20-40 sample plants in each of three species categories and relating this to diameter at ground level. The three species categories were:

1) *Rubus spectabilis*
2) *Rhododendron albiflorum*
3) *Vaccinium* sp.

Increment of the perennial stem was determined indirectly. A regression relating stem age to stem biomass minus the current year's twig growth was calculated. This permitted the determination of stem increment as a function of age. The relationship between stem age and diameter at ground level was then used to estimate the increment of each measured shrub stem.

However, this technique could not be used for *Vaccinium* species due to the difficulty in determining age (Flower-Ellis, 1971; Dale, 1968). For these shrubs it was necessary to assume that a fixed percentage of the total production was in woody perennial material. Whittaker (1962, 1963) and Whittaker and Marks (1975) present values of up to 52 percent for stemwood, stembark, branchwood and branchbark production in shrubs from the Great Smoky Mountains. Forrest (1971) reported that 67% of the new production in *Empetrum nigrum* L. was leaves. Mork (1946) reported that leaf production was 85 percent and 70 percent of total production in *Empetrum hermaphroditum* L. and *Vaccinium uliginosum* L. respectively. Based on these figures, perennial woody production was assumed to be 30 percent of total annual production for *Vaccinium* species. Similarly, the woody production of *Rubus spectabilis* was assumed to be 17 percent of stem biomass.

Total shrub production was then calculated by summing the three components. The production of *Phyllodoce empetriformis* (Sw.) D. Don, *Cassiope mertensiana* (Bong.) G. Don and the moss species was assumed to be 20 percent of their standing biomass (Tamm, 1953; Van Cleve and Dyrness, 1977).

### 3.2.4 Determination of Elemental Concentrations

After determination of oven dry weight, all biomass and productivity samples were ground to pass a 40-mesh screen in a Wiley mill. Prior to analysis the samples were redried at 70°C for 24 hours.

The concentration of calcium, magnesium, potassium, manganese, copper and zinc was determined from a one gram sample. The sample was ashed at 475°C in a muffle furnace for 4 hours. The resultant ash was dissolved in 7.5 ml of hot HCl 20 percent. This solution was then diluted to 100 ml with distilled water and stored in a polyethylene bottle until the cation concentrations were determined with a Varian - Techtron Atomic Absorption Spectrophotometer.

Nitrogen and phosphorus concentrations were determined from an 0.2 gram sample digested with 5 ml of digestion mixture (100 gm of potassium sulfate plus 1 gm of selenium plus 1 liter of concentrated $H_2SO_4$ heated until the solution is clear; approximately 24 hours). The resultant solution was then diluted to 100 ml with distilled water and stored in a polyethylene bottle. Concentrations of nitrogen and phosphorus were determined colorimetrically with a Technicon Industrial Automatic Analyser.

## 3.3 Results and Discussion

### 3.3.1 Understory Biomass

The equations used to calculate the biomass and production of understory vegetation for 1976 are presented in Tables 3.3 and 3.4. The total understory biomass ranged from a low of 39.8 $g \cdot m^{-2}$ for the hygric site to 331.1 $g \cdot m^{-2}$ for the xeric site (Table 3.5). The mesic site was intermediate at 54.3 $g \cdot m^{-2}$ (Table 3.5). The estimates for shrub and herb biomass were approximately 30 percent less in 1976 than 1975. The difference was considered to be the result of two factors: climate and sampling method.

TABLE 3.3.

Component Shrub Regressions by Species

| Species | Number of Observations | a | b | Standard Error of Estimate |
|---|---|---|---|---|
| Dependent Variable = Dry Leaf Weight | | | | |
| Rubus | 55 | 0.21059 | 0.30592 | 0.328 |
| Vaccinium | 122 | 0.19538 | 0.24005 | 0.211 |
| Rhododendron | 49 | 0.33812 | 0.15874 | 0.391 |
| Dependent Variable = Dry Stem Weight | | | | |
| Rubus | 13 | 0.32936 | 0.40231 | 1.016 |
| Vaccinium | 18 | 0.81219 | 0.32059 | 1.505 |
| Rhododendron | 20 | 3.3417 | 0.18102 | 1.223 |
| Dependent Variable = Dry Current Growth Weight | | | | |
| Rubus | 13 | 0.29387 | 0.19898 | 0.301 |
| Vaccinium | 18 | 0.030335 | 0.24858 | 0.134 |
| Rhododendron | 20 | 0.051209 | 0.12347 | 0.065 |
| Dependent Variable = Dry Petiole Weight | | | | |
| Rubus* | 13 | 0.0 | 0.071973 | 0.14815 |

* This relationship is y = a + bx; for all others y(grams per plant) = $ae^{bx}$ where x is basal stem diameter (mm).

TABLE 3.4.

Herbaceous Biomass Regressions*

Estimated from 1976 Data

| Species Code | Number of Observations | Coefficient | R-Square | Standard Error of Estimate |
|---|---|---|---|---|
| ARLA** | 20 | 0.060941 | 0.80362 | 0.27826 |
| ATFF | 20 | 0.10114 | 0.90749 | 0.68573 |
| CAME | 18 | 0.43038 | 0.84562 | 1.1713 |
| CANI | 17 | 0.09641 | 0.99007 | 0.19480 |
| GYDR | 20 | 0.047807 | 0.85843 | 0.19221 |
| LUPE | 16 | 0.05452 | 0.99231 | 0.01894 |
| OSCH | 20 | 0.06510 | 0.9854 | 0.02613 |
| PHEM | 17 | 0.44814 | 0.63536 | 2.8988 |
| RUPE | 45 | 0.035998 | 0.81324 | 0.26424 |
| STRO | 41 | 0.085449 | 0.84156 | 0.37236 |
| STST | 23 | 0.053366 | 0.91426 | 0.07195 |
| TIUN | 43 | 0.05790 | 0.77335 | 0.33173 |
| VASI | 21 | 0.078339 | 0.77943 | 0.35714 |
| VEVI | 21 | 0.39025 | 0.90566 | 1.3104 |
| VIGL | 20 | 0.12924 | 0.78098 | 0.15203 |

* The form of the relationship is $y = ax$, where $x$ is the estimated percent cover and $y$ is the species biomass in grams. All regressions were significant at the 0.05 level of probability.

** A complete list of species codes can be found in Appendix 1.

TABLE 3.5.

Understory Aboveground Biomass ($g \cdot m^{-2}$) by Species for Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| | PLANT ASSOCIATION | | | | | |
|---|---|---|---|---|---|---|
| | Streptopo - Abietetum amabilis | | Abieto - Tsugetum mertensianae | | Vaccinio - Tsugetum mertensianae | |
| Species Code | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 |
| Shrub Layer | | | | | | |
| ROAL | | | | | 147.606(60.1)[1] | 101.108 |
| RUSP | 2.634(1.91) | 5.237 | | | | |
| SOSI | | | 0.086(0.09) | 0.0 | | |
| VAAL | 3.442 | 2.848[2] | 29.956(11.33) | 18.925[2] | 80.763(43.1) | 54.548[2] |
| VAME | | | 1.440(0.88) | 0.910 | 126.347(27.8) | 85.336 |
| VAOV | | | 27.447(14.19) | 17.340 | 5.074(3.16) | 3.427 |
| VAPA | 0.080(0.06) | 0.066 | 0.549(0.41) | 0.347 | | |
| VASP | 0.047(0.03) | 0.039 | 0.006(0.01) | 0.004 | 48.603(16.07) | 32.827 |
| *Vaccinium* Total | 3.569 | 2.953 | 59.398 | 37.526 | 260.787 | 176.138 |
| Shrub Total | 6.203 | 8.190 | 59.484 | 37.526 | 408.393 | 277.246 |
| Herb Layer | | | | | | |
| ARLA | 3.746(1.01) | 1.087 | | | | |
| ATFF | 3.424(2.95) | 3.580 | | | | |
| CANI | | | | | 1.458(1.46) | 0.686 |
| CAME* | | | | | 2.171(1.87) | 1.741 |
| GYDR | 3.229(0.77) | 1.201 | 0.156(0.14) | 0.161 | | |
| LUPE | | | | | 0.0 | 0.066 |
| OSCH | 0.551(0.14) | 0.237 | | | | |
| PHEM* | | | | | 9.704(3.68) | 5.671 |
| RUPE* | 0.378(0.17) | 1.124 | 4.657(0.84) | 2.331 | 0.281(0.20) | 0.323 |
| STAM | 0.959(0.41) | 0.170 | | | | |
| STRO | 3.721(1.04) | 3.154 | 0.435(0.21) | 0.830 | | |
| STST | 0.078(0.08) | 0.113 | 0.973(0.40) | 0.512 | | |

TABLE 3.5 (Cont'd.)

| | PLANT ASSOCIATION | | | | | |
|---|---|---|---|---|---|---|
| | Streptopo - Abietetum amabilis | | Abieto - Tsugetum mertensianae | | Vaccinio - Tsugetum mertensianae | |
| Species Code | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 |
| Herb Layer Cont'd. | | | | | | |
| TIUN | 2.956(0.32) | 2.709 | 0.260(0.21) | 0.615 | | |
| TITR | 0.004(0.004) | 0.0 | | | | |
| VASI | 1.578(0.26) | 1.603 | | | | |
| VEVI | 10.195(3.47) | 5.669 | 0.129(0.13) | 0.523 | | |
| VIGL | 0.665(0.30) | 0.313 | | | | |
| Herb Total | 31.484 | 20.960 | 6.610 | 4.972 | 13.614 | 8.487 |
| Bryophytes | | | | | | |
| BRHO | | 1.662 | | | | |
| DIPA | | 1.658 | | 8.280 | | 32.433 |
| PLLA | | 0.995 | | | | |
| PTCA | | | | | | 4.801 |
| RHNU | | 5.794 | | 0.520 | | |
| RHRO | | 0.098 | | 1.326 | | 8.148 |
| HYCI | | | | 0.339 | | |
| Hepaticae | | 0.484 | | 1.326 | | |
| Bryophyte Total | | 10.691 | | 11.791 | | 45.382 |
| Shrub and Herb Total | 37.687 | 29.150 | 66.094 | 42.498 | 422.007 | 285.733 |
| Grand Total | | 39.841 | | 54.289 | | 331.115 |

[1] Standard Error of the mean.

[2] *Vaccinium* species values based on 1975 proportions.

* Although these species are not true herbs, they were located in the herbaceous layer and considered with the herbs as a group.

The below-average temperatures and relatively late snow melt undoubtedly caused a reduction in the standing biomass of herbs for 1976 compared to 1975. The second factor was related to the natural variability of the population and the method of sampling. Because of the nature of the random sample a larger proportion of plots containing higher biomass could have been sampled during the 1975 field season. Great variability has also been reported in yearly estimates of standing biomass in stands of billberry (*Vaccinium myrtillus* L.) by Flower-Ellis (1971).

Although there appears to be a 30 percent reduction in biomass from 1975 to 1976, the biomass structure of the shrub and herbaceous strata remained relatively constant (Tables 3.5 and 3.6). The three species that deviate from 1975 to 1976 (*Arnica latifolia* Bong., *Gymnocarpium dryopteris* (L.) Newm. and *Rubus spectabilis*) are probably distributed nonrandomly throughout the community. A random sample could easily result in an over or under estimate of their biomass (Mueller-Dombois and Ellenberg, 1974).

The amount of organic matter present in the understory was within the range reported in the literature (Tables 3.1 and 3.5). However, the amount of understory biomass expressed as a percentage of overstory biomass was below the average reported for temperate coniferous ecosystems. This reflects the relatively large overstory biomass (a function of stand age) on the study sites which reduces the contribution of the understory to total aboveground biomass (Table 3.7).

TABLE 3.6

Percent of Shrub and Herb Biomass

Contributed by Individual Species

| Species Code | % of Biomass 1975 | % of Biomass 1976 |
|---|---|---|
| Streptopo - Abietetum amabilis plant association | | |
| VEVI | 27.05 | 19.45 |
| ARLA | 9.94 | 3.73 |
| STRO | 9.87 | 10.82 |
| VAAL | 9.13 | 9.77 |
| ATFF | 9.09 | 12.28 |
| GYDR | 8.57(73.65)* | 4.12(60.17) |
| RUSP | 6.99(80.64) | 17.97(78.14) |
| Abieto - Tsugetum mertensianae plant association | | |
| VAAL | 45.32 | 44.53 |
| VAOV | 41.53 | 40.80 |
| RUPE | 6.91(93.76) | 5.48(90.81) |
| Vaccinio - Tsugetum mertensianae plant association | | |
| ROAL | 34.98 | 35.39 |
| VAME | 29.94 | 29.87 |
| VAAL | 19.19(84.11) | 19.09(84.35) |
| PHEM | 2.30(86.41) | 1.99(86.34) |

* Cumulative total

TABLE 3.7.

Relationship of Understory Biomass and Productivity to Overstory Biomass and Mean Annual Increment (MAI)

| Plant Association | BIOMASS | | NET PRIMARY PRODUCTION | | |
|---|---|---|---|---|---|
| | Understory Biomass ($g \cdot m^{-2}$) | Percent of Overstory Biomass | Understory NPP ($g \cdot m^{-2} \cdot yr^{-1}$) | Percent of Understory Biomass | Percent of Overstory MAI |
| Strepotopo - Abietetum amabilis | 39.841 (37.687)* | 0.065 (0.062) | 25.946 | 65.12 | 11.28 |
| Abieto - Tsugetum mertensianae | 54.289 (66.094) | 0.098 (0.119) | 14.187 | 26.13 | 6.06 |
| Vaccinio - Tsugetum mertensianae | 331.115 (422.007) | 0.972 (1.239) | 63.121 | 19.06 | 48.55 |

* 1975 Estimate..

The values reported in this study are in close agreement with the values reported by Turner and Singer (1976) for a subalpine coniferous forest ecosystem 320 km to the south. These values also reflect the age of the study stands; the literature clearly indicates that understory biomass is generally a small percentage of overstory biomass except in young forests or shrub dominated ecosystems.

3.3.2 Understory Net Primary Production

The net primary understory production for the hygric, mesic and xeric sites was 25.9, 14.2 and 63.1 $g \cdot m^{-2} \cdot yr^{-1}$ respectively (Table 3.8). Accurate estimation of net primary production for understory vegetation can be very timeconsuming, so a number of assumptions were made as discussed under methods. As a result of these assumptions the values reported for production should be considered as conservative.

Age counts of *Rhododendron albiflorum* were possible. Woody production was estimated to be 61 percent of total aboveground production or 11.0 $g \cdot m^{-2} \cdot yr^{-1}$ (Table 3.9). This value is relatively high when compared to values in the literature (see Whittaker, 1962, 1963), but annual production of the perennial stem accounts for only 12 percent of the standing biomass. Also, white rhododendron has a relatively small amount of leaf biomass (7 percent of the total aboveground biomass). However, this small quantity of leaves represents 39 percent of the total aboveground production (Table 3.9).

TABLE 3.8.

Aboveground Net Primary Production ($g \cdot m^{-2} \cdot yr^{-1}$) for Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| | PLANT ASSOCIATION | | | | | |
|---|---|---|---|---|---|---|
| | Streptopo - Abietetum amabilis | | Abieto - Tsugetum mertensianae | | Vaccinio - Tsugetum mertensianae | |
| Species Code | 1975 | 1976 | 1975 | 1976 | 1975 | 1976 |
| Shrub Layer | | | | | | |
| ROAL | | | | | | 19.202 |
| RUSP | | 2.191 | | | | |
| *Vaccinium* Total | | 0.714 | | 6.857 | | 32.286 |
| Shrub Total | | 2.905 | | 6.857 | | 51.488 |
| Herb Layer | | | | | | |
| ARLA | 3.746(1.01)* | 1.087 | | | | |
| ATFF | 3.424(2.95) | 3.580 | | | | |
| CAME | | | | | 0.434 | 0.348 |
| CANI | | | | | 1.458(1.46) | 0.686 |
| GYDR | 3.229(0.77) | 1.201 | 0.156(0.14) | 0.161 | | |
| LUPE | | | | | 0.0 | 0.066 |
| OSCH | 0.551(0.14) | 0.237 | | | | |
| PHEM | | | | | 1.941 | 1.134 |
| RUPE | 0.378(0.17) | 1.124 | 4.657(0.84) | 2.331 | 0.281(0.20) | 0.323 |
| STAM | 0.959(0.41) | 0.113 | | | | |
| STRO | 3.721(1.04) | 3.154 | 0.435(0.21) | 0.830 | | |
| STST | 0.078(0.08) | 0.113 | 0.973(0.40) | 0.615 | | |
| TIUN | 2.956(0.32) | 2.709 | 0.260(0.21) | 0.512 | | |
| TITR | 0.004(0.004) | | | | | |
| VASI | 1.578(0.26) | 1.603 | | | | |
| VEVI | 10.195(3.47) | 5.669 | 0.129(0.13) | 0.523 | | |
| VIGL | 0.665(0.30) | 0.313 | | | | |
| Herb Total | 31.484 | 20.903 | 6.610 | 4.972 | 4.114 | 2.557 |
| Bryophyte Total | | 2.138 | | 2.358 | | 9.076 |
| Shrub and Herb Total | | 23.808 | | 11.829 | | 54.045 |
| Grand Total | | 25.946 | | 14.187 | | 63.121 |

* Standard error of the mean.

TABLE 3.9.

Component Shrub Production for Three Plant Associations in the Mt. Hemlock Biogeoclimatic Zone

| Species Code | Annual Production ($g \cdot m^{-2} \cdot yr^{-1}$) Leaf | Twig | Stem* | Total |
|---|---|---|---|---|
| Streptopo - Abietetum amabilis plant association | | | | |
| RUSP | 1.1 | 0.5 | 0.6 | 2.2 |
| % of Total | 49.2 | 22.4 | 28.4 | 100.0 |
| VASP | 0.4 | 0.1 | 0.2 | 0.7 |
| % of Total | 57.1 | 14.3 | 28.6 | 100.0 |
| Abieto - Tsugetum mertensianae plant association | | | | |
| VASP | 4.1 | 0.7 | 2.1 | 6.9 |
| % of Total | 59.5 | 10.1 | 30.4 | 100.0 |
| Vaccinio - Tsugetum mertensianae plant association | | | | |
| ROAL | 7.4 | 0.8 | 11.0 | 19.2 |
| % of Total | 38.5 | 3.9 | 57.6 | 100.0 |
| VASP | 19.4 | 3.2 | 9.7 | 32.3 |
| % of Total | 60.1 | 9.9 | 30.0 | 100.0 |

* Stem production means all woody production exclusive of the new twig growth.

The relationship of understory net primary production to overstory mean annual increment is shown in Table 3.7. The hygric site supported a smaller standing biomass than the mesic site, although the latter had a smaller percentage of total site net primary production in the understory strata (Table 3.7). The values for net primary production as a percentage of understory biomass indicate that a greater proportion of the hygric site standing crop is produced annually when compared to the other two sites. This reflects the abundance of herbs and relative scarcity of shrubs on the hygric site.

The values for net primary production and net primary production expressed as a percentage of overstory mean annual increment are within the range of values found in the literature (Table 3.1 and Appendix 5). However, the values reported in this study should be considered as conservative. The net primary production of the overstory strata will be somewhat lower than the mean annual increment in an old growth stand; therefore the last column of Table 3.7 should be considered an underestimate. This leads to the conclusion that the understory of the xeric site produces 50 percent or more of the quantity produced by the overstory (Table 3.7).

The turnover of organic matter in understory vegetation tends to be faster than the turnover in overstory vegetation (Witherspoon, 1964; Ovington, 1965; Day and McGinty, 1975). Herbaceous layers generally produce 100 percent of their aboveground biomass every year. This yearly turnover of organic matter and nutrients is generally viewed as the major contribution of understory vegetation to the maintenance of the entire community. Almost 2/3 of the understory biomass on the hygric site is produced annually, while the figure for the xeric site is only 1/5 of the understory biomass (Table 3.7).

### 3.3.3 Understory Nutrient Standing Crop

The standing crop of nutrients is a function not only of the biomass but also of the elemental concentrations present in the various understory species. The second component is probably of far greater importance and is discussed in some detail.

The percent ash content and elemental concentrations of the eight elements determined generally decreases as one moves up the topographic sequence from the hygric to the xeric site (Tables 3.10, 3.11, 3.12). This trend is present in both the averages calculated for all species and in those species present on all three sites (Appendix 6). Similar trends were found by Klinka (1976) for characteristic species at the level of plant order in his classification of the Haney Research Forest.

The order of abundance in elemental concentrations for all species on each site is given below:

Streptopo - Abietetum amabilis site;

K>N>Ca>P>Mg>Mn>Zn>Cu

Abieto - Tsugetum mertensianae site;

K>N>Ca>P=Mg>Mn>Zn>Cu

Vaccinio - Tsugetum mertensianae site;

N>K>Ca>Mg>P>Mn>Zn>Cu

The above series are similar to those presented by Klinka (1976) and Remezov and Pogrebnyak (1969). The one noticeable difference is in

TABLE 3.10.

Elemental Concentrations and % Ash Content for Species Collected During 1975 and 1976 for the Streptopo - Abietetum amabilis Site

| Species Code | No. of** Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Elemental Concentration | | | | | | | |
| | | | % | | | | | ppm | | |
| ARLA | 11 | 14.59 | 3.67 | 0.38 | 0.80 | 0.23 | 5.48 | 302 | 49 | 21 |
| | | (0.53)* | (0.11) | (0.02) | (0.04) | (0.01) | (0.25) | (23.2) | (2.2) | (1.4) |
| ATFF | 5 | 12.83 | 4.13 | 0.39 | 0.34 | 0.40 | 5.11 | 184 | 50 | 20 |
| | | (0.44) | (0.10) | (0.05) | (0.05) | (0.03) | (0.17) | (40.4) | (3.8) | (3.0) |
| GYDR | 11/ 8 | 10.13 | 3.73 | 0.32 | 0.25 | 0.35 | 3.93 | 250 | 31 | 14 |
| | | (0.15) | (0.14) | (0.02) | (0.01) | (0.02) | (0.11) | (13.5) | (1.2) | (0.9) |
| LICO | 1/ 0 | | 4.18 | 0.38 | | | | | | |
| OSCH | 7/ 6/ 4 | 15.36 | 3.75 | 0.37 | 1.32 | 0.26 | 5.21 | 416 | 36 | 16 |
| | | (0.83) | (0.10) | (0.01) | (0.08) | (0.02) | (0.23) | (12.1) | (1.4) | (2.7) |
| RUPE | 6/ 2/ 3 | 7.24 | 3.21 | 0.33 | 0.38 | 0.37 | 2.25 | 969 | 66 | 13 |
| | | (0.64) | (0.17) | (0.03) | (0.01) | (0.04) | (0.05) | (132) | (3.4) | (1.7) |
| STAM | 8/ 5/ 4 | 15.57 | 3.13 | 0.34 | 0.91 | 0.20 | 4.98 | 184 | 70 | 13 |
| | | (1.00) | (0.12) | (0.02) | (0.11) | (0.02) | (0.76) | (9.1) | (6.4) | (4.4) |
| STRO | 12/12/10 | 15.86 | 3.14 | 0.39 | 0.93 | 0.22 | 5.86 | 223 | 61 | 13 |
| | | (0.36) | (0.09) | (0.02) | (0.05) | (0.01) | (0.17) | (25.4) | (2.9) | (1.6) |
| STST | 1 | 13.39 | 3.11 | 0.40 | 0.68 | 0.19 | 5.14 | 365 | 92 | 18 |
| TIUN | 12/ 7 | 10.62 | 3.52 | 0.35 | 0.94 | 0.29 | 3.40 | 394 | 57 | 15 |
| | | (0.48) | (0.13) | (0.02) | (0.04) | (0.01) | (0.12) | (61.6) | (3.0) | (1.6) |
| VASI | 10/ 9 | 13.30 | 3.46 | 0.36 | 0.73 | 0.21 | 5.18 | 181 | 39 | 13 |
| | | (0.40) | (0.15) | (0.01) | (0.03) | (0.01) | (0.15) | (15.0) | (1.6) | (1.0) |
| VASP | 4/ 4/ 3 | 5.08 | 3.85 | 0.28 | 0.60 | 0.29 | 1.51 | 3637 | 23 | 11 |
| | | (0.97) | (0.24) | (0.04) | (0.08) | (0.02) | (0.04) | (63.6) | (2.6) | (1.4) |
| VEVI | 13 | 14.87 | 3.71 | 0.38 | 0.69 | 0.17 | 5.06 | 133 | 58 | 22 |
| | | (1.13) | (0.15) | (0.02) | (0.05) | (0.01) | (0.11) | (11.2) | (4.7) | (2.3) |
| VIGL | 6/ 5/ 3 | 14.58 | 4.14 | 0.33 | 0.62 | 0.37 | 5.74 | 295 | 57 | 10 |
| | | (0.70) | (0.14) | (0.01) | (0.08) | (0.02) | (0.43) | (27.4) | (3.8) | (1.8) |

TABLE 3.10 (cont'd.)

| Species Code | No. of Samples | % Ash Content | Elemental Concentration N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | % | | | | | ppm | | |
| RUSP | 8 | 6.19 (0.54) | 4.94 (0.19) | 0.34 (0.02) | 0.54 (0.11) | 0.44 (0.03) | 2.07 (0.19) | 893 (73.6) | 45 (2.8) | 16 (1.4) |
| Average | | 12.12 | 3.71 | 0.36 | 0.70 | 0.29 | 4.35 | 602 | 52 | 15 |
| BRHO | 1 | 6.99 | 2.69 | 0.16 | 0.35 | 0.12 | 0.90 | 799 | 80 | 32 |
| DIPA | 1 | 4.59 | 2.11 | 0.19 | 0.18 | 0.08 | 0.86 | 390 | 35 | 20 |
| LIVE | 1 | 7.71 | 1.76 | 0.16 | 1.28 | 0.33 | 1.65 | 564 | 38 | 11 |
| PLLA | 1 | 7.07 | 1.94 | 0.17 | 0.45 | 0.11 | 1.29 | 2889 | 149 | 25 |
| RNNU | 1 | 8.69 | 3.13 | 0.17 | 0.48 | 0.08 | 1.90 | 779 | 50 | 25 |
| Bryophyte Average | | 7.01 | 2.33 | 0.17 | 0.55 | 0.14 | 1.32 | 1084 | 70 | 23 |
| Grand Average | | 10.78 | 3.36 | 0.31 | 0.66 | 0.25 | 3.55 | 729 | 57 | 17 |

* Standard error of the mean

** Number of observations for N and P/ cations/Zn and Cu, where sample sizes differ. If no sample size is present for Zn and Cu, then it was the same as all other cations.

TABLE 3.11.

Elemental Concentrations and % Ash Content of Foliage for Species Collected

During 1975 and 1976 for the Abieto - Tsugetum mertensianae Site

| Species Code | No. of** Samples | % Ash Content | Elemental Concentrations N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | % | | | | | ppm | | |
| GYDR | 2/ 1 | 10.69 | 2.41 (0.15)* | 0.21 (0.02) | 0.30 | 0.36 | 3.80 | 176 | 25 | 10 |
| LYPO | 1 | 5.54 | 1.06 | 0.12 | 0.09 | 0.07 | 2.03 | 147 | 34 | 8 |
| RUPE | 12/11 | 6.77 (0.26) | 2.44 (0.11) | 0.25 (0.01) | 0.40 (0.01) | 0.39 (0.01) | 2.11 (0.09) | 860 (54.2) | 49 (2.6) | 11 (1.3) |
| SOSI | 1 | 7.66 | 3.51 | 0.29 | 0.72 | 0.47 | 2.30 | 76 | 30 | 6 |
| STRO | 5/ 3 | 13.17 (0.76) | 2.63 (0.07) | 0.26 (0.02) | 0.60 (0.14) | 0.31 (0.03) | 5.09 (0.50) | 152 (17.7) | 60 (9.3) | 10 (4.4) |
| STST | 5/ 5/ 3 | 14.42 (0.49) | 2.54 (0.15) | 0.32 (0.02) | 0.54 (0.04) | 0.17 (0.02) | 5.72 (0.16) | 329 (4.6) | 69 (0.6) | 7 (1.6) |
| TIUN | 3/ 2/ 1 | 9.80 (0.16) | 2.39 (0.16) | 0.25 (0.02) | 0.80 (0.05) | 0.31 (0.03) | 3.67 (0.42) | 616 (107) | 60 | 10 |
| VASP | 22/22/17 | 5.99 (0.11) | 3.25 (0.05) | 0.24 (0.00) | 0.72 (0.02) | 0.36 (0.01) | 1.29 (0.04) | 1341 (116) | 21 (0.6) | 11 (0.7) |
| VEVI | 2/ 2/ 1 | 13.64 (1.93) | 2.61 (0.34) | 0.29 (0.01) | 0.46 (0.20) | 0.24 (0.06) | 5.13 (1.66) | 63 (13.1) | 25 | 10 |
| Average | | 9.74 | 2.54 | 0.25 | 0.51 | 0.30 | 3.46 | 418 | 41 | 9 |

TABLE 3.11 (cont'd.)

| Species Code | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Elemental Concentrations | | | | | | | |
| | | | % | | | | | ppm | | |
| DIPA | 2 | 4.87 (0.28) | 1.82 (0.54) | 0.18 (0.04) | 0.13 (0.06) | 0.06 (0.01) | 0.65 (0.22) | 219 (119) | 35 (5) | 24 (3) |
| LIVE | 1 | 7.97 | 2.23 | 0.17 | 0.35 | 0.07 | 0.86 | 638 | 55 | 26 |
| RHRO | 1 | 5.77 | 2.31 | 0.19 | 0.30 | 0.08 | 0.60 | 617 | 55 | 30 |
| RNNU | 1 | 8.58 | 3.57 | 0.25 | 0.35 | 0.10 | 1.54 | 652 | 52 | 26 |
| Bryophyte Average | | 6.80 | 2.48 | 0.20 | 0.28 | 0.08 | 0.91 | 532 | 49 | 27 |
| Grand Average | | 8.83 | 2.52 | 0.23 | 0.44 | 0.23 | 2.68 | 453 | 44 | 14 |

* Standard error of the mean

** Number of observations for N and P/cations/Zn and Cu where sample sizes differ.

TABLE 3.12

Elemental Concentrations and % Ash of Foliage for Species Collected During 1975 and 1976 for the Vaccinio - Tsugetum mertensianae Site

| Species Code | No. of** Samples | % Ash Content | Elemental Concentration N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | ------- | ------- | % | ------- | ------- | ------- | ppm | ------- |
| CAME+ | 7/ 7 | 2.16 | 1.12 | 0.10 | 0.23 | 0.12 | 0.46 | 160 | 28 | 8 |
| | | (0.11)* | (0.04) | (0.00) | (0.02) | (0.01) | (0.04) | (30.1) | (1.8) | (1.0) |
| CANI | 3/ 3 | 5.53 | 2.87 | 0.22 | 0.15 | 0.18 | 1.94 | 126 | 55 | 16 |
| | | (0.27) | (0.02) | (0.03) | (0.02) | (0.02) | (0.08) | (17.0) | (5.9) | (1.0) |
| LUPE+ | 1 | 2.80 | 1.70 | 0.16 | 0.23 | 0.12 | 0.86 | 109 | 62 | 16 |
| PHEM+ | 10/10 | 1.81 | 0.94 | 0.09 | 0.14 | 0.12 | 0.44 | 392 | 34 | 8 |
| | | (0.10) | (0.03) | (0.00) | (0.01) | (0.00) | (0.03) | (41.8) | (1.7) | (1.1) |
| ROAL | 13/13 | 5.78 | 2.81 | 0.25 | 0.68 | 0.39 | 1.53 | 163 | 42 | 9 |
| | | (0.22) | (0.14) | (0.01) | (0.03) | (0.01) | (0.08) | (32.6) | (1.5) | (0.7) |
| RUPE | 2/ 3 | 6.91 | 2.10 | 0.21 | 0.49 | 0.43 | 2.15 | 401 | 51 | 10 |
| | | (0.43) | (0.13) | (0.01) | (0.04) | (0.03) | (0.15) | (13.7) | (6.3) | (0.1) |
| VASP | 30/30 | 5.48 | 3.03 | 0.25 | 0.67 | 0.35 | 1.19 | 551 | 24 | 13 |
| | | (0.15) | (0.06) | (0.01) | (0.02) | (0.01) | (0.05) | (46.1) | (0.8) | (0.7) |
| Average | | 4.35 | 2.08 | 0.18 | 0.37 | 0.24 | 1.22 | 272 | 42 | 11 |
| DIPA | 3 | 3.82 | 2.34 | 0.20 | 0.16 | 0.09 | 0.92 | 169 | 32 | 18 |
| | | (0.39) | (0.25) | (0.01) | (0.02) | (0.01) | (0.12) | (37) | (5) | (6) |
| PTCA | 1 | 6.39 | 2.18 | 0.22 | 0.16 | 0.10 | 1.79 | 270 | 37 | 25 |
| RHRO | 1 | 5.10 | 2.26 | 0.19 | 0.49 | 0.08 | 0.75 | 240 | 40 | 28 |
| Bryophyte Average | | 5.10 | 2.26 | 0.20 | 0.27 | 0.09 | 1.15 | 226 | 36 | 24 |
| Grand Average | | 4.58 | 2.13 | 0.19 | 0.34 | 0.20 | 1.20 | 258 | 40 | 15 |

\+ Concentrations for the entire aboveground plant

* Standard error of the mean

** Number of observations for N and P/cations/Cu and Zn, where sample sizes differ.

the ranking of potassium. On the two sites which are influenced by seepage (Brooke et al., 1970), the hygric and mesic sites, potassium ranks higher than nitrogen.

The above series are more pronounced when the moss samples are excluded (Tables 3.10, 3.11, 3.12). The trends between sites that are present for the herbaceous and shrub strata are not clearly defined for the moss strata. This may reflect the difference in nutritional physiology of the layers. Mosses get most of their nutrition from throughfall precipitation and only a small proportion from the humus layer (Tamm, 1953; Weetman and Timmer, 1967). The average concentrations of the five macronutrients are lower in moss samples than the corresponding averages for shrub and herb foliage, while micronutrient (Mn, Zn, Cu) concentrations are higher. Bryophytes have been shown to be effective absorbers of metallic cations (Ruhling and Tyler, 1970). Since variation in chemical concentration has been suggested as an indicator of niche differentiation (Muller, 1975; Woodwell et al., 1975), it can be hypothesized that mosses play an important part in the micronutrient cycle in these ecosystems, and as such can be used as indicators of the micronutrient status of a given site. Further, it is entirely possible that the major source of micronutrients for other vascular plants on these sites may be from decomposing moss tissue, and therefore bryophytes could represent a very important nutrient source for other forest vegetation.

Multiplying the elemental concentrations (Appendix 6) by the appropriate biomass figure (Table 3.4) yields the nutrient standing crop. As with biomass, the standing crop of nutrients in the aboveground understory vegetation represents a relatively small portion of the total present in the vegetation on the three sites (Tables 2.7, 3.13, 3.14, 3.15). Turner and Singer (1976) present the following values for the standing nutrient crop in a subalpine coniferous forest in the Cedar River watershed:

| | $g \cdot m^{-2}$ |
|---|---|
| Nitrogen | 1.47 |
| Phosphorus | 0.17 |
| Calcium | 1.51 |
| Magnesium | 0.07 |
| Potassium | 1.58 |
| Manganese | 0.04 |

These values are consistent with the values obtained here for either the hygric or the mesic sites (Table 3.13, 3.14) with the exception of calcium. A greater quantity of nutrients was found in the understory of the xeric site due to its relatively high standing biomass; nutrient concentrations on the xeric site were generally lower than on other sites.

### 3.3.4 Nutrients Accumulated in Understory Net Primary Production

Organic matter and nutrients are accumulated in standing crops through the process of primary production. For this reason it is important to know the quantities of various nutrients present in annually produced tissues. The quantity of nutrients present in annual production on the three sites shows the same general pattern as the total quantity of nutrients present in biomass (Table 3.14). There are two exceptions that result from a difference in species composition on the three sites. First, the quantity of potassium is higher in the

TABLE 3.13.

Aboveground Understory Nutrient Standing Crop ($g \cdot m^{-2}$) in 1975 for Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Nutrient and Layer | Plant Association | | |
|---|---|---|---|
| | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
| Nitrogen | | | |
| Shrubs | 0.0941 | 0.5076 | 2.4704 |
| Herbs | 1.0841 | 0.1546 | 0.1592 |
| Total | 1.1782 | 0.6622 | 2.6296 |
| Phosphorus | | | |
| Shrubs | 0.0090 | 0.0453 | 0.2531 |
| Herbs | 0.1189 | 0.0172 | 0.0155 |
| Total | 0.1279 | 0.0625 | 0.2686 |
| Calcium | | | |
| Shrubs | 0.0177 | 0.1033 | 0.6842 |
| Herbs | 0.2154 | 0.0288 | 0.0226 |
| Total | 0.2331 | 0.1321 | 0.7068 |
| Magnesium | | | |
| Shrubs | 0.0075 | 0.0510 | 0.2739 |
| Herbs | 0.0783 | 0.0235 | 0.0182 |
| Total | 0.0858 | 0.0745 | 0.2921 |
| Potassium | | | |
| Shrubs | 0.0477 | 0.1795 | 0.8021 |
| Herbs | 1.5824 | 0.1995 | 0.0866 |
| Total | 1.6301 | 0.3750 | 0.8887 |
| Manganese | | | |
| Shrubs | 0.0079 | 0.0467 | 0.1660 |
| Herbs | 0.0078 | 0.0048 | 0.0045 |
| Total | 0.0157 | 0.0515 | 0.1705 |
| Zinc | | | |
| Shrubs | 0.0003 | 0.0020 | 0.0097 |
| Herbs | 0.0015 | 0.0004 | 0.0005 |
| Total | 0.0018 | 0.0024 | 0.0102 |
| Copper | | | |
| Shrubs | 0.0001 | 0.0003 | 0.0020 |
| Herbs | 0.0005 | 0.0002 | 0.0002 |
| Total | 0.0006 | 0.0005 | 0.0022 |

TABLE 3.14.

Aboveground Understory Nutrient Standing Crop ($g \cdot m^{-2}$) in 1976 for Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Nutrient and Layer | Plant Association | | |
|---|---|---|---|
| | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
| Nitrogen | | | |
| Shrubs | 0.1214 | 0.3388 | 2.2143 |
| Herbs | 0.7822 | 0.1414 | 0.0560 |
| Bryophytes | 0.2904 | 0.2292 | 1.0466 |
| Total | 1.1940 | 0.7094 | 3.3169 |
| Phosphorus | | | |
| Shrubs | 0.0093 | 0.0312 | 0.2032 |
| Herbs | 0.0705 | 0.0133 | 0.0093 |
| Bryophytes | 0.0185 | 0.0209 | 0.0915 |
| Total | 0.0983 | 0.0654 | 0.3040 |
| Calcium | | | |
| Shrubs | 0.0215 | 0.0725 | 0.5043 |
| Herbs | 0.1377 | 0.0283 | 0.0146 |
| Bryophytes | 0.0476 | 0.0215 | 0.0978 |
| Total | 0.2068 | 0.1223 | 0.6167 |
| Magnesium | | | |
| Shrubs | 0.0107 | 0.0259 | 0.1970 |
| Herbs | 0.0498 | 0.0137 | 0.0114 |
| Bryophytes | 0.0111 | 0.0076 | 0.0403 |
| Total | 0.0716 | 0.0472 | 0.2487 |
| Potassium | | | |
| Shrubs | 0.0491 | 0.1359 | 0.9426 |
| Herbs | 0.9791 | 0.1711 | 0.0522 |
| Bryophytes | 0.1607 | 0.0815 | 0.4452 |
| Total | 1.1889 | 0.3885 | 1.4400 |
| Manganese | | | |
| Shrubs | 0.0057 | 0.0426 | 0.2104 |
| Herbs | 0.0050 | 0.0025 | 0.0023 |
| Bryophytes | 0.0094 | 0.0038 | 0.0084 |
| Total | 0.0201 | 0.0489 | 0.2211 |
| Zinc | | | |
| Shrubs | 0.0003 | 0.0012 | 0.0075 |
| Herbs | 0.0010 | 0.0003 | 0.0003 |
| Bryophytes | 0.0008 | 0.0005 | 0.0015 |
| Total | 0.0021 | 0.0020 | 0.0093 |
| Copper | | | |
| Shrubs | 0.0001 | 0.0003 | 0.0021 |
| Herbs | 0.0003 | <0.0001 | 0.0001 |
| Bryophytes | 0.0003 | 0.0003 | 0.0009 |
| Total | 0.0007 | 0.0006 | 0.0031 |

TABLE 3.15.

Percent of Aboveground Plant Biomass Nutrient Content Present in the Understory of Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Nutrient and Year | Plant Association | | |
|---|---|---|---|
| | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
| Nitrogen | | | |
| 1975 | 1.44 | 0.89 | 4.93 |
| 1976 | 1.46 | 0.95 | 6.14 |
| Phosphorus | | | |
| 1975 | 0.92 | 0.49 | 2.34 |
| 1976 | 0.71 | 0.51 | 2.64 |
| Calcium | | | |
| 1975 | 0.23 | 0.14 | 1.19 |
| 1976 | 0.20 | 0.13 | 1.04 |
| Magnesium | | | |
| 1975 | 0.77 | 0.74 | 3.57 |
| 1976 | 0.66 | 0.47 | 3.06 |
| Potassium | | | |
| 1975 | 2.82 | 0.73 | 2.52 |
| 1976 | 2.07 | 0.75 | 4.02 |

annual production on the hygric site than in that on the xeric site (Table 3.16). This reflects the abundance of potassium-rich herbaceous production present on the hygric site. Second, the quantity of manganese on the mesic site is intermediate between the values for the xeric and hygric sites, whereas for other elements the mesic site has the lowest values (Table 3.16). This can be related to the higher concentrations of manganese in current *Vaccinium* production and the large amount of *Vaccinium* production on the mesic site.

The percentage of the total understory standing crop of nutrients present in the annual production is quite high compared to published values for mature coniferous forests (Rodin and Bazilevich, 1967; Mälkönen, 1974; Tables 3.16, 3.17). There was a decrease in the percentage of nutrients present in the annual production from the hygric to the mesic to the xeric site (Table 3.17). This trend was expected since the amount of annual production expressed as a percentage of standing biomass follows the same pattern. There also appears to be a difference in the functioning of the macro- and micro-nutrient cycles, since a considerable difference in the percentage values for these two groups of nutrients was observed (Table 3.17). Micronutrient values were only about 60 percent of the macronutrient values for all sites. Similar results have been reported for iron in five plant communities in Hardangervidda, Norway (Wielgolaski et al., 1975). Turner and Singer (1976) have suggested contrasting cycling patterns for potassium and manganese. Although there is relatively little evidence at present, there does appear to be some justification for hypothesizing a different

TABLE 3.16.

Quantity of Nutrients ($g \cdot m^{-2}$) Accumulated in Understory Aboveground Annual Production in Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Species Code and Component | Elemental Quantity ($g \cdot m^{-2}$) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | N | P | Ca | Mg | K | Mn | Zn | Cu |
| Streptopo - Abietetum amabilis plant association | | | | | | | | |
| RUSP | | | | | | | | |
| Leaf | 0.0561 | 0.0033 | 0.0076 | 0.0052 | 0.0201 | 0.0011 | * | * |
| Twig | 0.0066 | 0.0008 | 0.0017 | 0.0008 | 0.0074 | 0.0001 | * | * |
| Stem | 0.0052 | 0.0004 | 0.0011 | 0.0004 | 0.0017 | 0.0002 | * | * |
| Total | 0.0679 | 0.0045 | 0.0104 | 0.0064 | 0.0292 | 0.0014 | * | * |
| VASP | | | | | | | | |
| Leaf | 0.0141 | 0.0009 | 0.0026 | 0.0011 | 0.0055 | 0.0007 | * | * |
| Twig | 0.0010 | 0.0015 | 0.0003 | 0.0001 | 0.0005 | 0.0002 | * | * |
| Stem | 0.0010 | 0.0001 | 0.0002 | 0.0001 | 0.0004 | 0.0002 | * | * |
| Total | 0.0161 | 0.0025 | 0.0031 | 0.0013 | 0.0064 | 0.0011 | * | * |
| Shrub Total | 0.0840 | 0.0070 | 0.0135 | 0.0077 | 0.0356 | 0.0025 | * | * |
| Herb Total | 0.7822 | 0.0705 | 0.1377 | 0.0498 | 0.9791 | 0.0050 | 0.0010 | 0.0003 |
| Bryophyte Total† | 0.0581 | 0.0037 | 0.0095 | 0.0022 | 0.0321 | 0.0019 | 0.0002 | 0.0001 |
| Grand Total | 0.9243 | 0.0812 | 0.1607 | 0.0597 | 1.0468 | 0.0094 | 0.0012 | 0.0004 |
| Abieto - Tsugetum mertensianae plant association | | | | | | | | |
| VASP | | | | | | | | |
| Leaf | 0.1574 | 0.0103 | 0.0296 | 0.0119 | 0.0616 | 0.0082 | 0.0001 | 0.0001 |
| Twig | 0.0113 | 0.0013 | 0.0037 | 0.0009 | 0.0056 | 0.0017 | 0.0001 | * |
| Stem | 0.0109 | 0.0013 | 0.0025 | 0.0008 | 0.0044 | 0.0021 | 0.0001 | * |
| Total | 0.1796 | 0.0129 | 0.0358 | 0.0136 | 0.0713 | 0.0120 | 0.0003 | 0.0001 |
| Herb Total | 0.1414 | 0.0133 | 0.0283 | 0.0137 | 0.1711 | 0.0025 | 0.0003 | * |

TABLE 3.16 (cont'd.)

| Species Code and Component | Elemental Quantity ($g \cdot m^{-2}$) N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|
| Bryophyte Total | 0.0458 | 0.0042 | 0.0043 | 0.0015 | 0.0163 | 0.0008 | 0.0001 | 0.0001 |
| Grand Total | 0.3668 | 0.0304 | 0.0684 | 0.0288 | 0.2590 | 0.0153 | 0.0007 | 0.0002 |
| Vaccinio - Tsugetum mertensianae plant association | | | | | | | | |
| ROAL | | | | | | | | |
| Leaf | 0.2439 | 0.0178 | 0.0489 | 0.0274 | 0.1194 | 0.0007 | 0.0003 | 0.0001 |
| Twig | 0.0138 | 0.0016 | 0.0027 | 0.0013 | 0.0072 | 0.0001 | * | * |
| Stem | 0.0430 | 0.0044 | 0.0132 | 0.0055 | 0.0210 | 0.0011 | 0.0002 | 0.0001 |
| Total | 0.3007 | 0.0238 | 0.0648 | 0.0342 | 0.1476 | 0.0019 | 0.0005 | 0.0002 |
| VASP | | | | | | | | |
| Leaf | 0.7430 | 0.0485 | 0.1397 | 0.0563 | 0.2910 | 0.0388 | 0.0004 | 0.0003 |
| Twig | 0.0536 | 0.0061 | 0.0175 | 0.0042 | 0.0265 | 0.0081 | 0.0002 | 0.0001 |
| Stem | 0.0504 | 0.0058 | 0.0116 | 0.0039 | 0.0204 | 0.0097 | 0.0003 | 0.0001 |
| Total | 0.8470 | 0.0604 | 0.1688 | 0.0644 | 0.3379 | 0.0566 | 0.0009 | 0.0005 |
| Shrub Total | 1.1477 | 0.0842 | 0.2336 | 0.0986 | 0.4855 | 0.0586 | 0.0014 | 0.0007 |
| Herb Total | 0.0560 | 0.0093 | 0.0146 | 0.0114 | 0.0522 | 0.0023 | 0.0003 | 0.0001 |
| Bryophyte Total | 0.2093 | 0.0183 | 0.0196 | 0.0081 | 0.0890 | 0.0017 | 0.0003 | 0.0002 |
| Grand Total | 1.3130 | 0.1118 | 0.2678 | 0.1181 | 0.6267 | 0.0625 | 0.0020 | 0.0010 |

* Less than 0.1 mg

† Estimated as 20 percent of standing crop

TABLE 3.17.

Percent of Total Understory Nutrient Standing Crop Present in the Understory Net Primary Production in Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Nutrient | Plant Association | | |
|---|---|---|---|
| | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
| | % | | |
| Nitrogen | 77.4 | 51.7 | 42.6 |
| Phosphorus | 82.6 | 46.5 | 36.8 |
| Calcium | 77.7 | 55.9 | 43.4 |
| Magnesium | 83.4 | 61.0 | 47.5 |
| Potassium | 88.0 | 66.7 | 43.5 |
| Manganese | 46.8 | 31.3 | 28.3 |
| Zinc | 57.1 | 35.0 | 21.5 |
| Copper | 57.1 | 33.3 | 32.2 |

pattern of circulation of micronutrients compared to macronutrients. This will be discussed further in Chapter 5.

## 3.4 Summary

### 3.4.1 Biomass and Production

The average aboveground biomass of understory vegetation for the three sites was less than one percent of the aboveground overstory biomass. The two-year average biomass values for the three sites were:

| | |
|---|---|
| Streptopo - Abietetum amabilis | 44.1 $g/m^2$ |
| Abieto - Tsugetum mertensianae | 66.1 $g/m^2$ |
| Vaccinio - Tsugetum mertensianae | 399.3 $g/m^2$ |

The aboveground understory net primary production of the three sites represented a greater proportion of the site net primary production than simple biomass figures might suggest. A maximum value for understory production of 63.1 $g/m^2 \cdot yr$ was estimated for the Vaccinio - Tsugetum mertensianae site. This represented approximately 50 percent of the overstory production as indicated by overstory mean annual increment. The floristic structure of the three communities differed and resulted in a decreasing proportion of standing biomass present as annual production from the Streptopo - Abietetum amabilis site to the Vaccinio - Tsugetum mertensianae site (Table 3.7).

### 3.4.2 Nutrients

The understory nutrient standing crop was typical for high elevation forests (Tables 3.13, 3.14) in that it contributed only a small percentage of the total aboveground nutrients present in the vegetation. A maximum value of 6.1 percent was estimated for nitrogen on the Vaccinio - Tsugetum mertensianae site (Table 3.15). However, the understory cycles a much greater proportion of its total standing crop annually as compared to overstory. Approximately 80 percent of the macronutrients present in the standing crop are found in annual production on the Streptopo - Abietetum amabilis site. Micronutrients were found to be present in annual production at 60 percent of the macronutrient percentage (Table 3.17). This suggests that the micronutrient cycle functions differently than the macronutrient cycle in the understory strata.

Having considered the magnitude of the biomass and nutrient components of the understory, I will proceed to a discussion of two major recycling mechanism: litterfall and throughfall leaching.

# CHAPTER 4

# Understory Litterfall and Throughfall Leaching

## 4.1 Introduction

The prolonged use of limited resources from a fixed geographical area requires the repeated reutilization of certain portions of that resource. Nutrient reutilization within a vegetative community can take place through cycles that occur within the plant (internal cycling) and cycles which are outside the plant (external cycling). Two components of the external cycles are litterfall and throughfall.

### 4.1.1 Litterfall

Litterfall has received much attention in the past because of its relationship to site productivity (Bray and Gorham, 1964). Excellent reviews of overstory litterfall were presented by Bray and Gorham (1964) and Rodin and Bazelivich (1967), but relatively little attention has been given to the contribution of understory litterfall to total litterfall.

Ovington (1962) noted that litter cannot be considered in terms of a single component (e.g. foliage), nor should litterfall from only one vegetation stratum be considered representative of the total site.

He presented a figure (Figure 5, pg. 137) that shows the relative contribution of overstory and understory vegetation to total litterfall over an age sequence in stands of *Pinus sylvestris*. The trend generally reflects the contribution of understory vegetation to site productivity and standing biomass over the life of a forest stand (Switzer and Nelson, 1972; Marks, 1971; Ford and Newbould, 1977).

The importance of understory litterfall was first emphasized by Scott (1955), who suggested that it should not be judged solely upon a consideration of weight. The variability in the contribution of understory to litterfall biomass is quite large. For example, in a 70 to 200-year-old pine forest, understory contributed 53 percent of the total litterfall (P'Yavchenko, 1960) while in a 225-year-old whortleberry spruce forest on the Kola Peninsula understory contributed 39 percent of the total litterfall (Manakov, 1962). Yet, in contrast, understory contributed only 2 percent of the total site litterfall along an elevational series of northern hardwood stands in New Hampshire (Gosz et al., 1972).

In many cases the elemental concentrations of understory litter components are greater than elemental concentrations of overstory litter components (Scott, 1955; Gosz et al., 1972) which can result in a significant contribution by understory to the total elemental quantities returned in litterfall (Scott, 1955; Manakov, 1962). Tappeiner and Alm (1975) reported that there was a significant increase in the amount of nitrogen, calcium, and manganese in the litter layer of the forest floor when an understory canopy of hazel was present in a red pine (*Pinus resinosa* Ait.) stand. When an understory layer of herbaceous vegetation and hazel was present there was faster turnover of nutrients under red pine, and it was thought that the understory litter promoted faster decomposition of litter on the forest floor (Tappeiner and Alm, 1975). It has also been shown that it is necessary to consider understory litterfall when quantifying nutrient cycles in jack pine (*Pinus banksiana* Lamb.) stands (Foster, 1974) and red alder (*Alnus rubra* Bong.) stands (Turner et al., 1976).

### 4.1.2 Understory Throughfall Leaching[1]

Literature on leaching (throughfall and stemflow) of understory vegetation is very scarce. Stemflow and throughfall in a multilayered aspen community have been measured by Clements (1971, 1972). He found

[1] Throughfall leaching - the removal of substances from plants by the action of rain, dew, mist, or fog (Tukey, 1970) which subsequently falls freely to the ground from the plant surface.

that interception by all canopies was from 22 percent to 46 percent of incident rainfall, and that interception by a bracken fern (*Pteridium aquilium* (L.) Kuhn.) canopy alone was three to nine percent of incident rainfall (Clements, 1971). The importance of the bracken fern canopy was clearly shown by its ability to concentrate more rainwater per storm in the form of stemflow, than did the largetooth aspen (*Populus grandidentata* Michx.), red maple (*Acer rubrum* L.) and hazel canopies (Clements, 1972).

Carisle et al., (1967) found that by ignoring the *Pteridium aquilinum* layer in a sessile oak (*Quercus petraea* (Matluschka) Liebl.) woodland would yield an estimate of throughfall precipitation 26 percent above the actual value. They also found that a significant proportion of the potassium (31.6 percent) and phosphorus (9.8 percent) reaching the ground in solution in the woodland was being washed from the bracken fronds. Thus, it appears that understory vegetation can have a major effect on throughfall chemistry.

A well developed moss stratum can effectively remove a large portion of the nutrients from throughfall precipitation (Tamm, 1953). Ruhling and Tyler (1970) found that *Hylocomium splendens* (Hedw.) B.S.G. effectively removed both zinc and manganese from a water solution passing over the green tissues. They also found that these elements were incorporated into the moss tissues and became very resistant to further leaching. At the Washington Creek Research site in Alaska four bryophyte genera (*Sphagnum, Hylocomium, Pleurozium* and *Polytrichum*) were each found to have a cation exchange capacity which greatly exceeded the total yearly input of calcium, magnesium and potassium in throughfall precipitation (Van Cleve and Dyrness, 1977). Thus, unlike higher strata which in general tend to enrich throughfall precipitation, moss layers tend to remove nutrients from throughfall.

Generally stemflow has been shown to account for only relatively minor quantities of water and nutrients reaching the forest floor (Kittredge, 1948; Helvey, 1971). Eaton et al. (1973) found that stemflow added at most 12 percent to the quantity of potassium leached in a northern hardwood forest. Miller et al. (1976) reported that stemflow added an additional 5 percent and 2.7 percent to the quantity of nitrogen and potassium, respectively, reaching the forest floor in a 450 year old Douglas-fir stand. This agrees with data presented by Rothacher (1963) which indicated that stemflow was relatively unimportant in rough barked trees like Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Even in the multilayered aspen community studied by Clements (1971, 1972) where bracken fern concentrated more rain water per storm in the form of stemflow than the other three overstory canopies, stemflow was only 8 percent (range 3.8 percent to 12.4 percent) of the gross rainfall. For this reason, and because of the time-consuming nature of an understory stemflow study, it was decided to omit stemflow in the present study.

Considering the limited evidence on the effect of minor vegetation on total throughfall and litterfall, the objective of this portion of the study was to quantify the contribution of minor vegetation to throughfall and litterfall in the three Mt. Hemlock ecosystems.

## 4.2 Methods

### 4.2.1 Litterfall

Herbaceous litterfall was estimated by calculating a second set of percent cover - biomass regressions from a random sample of twenty 0.25 $m^2$ herbaceous clipping plots (Figure 3.1). The plots were clipped at the end of the growing season (end of September, 1976) and assumed to represent herbaceous senescent biomass. If the two sets of equations were found to differ significantly ($a = 0.05$), the senescent equation was then used to calculate senescent biomass on the entire set of first phase sample plots ($n = 70$) used to estimate peak standing biomass. If the equations were found to be the same then the midseason biomass value was used to represent senescent biomass.

The vegetation from the clipped plots was separated according to species, dried at 70° C until constant weight was obtained and weighed to the nearest 0.001 gram.

Overstory and shrub litterfall was estimated from 20 randomly located 0.25 $m^2$ (1 m x 0.25 m) littertraps per plant association. Litter collections were made at monthly intervals from June until October, 1976. The litter was separated into the following categories:

1) Lichens
2) Overstory
    a) Old foliage
    b) Green foliage
    c) Twigs
    d) Seeds and cones

e) Bark

3) Understory

a) Shrub leaves

b) Shrub twigs

c) Shrub fruits and flowers

4) Miscellaneous

The samples were sorted in the laboratory, dried at 70°C until constant weight was obtained and weighed to the nearest 0.001 gram.

During the October collection an estimate of leaf biomass remaining on the shrubs was made by removing all leaves within a vertical projection above the littertraps. They were dried at 70°C until constant weight was obtained and weighed to the nearest 0.001 gram.

#### 4.2.1.1 Litterfall Chemical Analysis

Chemical analysis was performed on bulked samples for each of the categories of litter collected from the littertraps for each month on each site. Herbaceous material collected for the second set of percent - cover biomass relationships was also bulked and analyzed by species. The samples were analyzed for N, P, Ca, Mg, K, Mn, Zn, and Cu. Methods of chemical analysis are described in Chapter 3. Due to the late snowfall during 1976 a second set of samples was collected for chemical analysis from the Streptopo - Abietetum amabilis site at the end of October, slightly before the first snowfall.

### 4.2.1.2 Litterfall Statistical Analysis

Statistical differences between the two sets of percent cover - biomass relationships were determined by use of a t-test. The slopes of the regression equations which had noninclusive confidence intervals were tested to see if they were statistically (a = 0.05) different. A t-test was also used to determine if there were statistical differences between chemical concentrations of midseason and senescent herbaceous vegetation.

### 4.2.2 Throughfall

Throughfall was collected in 7.62 cm diameter funnels connected to one-liter plastic bottles. A piece of glass wool was inserted in each funnel to reduce contamination of the sample by foreign material.

A paired two-stage sampling design (Cochran, 1963) was used. Ten randomly selected 16 $m^2$ plots were selected for the first stage units in each plant association. The second stage units consisted of two sets of paired collectors. These were randomly located within each first stage unit.

The collectors were set up so that one of the pair collected throughfall beneath the overstory but above the understory. The second was placed in close proximity to the first, but below the level of the understory foliage (Figures 4.1 and 4.2). The difference between the two collectors was thus an indication of the effect of the understory at that point. The percent cover of the shrub layer was estimated on the mesic site within each second stage unit sampled. The calculated

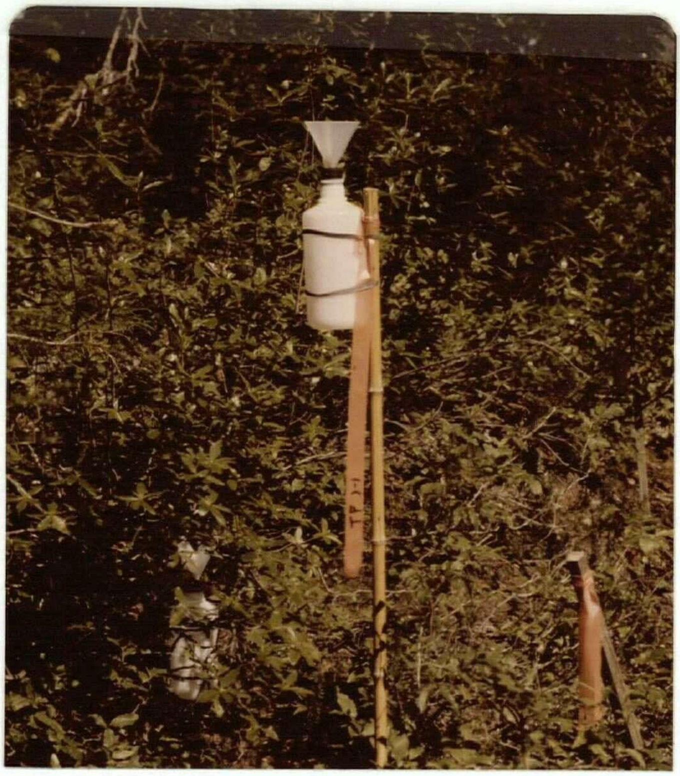


Figure 4.1. Understory and Overstory Throughfall Collectors on the Vaccinio - Tsugetum mertensianae Site

Figure 4.2. Understory and Overstory Throughfall Collectors on the Streptopo - Abietetum amabilis Site

values of throughfall nutrients reaching the moss layer per $m^2$ were then corrected according to the percent cover values of the shrub layer on this site. Due to the evenness of the understory cover on the hygric and xeric sites a correction for percent cover was not considered necessary.

One set of collectors was placed in an opening adjacent to the Vaccinio - Tsugetum mertensianae site, to determine the input of nutrients in precipitation in the open.

Three collections were made from all sites: monthly at the end of August, September and October.

Due to time constraints and the relative difficulty of the study, the effects of bryophytes on throughfall and the estimation of shrub and herbaceous stemflow was not determined.

4.2.2.1 Throughfall Chemical Analysis

The volume of throughfall in each collector was measured to the nearest milliliter in the field. A 100 ml subsample was retained for chemical analysis.

The pH was determined within 24 hours on an Orion model 404 specific ion meter with standard glass and silver/silver chloride reference electrodes. The samples were then stored for a maximum of six weeks at 0°C prior to cation and anion analysis.

Ammonium, phosphate, nitrate and sulphate concentrations were determined on a Technicon Autoanalyzer II using standard colorimetric methods (Technicon Industrial Systems 1971a, 1971b, 1971c; Johnson, 1972).

Calcium, magnesium and potassium concentrations were determined directly from the 100 ml subsample using a Varian - Techtron Atomic Absorption Spectrophotometer.

4.2.2.2 Throughfall Statistical Analysis

The significance of the effect of the understory was tested by a paired t-test according to procedures outlined by Cochran (1963). A one-way analysis of variance was performed on the twenty observations per plant association for both overstory and the understory to test the differences between the three sites during each sampling period and for the total three month sampling period.

4.3 Results and Discussion

In ecosystems where snow cover can last from six to eight months a year, external elemental recycling is divided into two components; (1) throughfall and litterfall which occurs during the snow free period, and (2) throughfall and litterfall which occurs during the period of snow cover. Generally these two components correspond to the periods when throughfall takes the form of either rain or snow, respectively. During the latter period foliar leaching is largely eliminated and external cycling is limited to litterfall. However, periods of snow melt and rain are common during the snow period in the coastal Mt. Hemlock Zone increasing the importance of foliar leaching during this period. Time limitations and the problems of accurate estimates of throughfall and litterfall during the winter prevented the measurement of foliar leaching during the snow period, and since this study was mainly concerned with deciduous vegetation the study was limited to the snow free period. Also, the apparent aboveground elemental cycling role of minor vegetation in the Mt. Hemlock biogeoclimatic zone is confined almost entirely to the snow free period.

4.3.1 Litterfall

The relationship between midsummer and autumn herbaceous percent cover - biomass equations varied according to the species concerned (Table 4.1). Of the 15 species studied, 7 showed no significant differences, while 8 were found to differ significantly. A significant difference between the slopes of the midseason and senescent equations would indicate a change in weight of that species between the two sampling periods. Of the 8 species which did show significant weight changes, 5 increased in weight and 3 decreased in weight (Table 4.1).

The herbaceous litterfall biomass was calculated using all herbaceous species on the hygric and mesic sites and using *Carex nigricans* Retz., *Rubus pedatus* and *Luetkea pectinata* (Pursh) Kuntze from the xeric site. Both *Phyllodoce empetriformis* and *Cassiope mertensiana* contribute very little of their standing biomass to litterfall each year. Thus, omitting them probably results in an underestimate of less than 10 percent. The herbaceous litterfall for each of the three sites was estimated to be 14.2, 1.8 and 0.3 $g \cdot m^{-2} \cdot yr^{-1}$ for the hygric, mesic and xeric sites, respectively (Table 4.2). Total minor vegetation

TABLE 4.1.

Statistical Comparison of Midseason and Senescent Percent Cover - Biomass Regressions for Fifteen Herbaceous Species

| Species | Midsummer Equation | | Senescent Equation | | | Calculated |
|---|---|---|---|---|---|---|
| Code | Slope | Confidence Limits | Slope | Confidence Limits | n | t |
| ARLA | 0.06094 | 0.04931 - 0.07258 | 0.05494 | 0.03603 - 0.07385 | | |
| ATFF | 0.10114 | 0.08710 - 0.11518 | 0.14949 | 0.13794 - 0.16104 | 38 | 5.3771* |
| CAME | 0.43038 | 0.34653 - 0.51423 | 0.74076 | 0.45062 - 1.03090 | | |
| CANI | 0.09641 | 0.09143 - 0.10139 | 0.15150 | 0.13634 - 0.16666 | 31 | 7.8037* |
| GYDR | 0.04781 | 0.04018 - 0.05544 | 0.10493 | 0.07431 - 0.13555 | 38 | 5.0187* |
| LUPE | 0.05452 | 0.05195 - 0.05709 | 0.08460 | 0.07806 - 0.91135 | 30 | 9.1880* |
| OSCH | 0.06510 | 0.06163 - 0.06857 | 0.05829 | 0.03492 - 0.08166 | | |
| PHEM | 0.44814 | 0.31012 - 0.58616 | 0.36713 | 0.25342 - 0.48084 | | |
| RUPE | 0.03599 | 0.03173 - 0.04027 | 0.04385 | 0.04117 - 0.04653 | 97 | 3.2496* |
| STRO | 0.08545 | 0.07561 - 0.09529 | 0.04988 | 0.04184 - 0.05792 | 76 | 4.5293* |
| STST | 0.05337 | 0.04685 - 0.05988 | 0.02193 | 0.01188 - 0.03198 | 38 | 5.6603* |
| TIUN | 0.05790 | 0.04991 - 0.06589 | 0.05774 | 0.04487 - 0.07061 | | |
| VASI | 0.07834 | 0.06300 - 0.09368 | 0.06108 | 0.03777 - 0.08439 | 39 | 1.1973 |
| VEVI | 0.39025 | 0.34250 - 0.43799 | 0.37168 | 0.30456 - 0.43880 | 39 | 0.4055 |
| VIGL | 0.12924 | 0.10067 - 0.15781 | 0.06703 | 0.05716 - 0.07690 | 38 | 10.6981* |

* Significant at the 0.05 percent level of probability.

TABLE 4.2.

Herbaceous Aboveground Litterfall Biomass and Elemental Quantities ($g \cdot m^{-2}$) for Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Item | Plant Association: Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
|---|---|---|---|
| Biomass | 14.202 | 1.815 | 0.348 |
| Nitrogen | 0.5284 | 0.1292 | 0.0344 |
| Phosphorus | 0.0364 | 0.0120 | 0.0028 |
| Calcium | 0.3032 | 0.0280 | 0.0036 |
| Magnesium | 0.0688 | 0.0144 | 0.0040 |
| Potassium | 0.8340 | 0.1276 | 0.0316 |
| Manganese | 0.0100 | 0.0028 | * |
| Zinc | 0.0012 | 0.0004 | * |
| Copper | 0.0004 | * | * |

* Less than 0.4 $mg/m^2$

litterfall, including lichens but excluding mosses, was 17.6, 8.3 and 20.6 $g \cdot m^{-2}$ for the hygric, mesic and xeric sites, respectively, for the entire sampling period. At the end of October shrub leaves which amounted to another 2.16 $g \cdot m^{-2}$ remained on the shrubs on the xeric site.

On the three sites studied both understory and overstory show an autumn (October) seasonal peak in litterfall (Figure 4.3). This peak would normally occur just before the winter snow pack begins to accumulate, which would trap a small portion of shrub leaves in the snow above the forest floor until spring.

The October increase in litterfall is relatively small on the mesic site (Figure 4.3) because of the lack of a large quantity of either shrub or herbs. The increase in understory litterfall on the xeric site is caused by the shedding of shrub leaves, while the peak on the hygric site is caused by the inclusion of the herbaceous strata in the litterfall estimates. In most years the entire herbaceous standing crop becomes litterfall during the first wet snowfall of the year, and therefore probably represents the greatest single pulse of nutrient-rich, easily decomposable litter throughout the entire year.

The changes in elemental composition of the herbaceous species between midsummer and autumn were much more consistent than the biomass changes. All the herbaceous species, with the exception of *Rubus pedatus*, displayed significant changes in elemental composition between the two sampling periods on the hygric site, while fewer significant changes were found on the mesic and xeric sites (Table 4.3, Appendix 6).

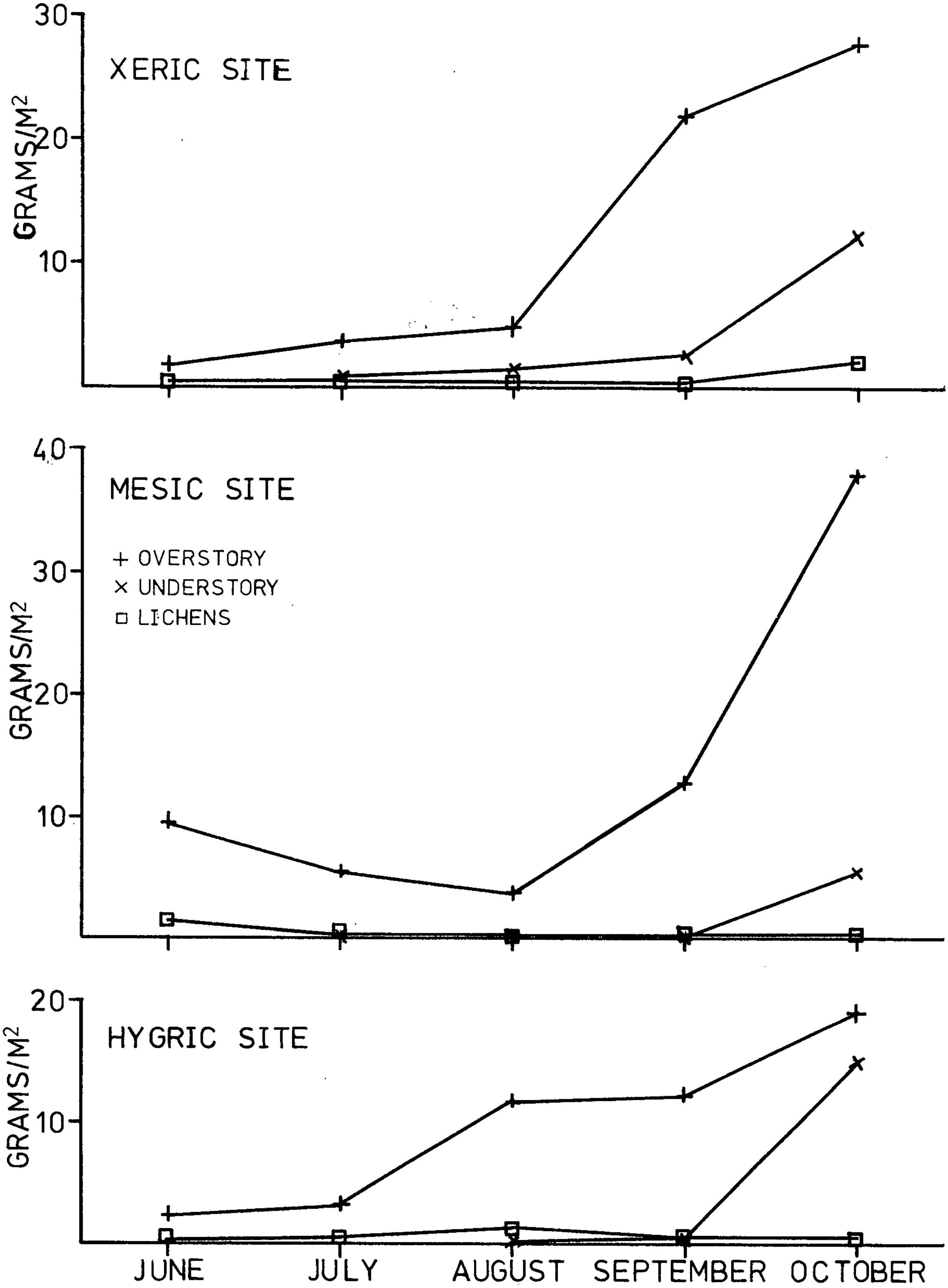



Figure 4.3. Monthly litterfall biomass in three categories for three forested Mt. Hemlock ecosystems.

TABLE 4.3.

Statistical differences (a=0.05) Between Midseason and Senescent Elemental Concentrations for the Sampled Herbaceous Species of Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Species Code | df | Element | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | N | P | Ca | Mg | K | Mn | Zn | Cu |
| Streptopo - Abietetum amabilis plant association | | | | | | | | | |
| ARLA | 10 | - | - | + | | - | + | | - |
| ATFF | 4 | - | - | + | | | | | |
| GYDR | 11/ 9* | - | - | + | | - | + | | - |
| OSCH | 6/ 5/ 3 | - | - | + | - | - | + | | |
| RUPE | 5/ 1/ 2 | | | | | | | | |
| STRO | 11/11/ 9 | - | - | + | - | - | + | - | |
| TIUN | 11/ 6 | | - | + | + | | | | - |
| VASI | 9/ 8 | - | - | + | + | - | + | | - |
| VEVI | 12 | - | - | + | + | - | + | | - |
| VIGL | 5/ 4/ 2 | - | - | + | + | + | + | | |
| Abieto - Tsugetum mertensianae plant association | | | | | | | | | |
| RUPE | 11/10 | | | | | | | | |
| STRO | 4/ 2 | - | - | + | | - | + | | |
| STST | 4/ 4/ 2 | | - | + | | - | + | + | + |
| Vaccinio - Tsugetum mertensianae plant association | | | | | | | | | |
| CAME | 6/ 6 | | | | + | | | | + |
| CANI | 4/ 4 | - | | | | | | | |
| PHEM | 11 | | | | | | | - | |

\- = Significant decrease in concentration
\+ = Significant increase in concentration
* Degrees of freedom for N and P/cations/Zn and Cu where sample sizes differ

The quantities ($mg \cdot m^{-2}$) of nutrients returned during the sampling period in understory litterfall (exclusive of mosses but including lichens) on the hygric, mesic and xeric sites were 571.8, 220.7, 433.1 for nitrogen; 39.6, 18.2, 29.8 for phosphorus; 318.7, 66.0, 162.3 for calcium; 72.0, 27.3, 45.3 for magnesium; 845.7, 165.9, 76.4 for potassium; 15.0, 20.8, 11.5 for manganese; 1.33, 0.35, 0.81 for zinc; and 0.181, 0.084, 0.312 for copper, respectively.

Using the months of August, September and October to represent the growing season for 1976, understory litterfall biomass was 28.3 percent, 10.5 percent and 26.1 percent of the total aboveground growing season litterfall for the hygric, mesic and xeric sites, respectively (Figure 4.4). However, as already indicated, biomass gives only an approximate indication of the effect of understory litterfall on the site (Scott, 1955). A substantially higher percentage of nitrogen, phosphorus, magnesium, potassium, zinc and copper was returned as understory litterfall during the growing season than biomass alone would indicate (Figure 4.4). Understory returned a larger quantity of all elements studied on the hygric site than on the mesic or xeric sites. The minor vegetation on the mesic site generally returned the smallest quantity of nutrients in litterfall except for potassium and manganese for which it was intermediate between the hygric and xeric sites.

The proportion of total nutrient return by litterfall that can be ascribed to the understory over the three month period is substantial for both the hygric and xeric sites (Figure 4.4). A maximum of 96 percent of the litterfall potassium can be attributed to understory

Figure 4.4. Relative contribution of understory and overstory litter to the total litterfall during the growing season for three forested Mt. Hemlock ecosystems.

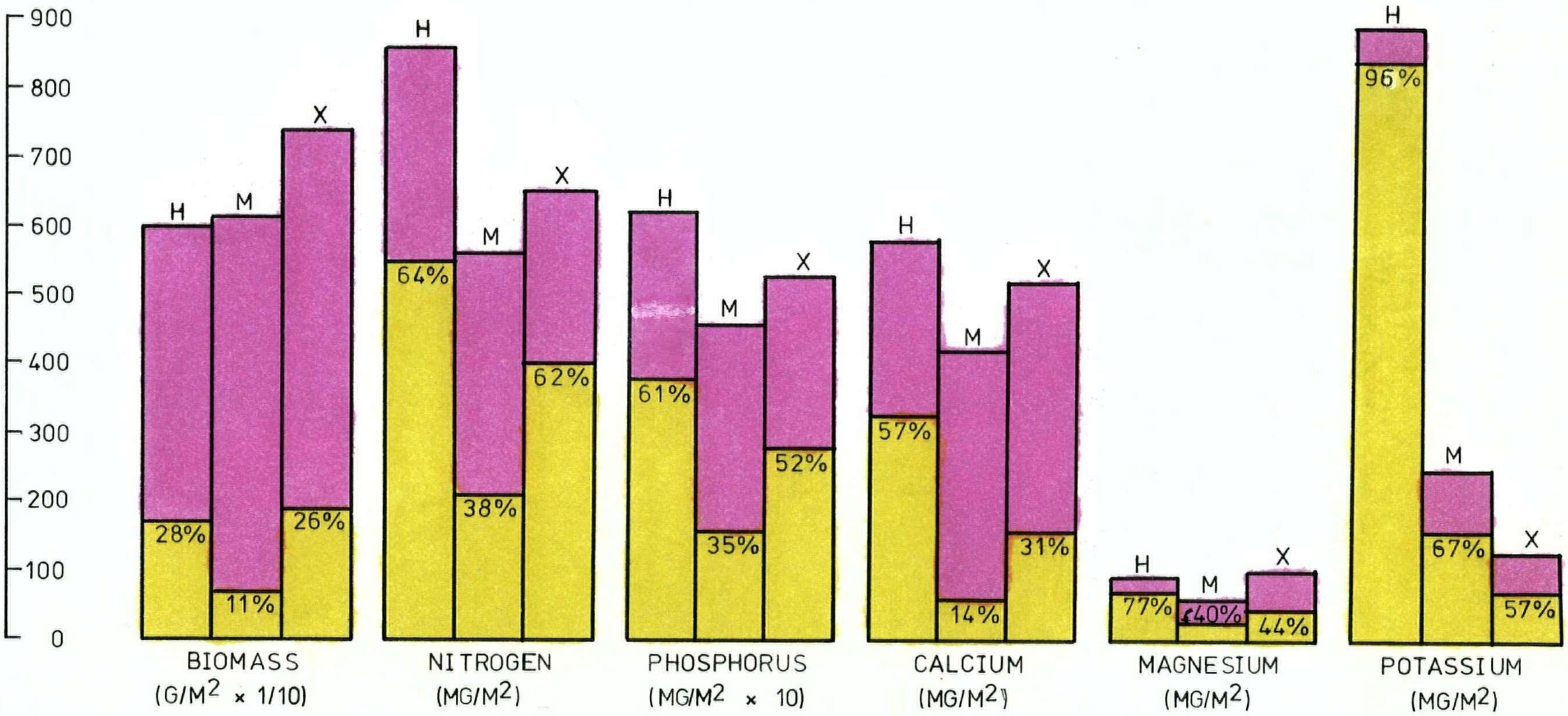
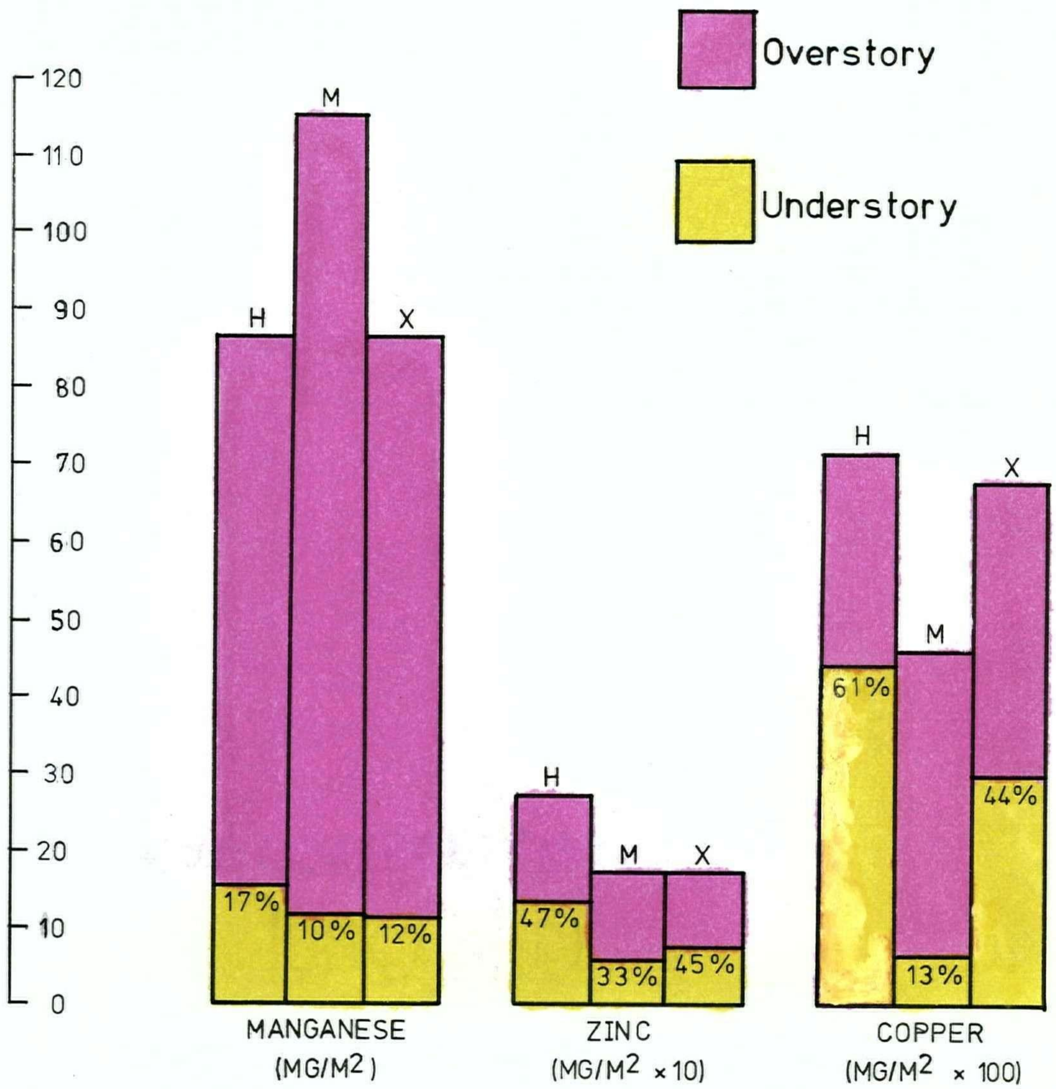


Figure 4.4 (Cont'd.)



vegetation. Manganese appears to be the only element which was cycled predominately by overstory vegetation; a maximum of only 17 percent of the litterfall manganese was contributed by understory vegetation on the hygric site (Figure 4.4). Thus, it appears that understory contributes a substantial portion of the total litterfall during the snow free period.

To permit a valid comparison between the litterfall contributions of overstory and understory vegetation it was necessary to expand the litterfall estimates to a yearly basis. The understory estimates were considered to represent the annual contribution to total litterfall. The five month overstory estimates were assumed to represent 41.7 percent, 35.0 percent, 50.0 percent and 41.7 percent of the total yearly input of foliage, twigs, cones and bark, respectively. These proportions were obtained from studies in old growth Douglas-fir stands in Oregon (Abee, 1973) and from detailed litterfall studies in stands adjacent to the study area (Krumlik, 1978). The resulting component estimates were then summed to give yearly estimates; these were relatively low compared with published values for stands of comparable age (Abee, 1973; Turner and Singer, 1976; Rodin and Bazilevich, 1967; Krumlik, 1978; Figure 4.5).

Considering the data on an annual basis we find that understory litterfall represents a relatively small proportion of total litterfall biomass, but a significant proportion of the litterfall nutrients (Figure 4.5). The importance of understory litterfall in potassium recycling is still obvious on an annual basis. The values reported

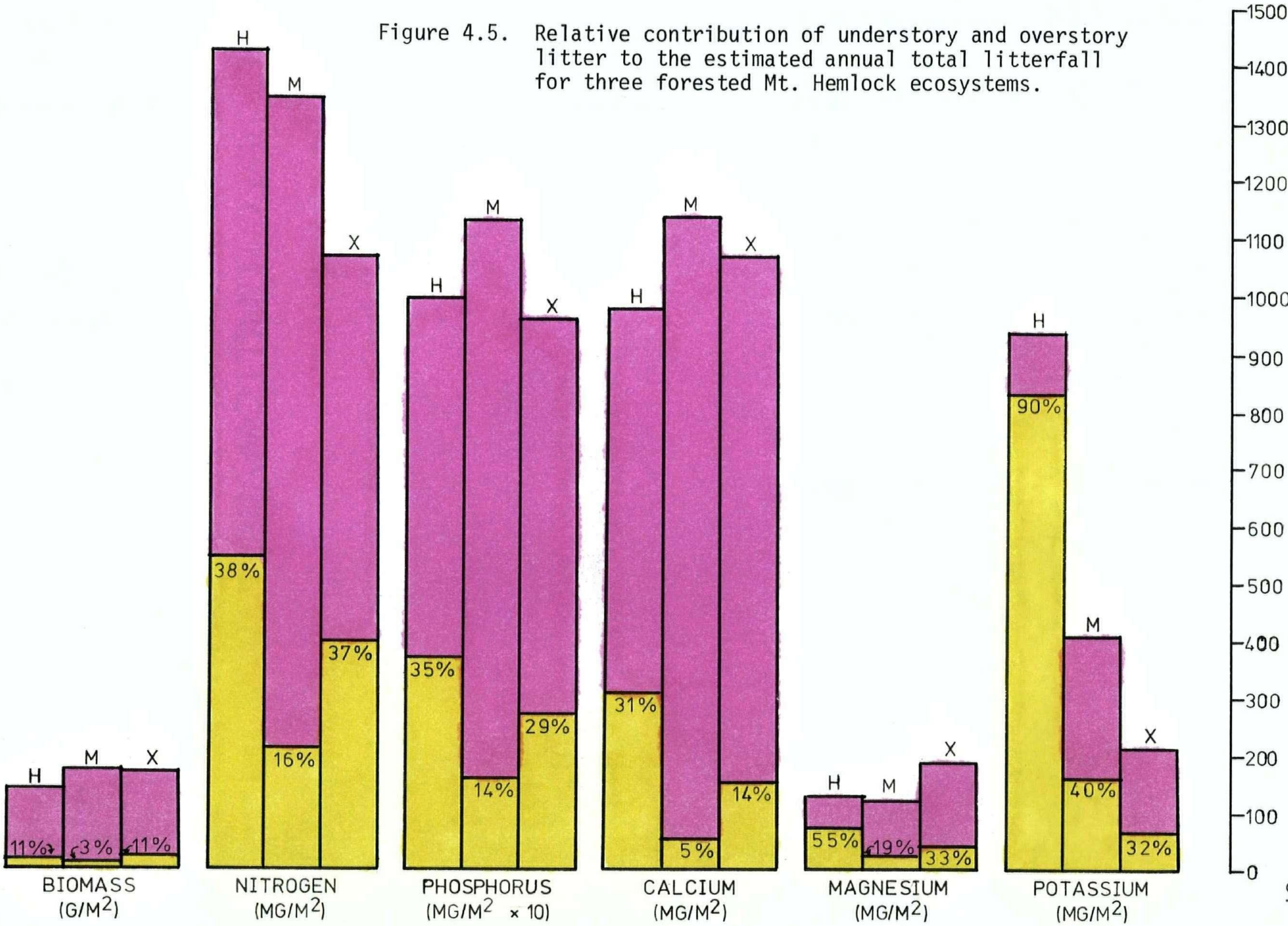
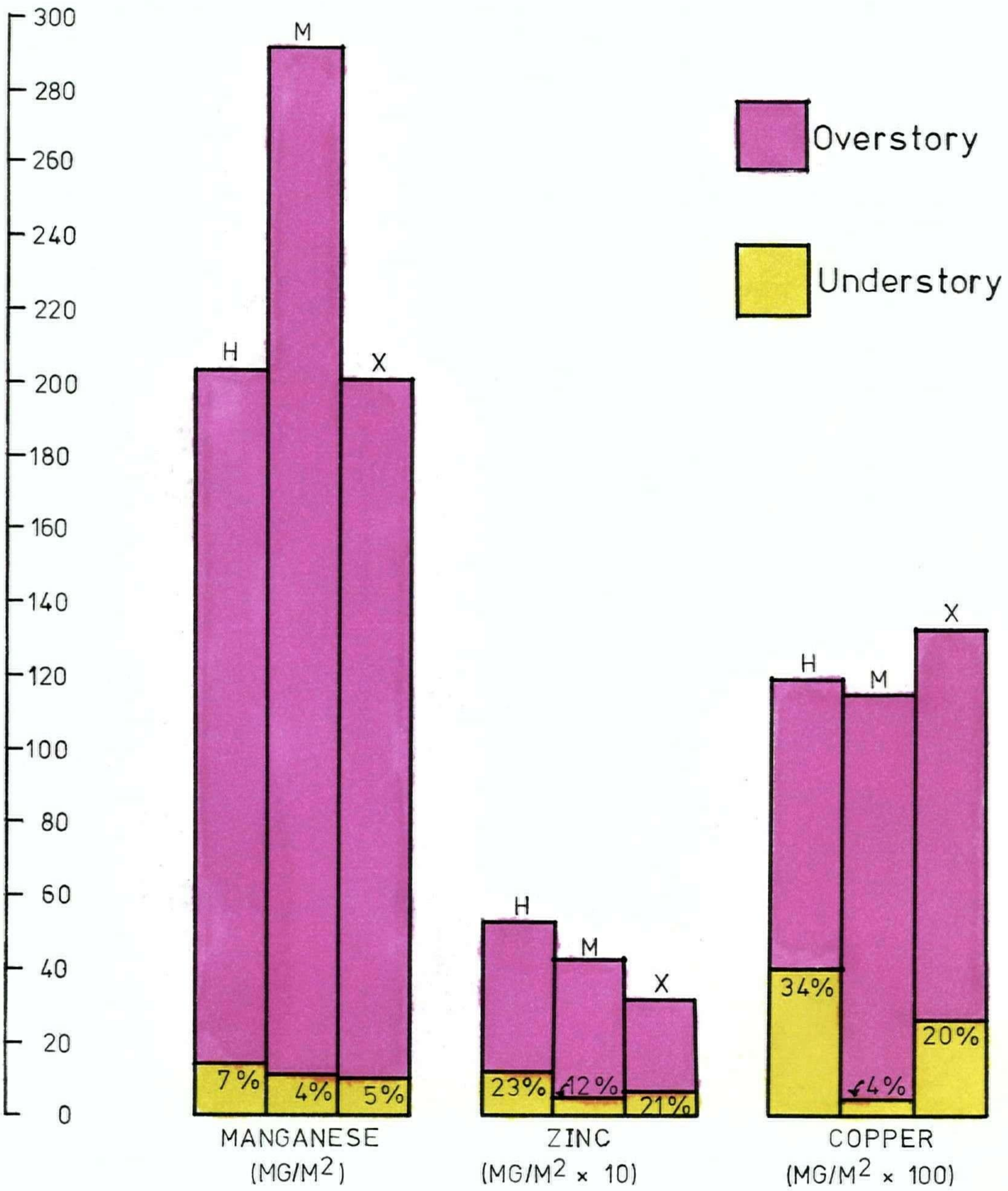



Figure 4.5. Relative contribution of understory and overstory litter to the estimated annual total litterfall for three forested Mt. Hemlock ecosystems.

Figure 4.5 (Cont'd.)



for quantities of understory litterfall nutrients are well within the range of values previously reported (Scott, 1955; Manakov, 1962; Gosz et al., 1972).

### 4.3.2 Throughfall

The effect that understory vegetation has on throughfall is, by necessity, seasonal in nature. The effect is limited to the snow free period, which was approximately four months long during the study period.

The effect of understory vegetation on overstory throughfall followed the same pattern on all three sites throughout the sampling period. During the first month of ontogeny (August), understory vegetation removed phosphate-phosphorus, nitrate-nitrogen and ammonium-nitrogen from overstory throughfall (Table 4.4). There was relatively little effect in September except for ammonium-nitrogen and nitrate-nitrogen removal on the xeric site. During senescence in October, the understory added calcium, magnesium and potassium to overstory throughfall (Table 4.4). In addition, ammonium-nitrogen was added on the hygric site and phosphate-phosphorus was added on the mesic site.

It should be apparent that ignoring the effect of understory on throughfall can yield significantly erroneous results (Table 4.4). Understory reduces the amount of phosphate-phosphorus reaching the moss layer by 80 percent, 35 percent and 64 percent on the hygric, mesic and xeric sites, respectively, in August. In September, a reduction of 90 percent and 71 percent occurs for nitrate-nitrogen and

TABLE 4.4.

Statistical Comparison of Overstory and Understory Throughfall Quantities ($mg \cdot m^{-2}$) by Stratum

| Item | PLANT ASSOCIATION | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Streptopo - Abietetum amabilis | | | Abieto - Tsugetum mertensianae | | | Vaccinio - Tsugetum mertensianae | | |
| | AUG | SEPT | OCT | AUG | SEPT | OCT | AUG | SEPT | OCT |
| Overstory | | | | | | | | | |
| Quantity (cm) | 13.11* | 14.66 | 10.12 | 12.87 | 13.78 | 8.67 | 13.82 | 14.08 | 11.05 |
| $PO_4$-P | 2.97 | 1.35 | 0.19 | 5.77 | 11.32 | 0.21 | 3.77 | 1.46 | 0.47 |
| $NO_3$-N | 0.83[a] | 0.20[a] | 0.24 | 3.55[b] | 0.49[a] | 0.31 | 5.43[b] | 2.28[b] | 1.10 |
| $NH_4$-N | 20.22 | 1.64 | 0.29 | 37.59 | 36.68 | 0.19 | 21.18 | 8.17 | 0.32 |
| $SO_4$-S | 82.85 | 30.68 | 54.71 | 65.96 | 23.21 | 47.70 | 72.80 | 28.62 | 61.82 |
| Ca | 43.46[a] | 23.78[a] | 21.73 | 24.09[b] | 13.55[b] | 16.40 | 25.09[b] | 10.05[b] | 18.23 |
| Mg | 14.63 | 9.82[a] | 8.77 | 8.46 | 4.74[b] | 7.16 | 9.52 | 5.58[b] | 10.43 |
| K | 127.2[a] | 90.18[a] | 123.30[a] | 88.50[ab] | 60.46[b] | 85.61[ab] | 67.42[b] | 41.72[b] | 68.15[b] |
| Understory | | | | | | | | | |
| Quantity (cm) | 9.58 | 10.71 | 8.25 | 11.98 | 13.03 | 8.12 | 11.59 | 12.69 | 10.03 |
| $PO_4$-P | 0.59[a] | 0.99 | 0.79 | 3.77[b] | 1.40 | 0.46 | 1.36[a] | 1.20 | 2.94 |
| $NO_3$-N | 0.34[a] | 0.05 | 0.35 | 1.60[ab] | 0.31 | 0.22 | 2.22[b] | 0.23 | 0.02 |
| $NH_4$-N | 7.48[a] | 1.20 | 0.74 | 22.88[b] | 2.24 | 0.26 | 6.06[a] | 2.34 | 0.75 |
| $SO_4$-S | 65.96 | 22.49 | 58.54[ab] | 61.73 | 19.98 | 47.76[a] | 75.10 | 30.93 | 75.94[b] |
| Ca | 40.73 | 23.35[a] | 39.79[ab] | 23.30 | 13.22[b] | 22.48[a] | 28.55 | 11.74[b] | 59.54[b] |
| Mg | 10.48 | 7.56 | 18.44[a] | 8.86 | 4.84 | 12.04[a] | 12.18 | 7.39 | 58.79[b] |
| K | 109.70 | 79.15 | 204.30 | 89.81 | 66.89 | 113.6 | 78.99 | 57.53 | 239.30 |

* Parameters underlined were significantly different (a=0.05) between the understory and overstory. Parameters superscripted by the same letter were not significantly different (a=0.05) between sites for the same month within each stratum. Only items having at least one significant difference are superscripted.

ammonium-nitrogen, respectively, on the xeric site (Table 4.4). Increases ranging from 33 percent for potassium on the mesic site to 82 percent for magnesium on the xeric site can be attributed to understory vegetation in October (Table 4.4).

Considering the entire sampling period a net reduction in ammonium-nitrogen and nitrate-nitrogen and an increase in calcium, magnesium and potassium can be attributed to the effect of understory vegetation above the moss layer (Table 4.5). The understory reduced the amount of ammonium reaching the moss layer by 55 percent on the hygric site. On the mesic site there was a reduction of 51 percent in throughfall nitrate-nitrogen and an increase of 21 percent in magnesium reaching the moss layer.

Two possible reasons can be hypothesized which could account for the effect that understory vegetation has on overstory throughfall. Firstly, it is possible that understory vegetation cannot compete successfully for certain nutrients (e.g. nitrogen and phosphorus) in the soil during spring and has adapted to remove those nutrients from throughfall precipitation. The source of this competition could be a combination of the nutrient demand by the tree strata plus the demand by microbial and fungal organisms. Secondly, the process could be the result of a concentration gradient into the plant cells. At lower concentrations of $NO_3$-N and $NH_4$-N in open precipitation, it has been found that nitrogen is leached from the plant into throughfall, at least at the overstory level (Abee, 1973; Kimmins and Feller, 1976). Then in the autumn when the understory vegetation is senescening certain

TABLE 4.5.

Statistical Comparison of Overstory and Understory Throughfall Quantities ($mg \cdot m^{-2}$) by Stratum and Sites Within Stratum for the Entire Sampling Period

| Item | Plant Association | | |
|---|---|---|---|
| | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
| Overstory | | | |
| Quantity (cm) | 37.89* | 34.95 | 38.95 |
| $PO_4$-P | 4.51 | 17.30 | 5.69 |
| $NO_3$-N | 1.27$^{a}$ | 4.35$^{a}$ | 8.81$^{b}$ |
| $NH_4$-N | 22.15 | 74.47 | 29.67 |
| $SO_4$-S | 167.90 | 136.89 | 163.23 |
| Ca | 88.96$^{a}$ | 54.04$^{b}$ | 53.38$^{b}$ |
| Mg | 33.22 | 20.36 | 25.52 |
| K | 340.61$^{a}$ | 234.57$^{ab}$ | 177.28$^{b}$ |
| Understory | | | |
| Quantity (cm) | 28.99 | 32.01 | 34.31 |
| $PO_4$-P | 2.37 | 5.63 | 5.50 |
| $NO_3$-N | 0.74 | 2.13 | 2.47 |
| $NH_4$-N | 9.40$^{a}$ | 25.38$^{b}$ | 9.15$^{a}$ |
| $SO_4$-S | 148.81 | 129.48 | 182.00 |
| Ca | 109.29$^{a}$ | 59.01$^{b}$ | 99.83$^{a}$ |
| Mg | 39.64$^{a}$ | 25.73$^{a}$ | 78.36$^{b}$ |
| K | 389.71 | 270.25 | 375.78 |

* Parameters underlined were significantly different (a = 0.05) between understory and overstory. Parameters superscripted by the same letter were not significantly different (a = 0.05) between sites within each stream. Only items having at least one significant difference are superscripted.

cations (e.g. calcium and magnesium) can be leached easily from the vegetation. Also, considering the significant effect that understory vegetation has on the quantities of nutrients passing through its canopy, it should be apparent that any throughfall study examining the return of nutrients to the humus layer must estimate this parameter below the level of the understory layer. Conclusions drawn about the relative effectiveness of the humus layer as a nutrient filter should take into account the effects of the understory layer on the chemistry of water reaching the ground.

Differences between sites were relatively inconsistent within and between each stratum both on a monthly basis (Table 4.4) and considering the entire growing season (Table 4.5). A tentative explanation of between-site differences in the understory throughfall data can be based on total understory cover and species composition. Generally, the greatest quantities of $PO_4$-P, $NO_3$-N and $NH_4$-N to reach the moss layer were found on the mesic site due to a lack of absorbing leaf surface in the vascular plant strata. Conversely, the smallest quantities of $SO_4$-S, Ca and K to reach the moss layer were found on the mesic site due to a lack of available leaf surface for leaching. The quantities of magnesium reaching the moss layer appears to be related to both the relative abundance of total leachable leaf surface and the quantity of shrubs on the site. The quantity of magnesium reaching the moss layer on the xeric site was two to three times the quantity reaching the moss layer on the hygric and mesic sites.

## 4.4 Summary

### 4.4.1 Understory Litterfall

Estimates of 17.6, 8.3, and 20.6 $g \cdot m^{-2} \cdot yr^{-1}$ of understory litterfall (exclusive of the moss layer) were obtained for the hygric, mesic and xeric sites, respectively. These are underestimates for the whole layer because an estimate of moss litterfall was not obtained. The majority of understory litter fell in the month of October (Figure 4.3). The biomass of litterfall was shown to be a poor indicator of either the quantity of nutrients in litterfall or the proportional contribution of understory to aboveground site litterfall (Figures 4.4, 4.5). Understory was shown to return a significant proportion of the litterfall nutrients on a yearly basis, the bulk of which was returned as a single pulse in October (Figure 4.3).

### 4.4.2 Understory Throughfall

Understory vegetation above the moss layer was shown to have a significant effect on the quantity of nutrients present in throughfall precipitation. The effect was seasonal in nature with phosphate, nitrate and ammonium being removed in the spring and calcium, magnesium and potassium being added to throughfall in the fall. Two possible explanations were hypothesized to account for the effect that understory vegetation has on overstory throughfall. First, it was suggested that the removal of nutrients, such as nitrogen and phosphorus from throughfall could be a mechanism adapted because understory vegetation could not compete successfully for these nutrients during the spring. Second, the process could merely be the result of diffusion due to a concentration gradient. Also, it was suggested that any study investigating the filtering capacity of the humus layer should account for all possible aboveground influences on incoming throughfall. Modifications of water chemistry previously attributed to the forest floor may in some cases reflect unmeasured influences of understory vegetation.

# CHAPTER 5

## The Understory Nutrient Cycle

### 5.1 Introduction

The major components of the aboveground understory nutrient cycle (excluding litter decomposition) have been considered in Chapters 3 and 4. In this chapter, the results already presented will be combined to permit an examination of the overall understory nutrient cycle and a consideration of its role in the functioning of the ecosystem.

### 5.2 Understory Nutrient Cycle

The quantification of the understory nutrient cycle requires at least a fragmentary consideration of the overstory cycle (i.e. as a very minimum, overstory throughfall must be measured). In the past, only selected parts of the understory nutrient cycle have received consideration in "ecosystem" nutrient cycling investigations (e.g. Cole et al., 1968; Turner and Singer, 1976); studies of understory generally have been limited to the relatively minor contribution of understory biomass and productivity, ignoring the more significant contribution to throughfall and litterfall (cf. Chapters 3 and 4). Emphasis, in the present study, was placed on the quantification of the understory nutrient cycle, while overstory was considered only to permit broad comparisons with the understory data. A more detailed study of the overstory nutrient cycle has been carried out by Krumlik (1978).

The description of the understory nutrient cycle which follows is based on estimates of components from only a portion of a year. However, this lack of data from a complete year is not considered to be a serious weakness, because of the prolonged duration of snow cover and the short growing season. During the period of snow cover the aboveground portion of the understory can have, at most, only a minor effect on the function of the total ecosystem. Similarly, the aboveground function of the overstory is probably largely restricted to litterfall during this period.

In describing the understory nutrient cycle a number of terms were used according to the following definitions:

1) Overstory Throughfall - precipitation falling and/or dripping through the overstory canopy but collected above the understory canopy for the months of August, September, and October (the growing season).

2) Understory Throughfall - throughfall which was collected below the shrub and herbaceous layer but above the moss layer during the growing season.

3) Standing Crop and Annual Production - are defined as described in Chapter 3. The standing crop values for the shrub and herbaceous layers are the average of estimates for 1975 and 1976.

4) Understory Litterfall - was estimated as described in Chapter 4.

5) Annual Requirement - shrub and herb requirement was calculated as the sum of: (a) shrub annual production, (b) herbaceous annual production or litterfall, whichever was greater, and (c) the quantity of nutrients removed from or added to overstory throughfall.

6) Internal Redistribution - is defined as the difference between midseason standing crop and senescent standing crop minus any loss due to defoliation* and throughfall. If the value for senescent standing crop was the larger of the two then internal redistribution was assumed to be zero. Internal redistribution was assumed to represent that portion of the annual requirement which could be satisfied by redistribution of nutrients within the plant.

The understory aboveground nutrient cycle can then be described as follows. Overstory throughfall encounters the understory aboveground standing crop of nutrients which is made up of two components (1) the perennial standing crop (e.g. in shrub stems, etc.) and (2) the current annual production (e.g. in aboveground herbaceous vegetation, shrub leaves, etc). The nutrients in the current annual production originate from two main sources (1) the annual uptake from the soil layers (belowground), from the atmosphere, and from throughfall, and (2) any nutrients internally redistributed from belowground and

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* Defoliation was visually estimated to effect less than 1% of the vegetation on the three study sites.

perennial aboveground standing crop (Figure 5.1). That portion of the overstory throughfall which passes through the understory standing crop becomes understory throughfall (Figure 5.1). Also, those portions of the understory standing crop which falls as litter becomes understory litterfall (Figure 5.1).

There appear to be two different cycling patterns for the five macronutrients studied. The first includes the nitrogen and phosphorus cycles (Figures 5.2 and 5.3, respectively). The second is typical of the calcium and magnesium cycles (Figures 5.4 and 5.5, respectively). The potassium cycle (Figure 5.6) has characteristics of both. The two patterns differ in the following ways:

1) Effect on overstory throughfall,
2) the relationship of understory throughfall to bryophyte annual production, and
3) the proportion of the annual requirement accounted for by internal redistribution.

There was a net removal of phosphorus in the spring and of nitrogen for the entire sampling period from overstory throughfall by understory vegetation, thus increasing the total filtering action of aboveground structures. The nutrient demand of the estimated annual bryophyte production was sufficient to account for the remaining quantity of throughfall nitrogen and phosphorus, suggesting that little of these two elements may reach the litter layer in throughfall where there is a well developed bryophyte layer. The absorption of nitrogen

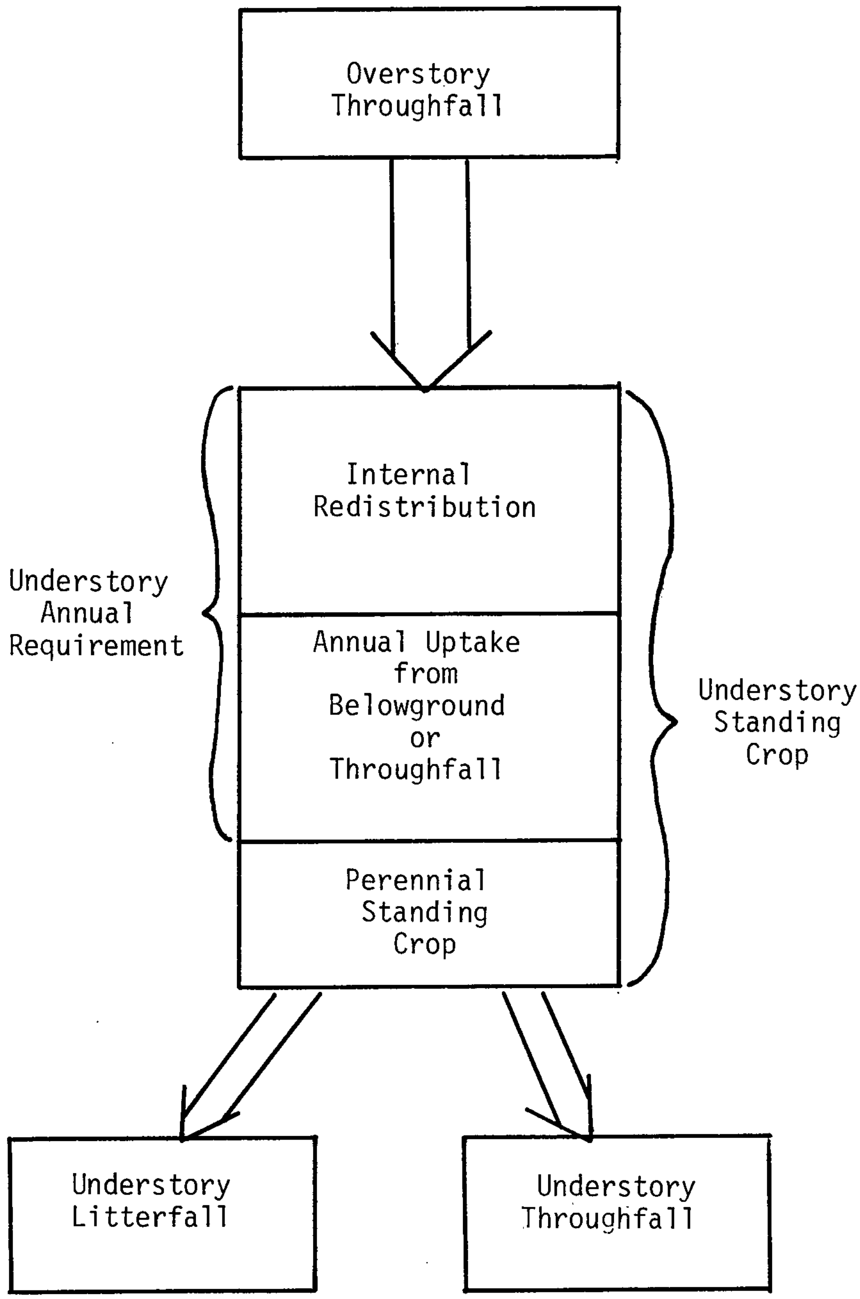


Figure 5.1. An understory nutrient cycle.

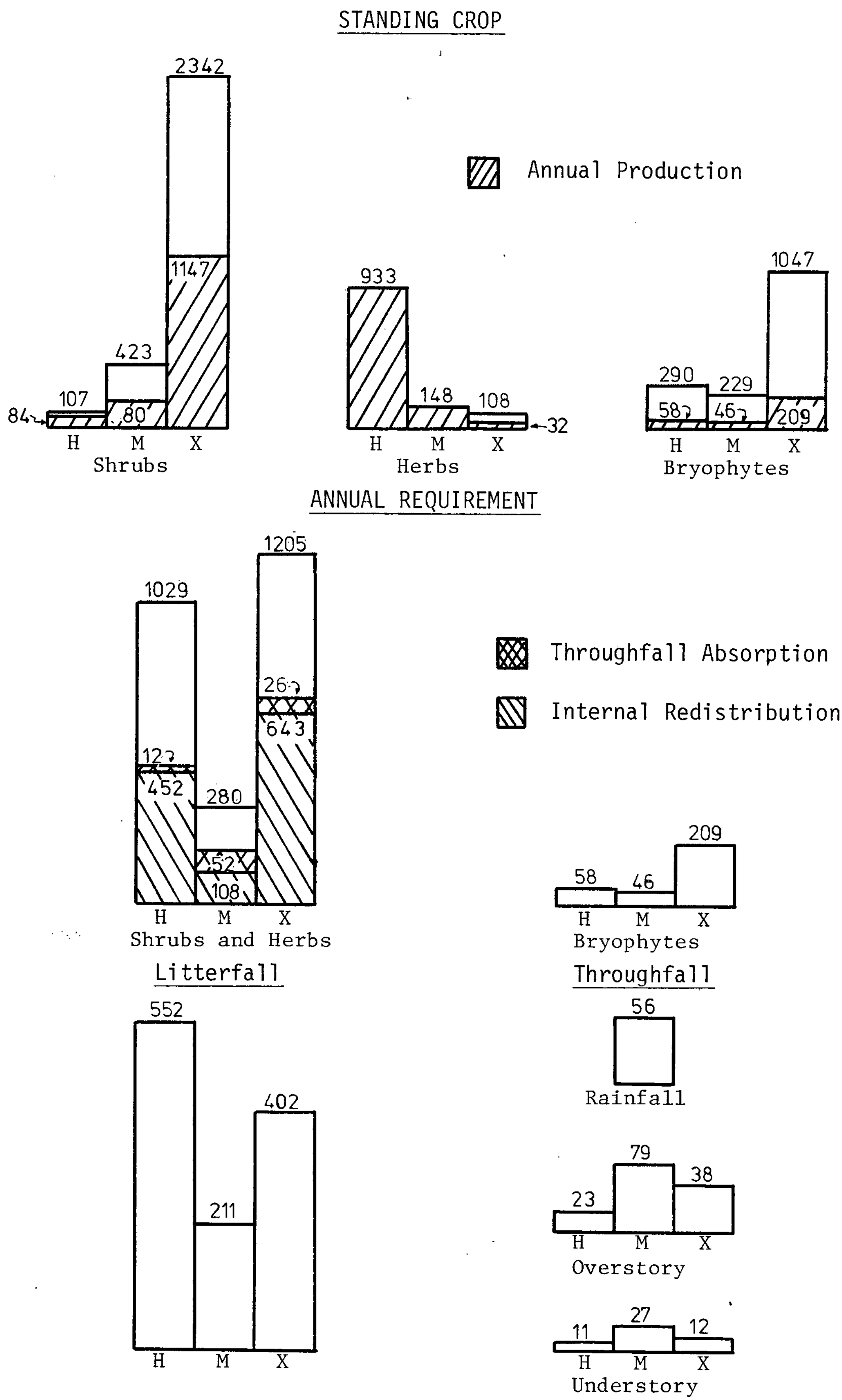


Figure 5.2. The understory nitrogen cycle (values in mg/m²).

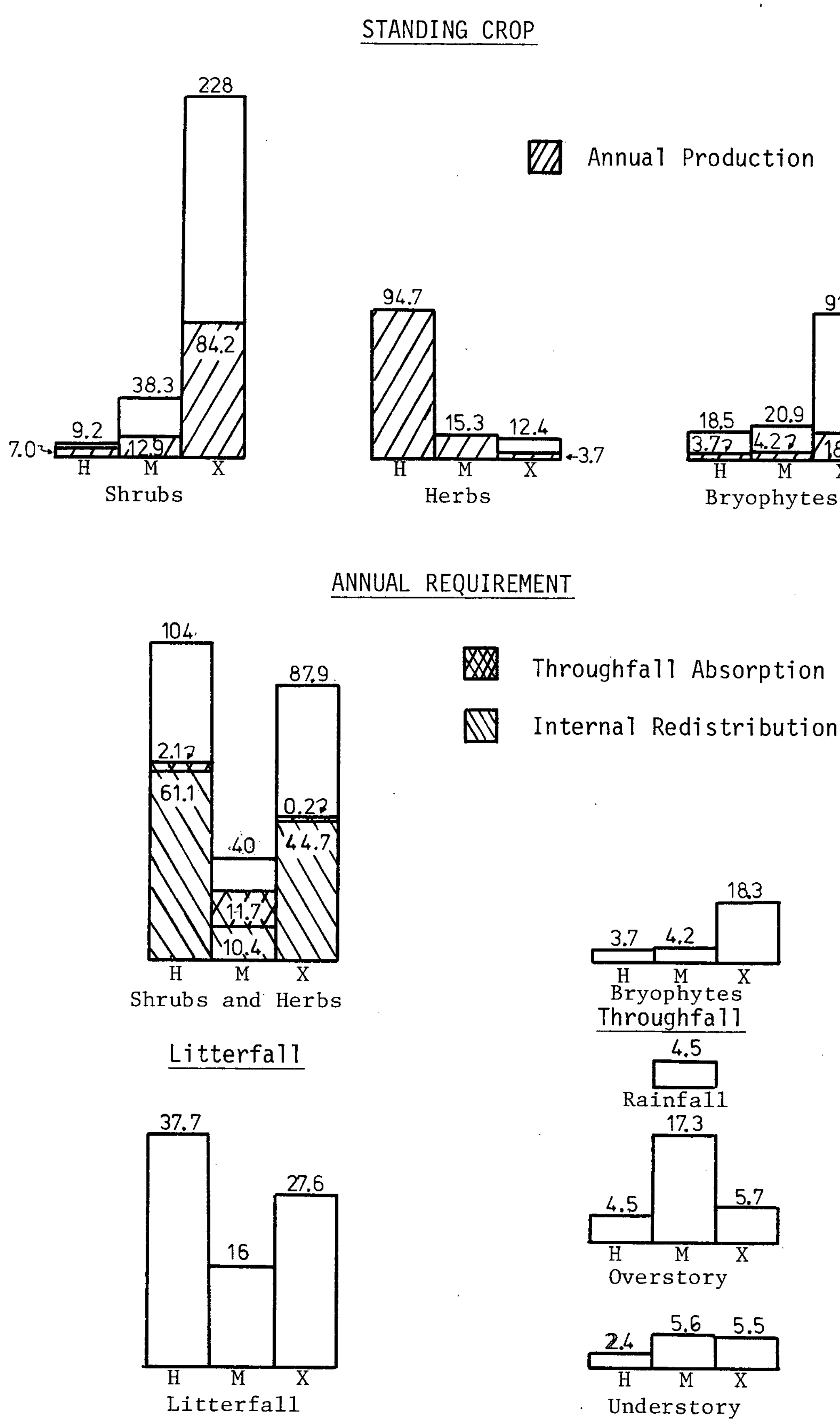


Figure 5.3. The understory phosphorus cycle (values in mg/m²).

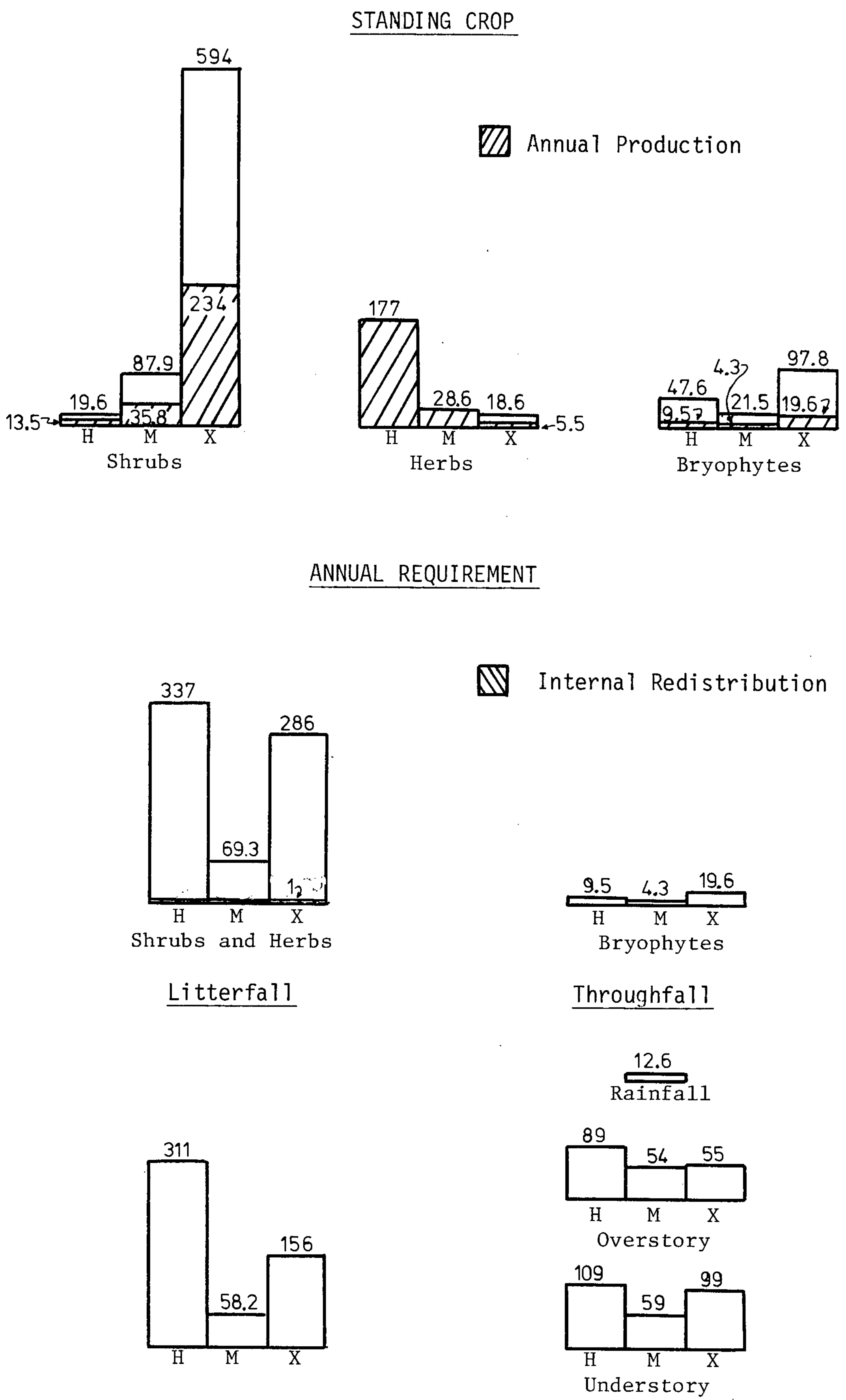


Figure 5.4. The understory calcium cycle (values in mg/m²).

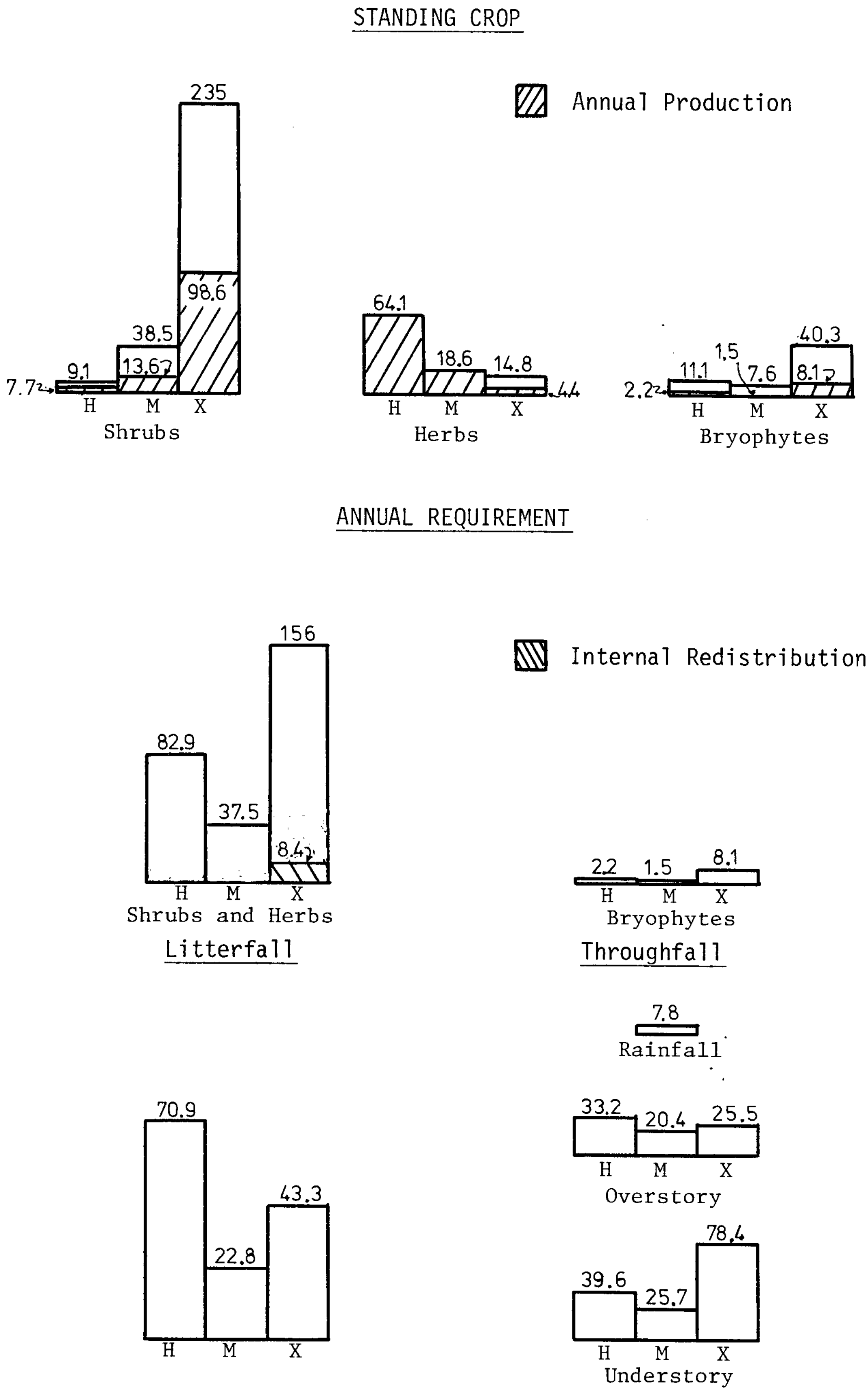


Figure 5.5. The understory magnesium cycle (values in mg/m$^2$).

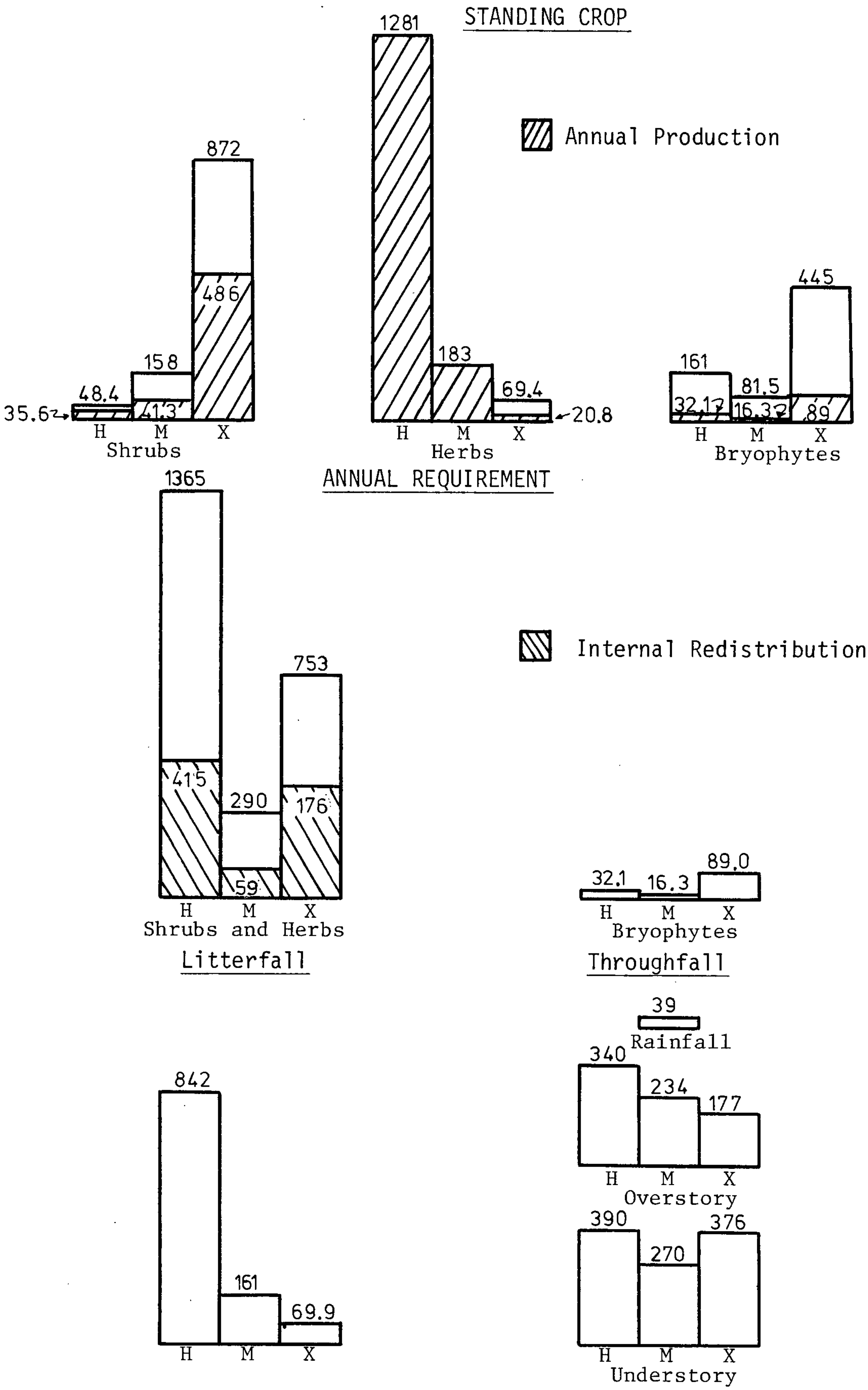


Figure 5.6. The understory potassium cycle (values in mg/m²).

and phosphorus from precipitation by vegetation appears to be a general phenomenon since it has been reported for a large variety of ecosystems (Likens et al., 1977; Krumlik, 1978). Finally, a large portion of the annual requirement of nitrogen and phosphorus can be ascribed to internal redistribution. Considering the above three attributes, it appears that understory vegetation within these ecosystems conserves nitrogen and phosphorus within the living plant biomass.

Considering the entire sampling period, calcium, magnesium, and potassium are added to overstory throughfall by understory vegetation (Figures 5.4, 5.5, 5.6, respectively). The leaching of these elements from the overstory layer has been reported for a large variety of ecosystems (Likens et al., 1977; Krumlik, 1978). The quantity of nutrients contained in the annual production of bryophytes is substantially less than the quantity contained in understory throughfall. Finally, a large portion of the annual requirement is obtained from external pools. However, potassium does show similarities to nitrogen and phosphorus in that internal redistribution accounts for 20 percent to 30 percent of the annual potassium requirement. Thus, it appears that calcium, magnesium, and potassium move in more open understory cycles than nitrogen or phosphorus, but that potassium also moves in a fairly well developed internal cycle.

The manganese cycle (Figure 5.7) appears to represent a third cycling pattern which may result from the utilization of manganese by woody perennials. The manganese cycle differs from the calcium and

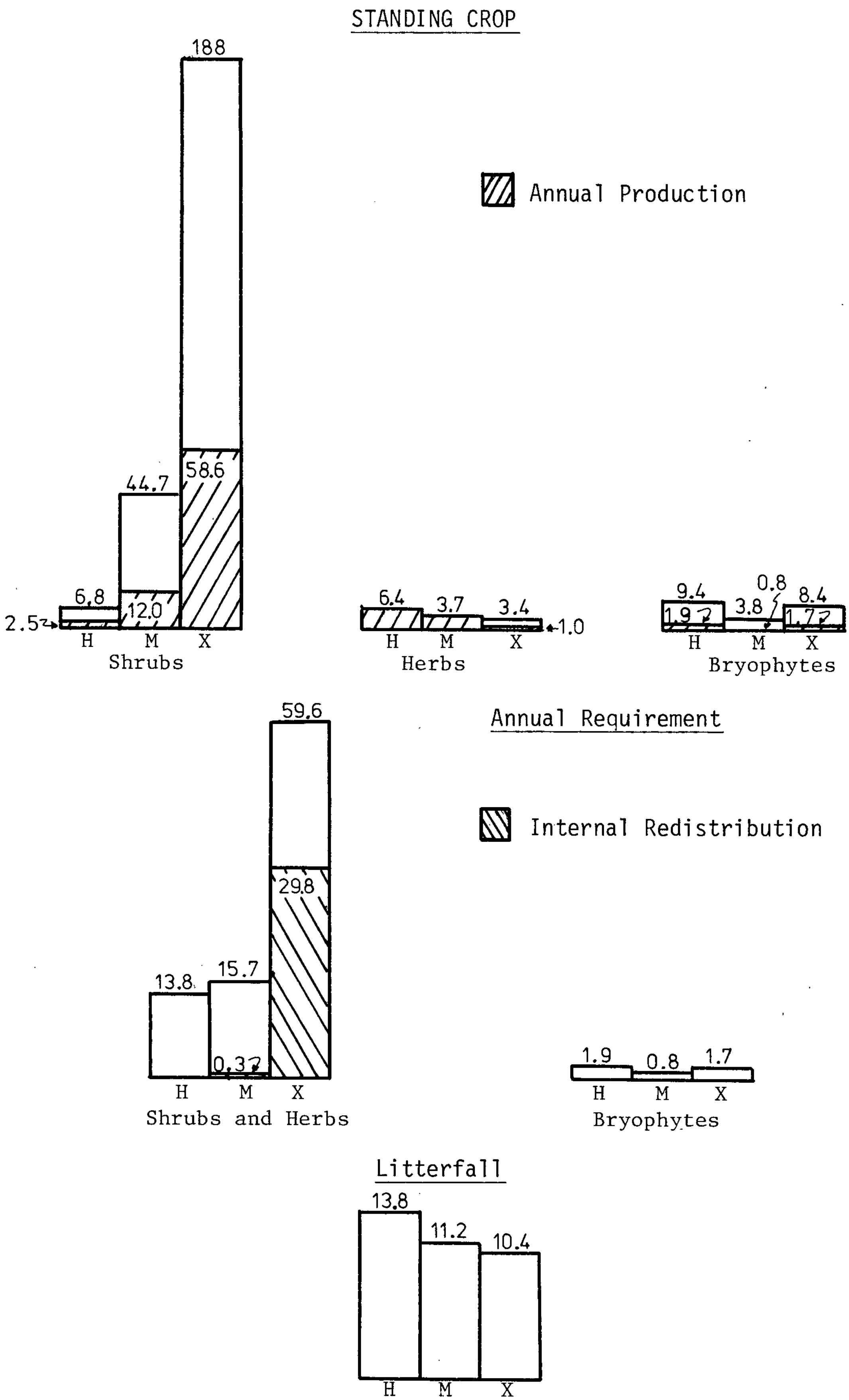


Figure 5.7. The understory manganese cycle (values in mg/m$^2$).

magnesium cycles in two respects. Firstly, the quantity of manganese in shrub annual production is relatively high compared to the moss and herbaceous species. This can be attributed to the high concentrations of manganese in *Vaccinium* sp. (Tables 3.10, 3.11, 3.12, and Appendix 6). Secondly, a large portion (50 percent) of the annual requirement on the xeric site can be accounted for by internal redistribution (Figure 5.7). This could be explained if the availability of manganese to woody perennials were relatively low, resulting in a cycling pattern similar to that of nitrogen and phosphorus (Figures 5.2, 5.3, and 5.7).

The zinc and copper cycles (Figures 5.8 and 5.9, respectively) appear to be similar to the potassium cycle (Figure 5.6). Although internal redistribution does satisfy a portion of the annual requirement, it is intermediate in importance when compared to the nitrogen or phosphorus and calcium or magnesium cycles. One point worthy of mention is the increased importance of bryophytes in accumulation, especially in comparison to the herbaceous strata. For example, if we look at the ratio of herbaceous to bryophyte standing crop for the elements studied on the hygric site, the following values can be calculated:

| Element | Herbaceous Standing Crop / Bryophyte Standing Crop |
|---|---|
| Nitrogen | 3.22 |
| Phosphorus | 5.10 |
| Calcium | 3.72 |

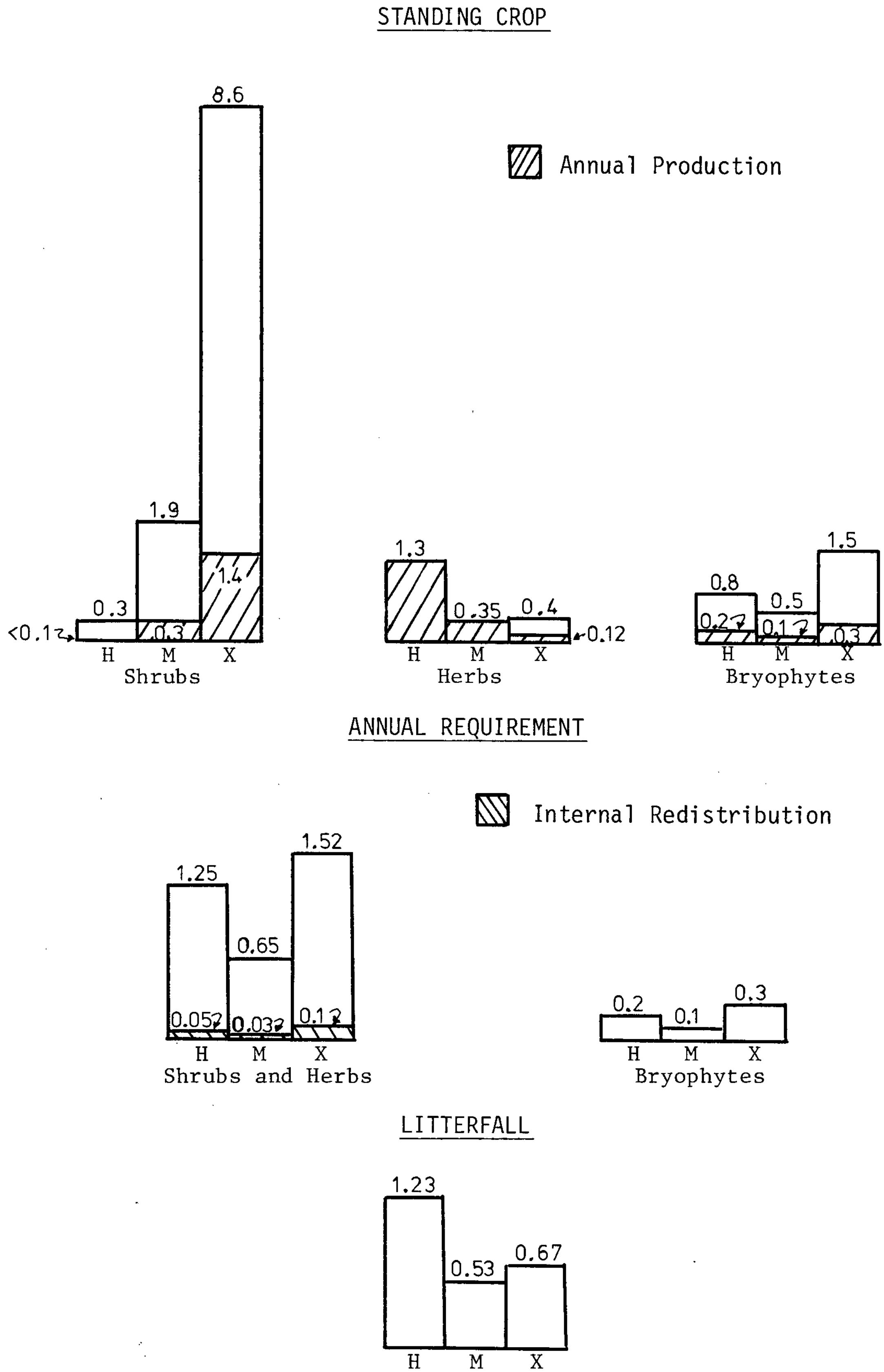


Figure 5.8. The understory zinc cycle (values in mg/m$^2$).

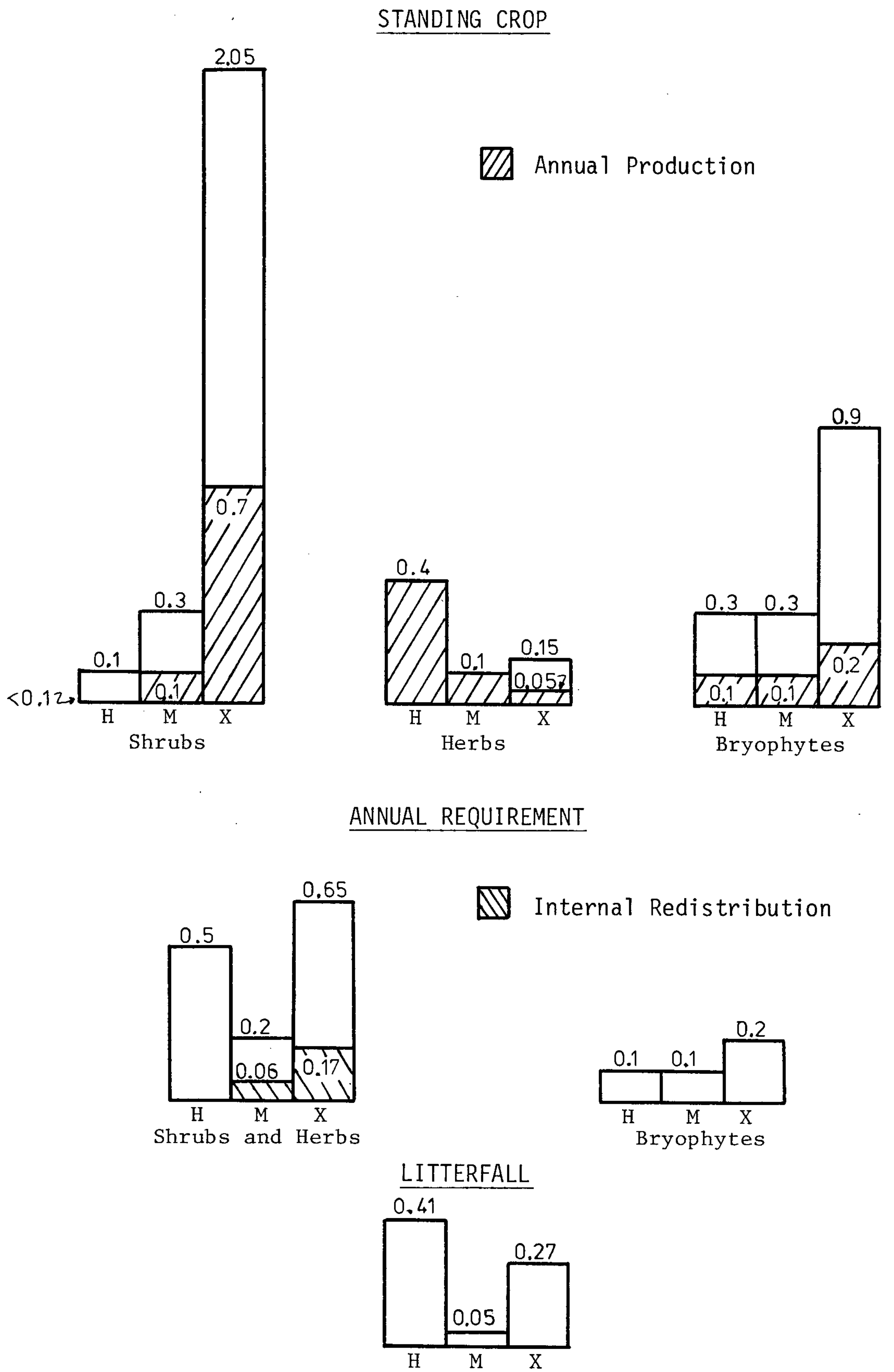


Figure 5.9. The understory copper cycle (values in mg/m$^2$).

| Element | Herbaceous Standing Crop / Bryophyte Standing Crop |
|---|---|
| Magnesium | 5.77 |
| Potassium | 7.96 |
| Manganese | 0.68 |
| Zinc | 1.62 |
| Copper | 1.33 |

The ratio is greater than 3.0 for the five macronutrients and less than 1.75 for the micronutrients. Any future studies of micronutrient cycles must seriously consider the role of bryophytes.

This concludes the basic description of the understory nutrient cycle. We will now consider the functional role of this cycle within the ecosystem.

## 5.3 Discussion

The role of understory vegetation in a community must be considered within the framework of the entire ecosystem, because the community itself has evolved as an integrated unit (Whittaker and Woodwell, 1972). An ecosystem can be considered as an energy processing system (Lindeman, 1942; Odum, 1971; Golley, 1972), whose basic strategy[1]

[1] The use of the term strategy in this context does not imply that the ecosystem has the power to choose one of several alternative structures or functional mechanisms; but that of the several alternatives one particular one has evolved through natural selection. Thus, the "nutrient cycling strategy" observed in a particular ecosystem or ecosystem component is the particular pathway of nutrient movement that has evolved in that ecosystem or ecosystem component to the exclusion of alternative "strategies" or alternative pathways.

is to maintain maximum persistent organic matter (Whittaker and Woodwell, 1972; O'Neill et al., 1975). If there is an adequate supply of energy and water, then maximum persistent organic matter should be determined by the supply of nutrients and the nutrient recycling mechanisms present (O'Neill et al., 1975). For many ecosystems, the most important consideration regarding ecosystem function is the efficiency of the recycling mechanisms.

A number of levels of recycling can be identified corresponding to the polycyclic nature of ecosystem functioning (Ovington, 1968; Switzer and Nelson, 1972; Day and McGinty, 1975) within the framework of environmental variability. The environment plays a key role within each level in determining the complexity and structure of the recycling mechanisms. Considering just biotic recycling we can use the previous description of understory nutrient cycles as an example.

Biotic recycling of nutrients can occur through a combination of internal and external mechanisms. The importance of each mechanism will depend upon the nutrient (Figures 5.2 through 5.9; Switzer and Nelson, 1972) and its scarcity in the environment (Turner, 1977). Nitrogen and phosphorus are two nutrients which are relatively scarce. Thus, as a result of this scarcity the understory must obtain a significant portion (approximately 50 percent) of its annual requirement from internal sources (Figures 5.2 and 5.3). In contrast, cations, which are generally more available in the external environment, are cycled outside of the plant to a much greater degree (Figures 5.4 through 5.9; Switzer and

Nelson, 1972; Turner and Singer, 1976).

Internal redistribution is a process which has a selective advantage when nutrients are in short supply (Figures 5.2, 5.3; Turner, 1977). The shortage might be the result of either a lack of the nutrient in the environment or of a slow rate of decomposition and thus a low availability. Considering the three sites studied, nutrient scarcity is probably the result of differential rates of decomposition. If this is true, then the decomposition rates for the three sites should be inversely related to the relative rates of internal redistribution. This assumption was found to be appropriate. The proportion of internal redistribution was found to be least on the mesic site (Figures 5.2 and 5.3) where decomposition of *Abies* and *Tsuga* needle litter was found to be greatest (Kimmins, unpublished data). The pattern for the hygric and xeric sites is slightly different dependent on the species. Decomposition of *Tsuga* needle litter was inversely related to nitrogen redistribution, while decomposition of *Abies* needle litter was inversely related to phosphorus redistribution. Final analysis of these two trends will have to wait until the completion of the decomposition study.

It can now be hypothesized that in the functioning of these ecosystems, the major role of the herbaceous and shrub understory is the maintenance of a supply of nutrients in a readily available form. Although this hypothesis cannot be tested by the data obtained in this study, evidence has been presented in the literature which supports the hypothesis. Tappeiner and Alm (1975) have shown that understory vegetation increases pine litter decomposition, and Gosz et al. (1972) have suggested a similar process. Also, as the proportion of understory internal redistribution of nitrogen increases we find that:

1) understory production increases
2) understory litterfall increases
3) the percentage removal of nitrogen by understory vegetation from overstory throughfall increases
4) bryophyte biomass increases

Although the four factors are not totally independent, they do indicate an increase in the quantities of nutrients circulated within the understory.

Assuming that an ecosystem is an energy processing system (Lindeman, 1942; Odum, 1971; Golley, 1972) whose basic strategy is the maintainance of maximum persistent organic matter (Whittaker and Woodwell, 1972; O'Neil et al., 1975), and that maintainance of the organic matter will be achieved through the currently most efficient means of energy processing (Margalef, 1968); then maximum organic matter can be most efficiently maintained by large individuals which require relatively small quantities of nutrients to produce a given quantity of organic matter. The most efficient utilization of nutrient resources is achieved by the overstory tree strata (Table 5.1, Mälkönen, 1974).

Because most nutrients would be exhausted in a very short period of time if recycling did not occur, the decomposition process is an extremely important part of the nutrient cycle. Since overstory

TABLE 5.1

Nutrient Utilization Per Unit of Dry Matter

Produced (g nutrient per kg dry matter)

| Strata and Forest Type | Ref. | Nutrient | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | N | P | Ca | Mg | K | Mn | Zn | Cu |
| Understory | | | | | | | | | |
| Hygric | A | 71.6 | 7.2 | 13.4 | 5.1 | 92.7 | 0.6 | 0.1 | 0.04 |
| Mesic | A | 25.8 | 2.2 | 5.1 | 2.5 | 20.1 | 1.2 | 0.05 | 0.02 |
| Xeric | A | 22.4 | 1.7 | 4.5 | 2.0 | 9.6 | 1.1 | 0.03 | 0.01 |
| Understory | | | | | | | | | |
| Scots Pine | B | 8.9 | 0.88 | 3.60 | | 3.99 | | | |
| Scots Pine | B | 7.59 | 0.86 | 3.21 | | 2.94 | | | |
| Scots Pine | B | 11.34 | 1.36 | 4.06 | | 6.42 | | | |
| Overstory | | | | | | | | | |
| Scots Pine | B | 4.60 | 0.64 | 2.29 | | 2.65 | | | |
| Scots Pine | B | 4.38 | 0.52 | 1.42 | | 2.00 | | | |
| Scots Pine | B | 4.35 | 0.50 | 1.81 | | 2.41 | | | |
| Understory | | | | | | | | | |
| Birch Stand | C | 14.32 | 1.85 | 6.37 | | 16.97 | | | |
| Overstory | | | | | | | | | |
| Birch Stand | C | 9.34 | 0.83 | 3.95 | | 4.82 | | | |

References: A, this study; B, Mälkönen, 1974; C, Mälkönen, 1977.

litterfall decomposition, as measured by litter bag studies, proceeded at a faster rate on the mesic site than on the hygric or xeric sites (Kimmins, unpublished data), we can assume that the environment was more favorable to decomposition on the mesic site. Also, the faster decomposition on the mesic site was associated with a slightly higher quantity of tree crown biomass (small branches, twigs, and foliage) (Appendix 4), and a greater percentage of overstory cover (Table 2.3). The greater percent cover will allow for greater energy utilization and greater production as indicated by the MAI (Table 2.3) and litterfall quantities (Table 4.4)..

Understory vegetation plays a more important role in nutrient recycling on the hygric and xeric sites as a result of the slower rates of decomposition of overstory litterfall which will result in slower nutrient turnover on these two sites. As a result of this slower turnover the availability of nutrients will decrease, and this is reflected in the relative rates of internal redistribution already discussed. The slower decomposition rates will also result in the necessity for the system to develop alternative mechanisms for maintaining a supply of available nutrients. It has already been hypothesized that this alternative mechanism is provided by the understory vegetation.

Although the preceding model is not directly testable by the scientific method, a number of hypotheses can be generated which, if not proven false, would give support to the model, and specifically to the hypothesized role of understory vegetation. They are:

1) The seasonal input of understory litter helps to promote the decomposition of overstory litter.
   1a) Removal of understory vegetation will result in an increase in the relative importance of internal cycling within the overstory strata as a result of decreased litter decomposition.
2) Relative rates of internal redistribution in overstory and understory vegetation are directly related.
3) Environmental conditions for heterotrophic decomposition are most favorable on mesic sites within similar climatic regions.

In summary, we can say that within the framework of the proposed model, the role of the understory has been shown to be very important in maintaining a readily available nutrient supply on sites where slow rates of heterotrophic decomposition result in a scarcity of nutrients. This role in nutrient availability will then help to maintain the maximum persistent organic matter of the community and thus the stability of the community (Webster et al., 1975).

## 5.4 Summary

The understory nutrient cycles for three plant associations within the Mt. Hemlock biogeoclimatic zone are described. It was shown that the nitrogen and phosphorus cycles are relatively conservative and function in a "closed" (e.g. large amounts of internal redistribution and seasonal removal of nitrogen and phosphorus from throughfall) manner. In contrast, the calcium and magnesium cycles are more "open" (e.g. little internal redistribution and seasonal leaching of calcium and magnesium) in character. The potassium cycle was found to be intermediate between the "open" and "closed" cycles; although there was a significant amount of internal redistribution some potassium was also leached from the understory vegetation. Brief descriptions were presented for the manganese, zinc, and copper cycles.

A generalized model of ecosystem function was presented in which the role of nutrient recycling was seen to be of primary importance. It was assumed that the basic strategy of an ecosystem was to maintain maximum persistent organic matter. Recycling of nutrients is necessary to maintain this persistent biomass. Two mechanisms of recycling, litter decomposition and internal redistribution appear to be inversely related. It also appears that the quantity of understory vegetation is inversely proportional to the amount of internal redistribution and it is hypothesized that understory vegetation helps to maintain a supply of nutrients in an easily decomposable form (e.g. readily available) and that this helps to maintain the stability of the community (Webster et al., 1975).

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# APPENDIX 1

## Plant Species Abbreviations

# SPECIES CODES

| Code | Species |
|---|---|
| ARLA | *Arnica latifolia* |
| ATFF | *Athyrium filix-femina* |
| BRHO | *Brachythecium holzingeri* |
| CAME | *Cassiope mertensiana* |
| CANI | *Carex nigricans* |
| DIPA | *Dicranum pallidisetum* |
| GYDR | *Gymnocarpium dryopteris* |
| HYCI | *Hypnum circinale* |
| OSCH | *Osmorhiza chilensis* |
| PHEM | *Phyllodoce empetriformis* |
| PLLA | *Plagiothecium laetum* |
| PTCA | *Ptilidium californicum* |
| RHNU | *Rhyzomnium nudum* |
| RHRO | *Rhytidiopois robusta* |
| ROAL | *Rhododendron albiflorum* |
| RUPE | *Rubus pedatus* |
| RUSP | *Rubus spectabilis* |
| SOSI | *Sorbus sitchensis* |
| STAM | *Streptopus amplexifolius* |
| STRO | *S. roseus* |
| STST | *S. streptopoides* |
| TITR | *Tiarella trifoliata* |
| TIUN | *T. unifoliata* |
| VAAL | *Vaccinium alaskaense* |
| VAME | *V. membranaceum* |
| VAOV | *V. ovalifolium* |
| VAPA | *V. parvifolium* |
| VASI | *Valeriana sitchensis* |
| VASP | *Vaccinium sp.* |
| VEVI | *Veratrum viride* |
| VIGL | *Viola glabella* |
| LICO | *Listera cordata* (L.) R. Br. |
| LIVE | *Hepaticae* sp. |
| LYPO | *Lycopodium* sp. |

# APPENDIX 2

## Climatic Data for the Study Sites

Average Monthly Minimum, Maximum and Mean Temperatures

for the Study Sites During the Study Period

| Month and Year | Station One | | | Station Two | | |
|---|---|---|---|---|---|---|
| | Minimum Temp °C | Maximum Temp °C | Mean Temp °C | Minimum Temp °C | Maximum Temp °C | Mean Temp °C |
| 1975 | | | | | | |
| August | 6.7 | 10.9 | 8.8 | 6.2 | 12.1 | 9.1 |
| September | 8.7 | 13.7 | 11.2 | 7.0 | 14.5 | 10.8 |
| October | 1.1 | 3.3 | 2.2 | 0.7 | 3.6 | 2.1 |
| November | -4.0 | -1.3 | -2.7 | * | * | * |
| December | -4.3 | -1.3 | -2.8 | * | * | * |
| 1976 | | | | | | |
| January | -3.1 | -0.2 | -1.6 | -2.1[1] | 2.8[1] | 0.2[1] |
| February | -4.6 | -1.9 | -3.3 | -4.9 | -1.3 | -3.1 |
| March | -5.4 | -2.1 | -3.7 | -7.8[1] | -1.8[1] | -5.0[1] |
| April | -1.4 | 2.8 | 0.7 | * | * | * |
| May | 0.8 | 4.8 | 2.8 | 0.1 | 5.8 | 2.9 |
| June | 2.2 | 6.5 | 4.3 | 2.1 | 8.3 | 5.2 |
| July | 5.9 | 10.6 | 8.3 | 4.2 | 10.9 | 7.5 |
| August | 6.5 | 10.6 | 8.6 | 6.1 | 12.2 | 9.1 |
| September | 8.6 | 12.6 | 10.6 | 6.9 | 12.8 | 9.8 |
| October | 3.1 | 6.3 | 4.7 | 1.4 | 6.2 | 3.8 |
| November | 0.5 | 6.9 | 2.4 | -2.2 | 3.6 | 0.4 |
| December | -1.4 | 1.4 | -0.2 | -2.6 | 0.9 | -0.8 |
| 1977 | | | | | | |
| January | -2.9 | 0.2 | -1.3 | -3.9 | 1.2 | -1.4 |
| February | -1.4 | 1.4 | 0.0 | -2.2 | 2.6 | 0.2 |
| March | -5.0 | -1.2 | -3.2 | -5.9 | -0.6 | -3.3 |
| April | 0.3 | 4.9 | 2.6 | -0.4 | 6.2 | 2.9 |
| May | 0.8 | 4.7 | 2.7 | -0.1 | 5.3 | 2.6 |

* No data available.

[1] Based on one-half month's data.

Precipitation for the Study Period at an Adjacent Sampling Site

| Month | 1975 (cm) | 1976 (cm) | 1977 (cm) |
|---|---|---|---|
| January | | 24.00 | 12.09 |
| February | | 27.18 | 19.51 |
| March | | 34.16 | 16.87 |
| April | | 9.14 | 10.67 |
| May | | 15.32 | 16.36 |
| June | | 8.69 | 5.18 |
| July | | 8.36 | |
| August | 19.35 | 12.29 | |
| September | 1.02 | 13.94 | |
| October | 43.00 | 14.35 | |
| November | 38.07 | 15.37 | |
| December | 32.64 | 26.44 | |
| Total | | 209.24 | |

April Snow-course Measurements for Adjacent Areas

| Snow Course | Mean Snow Depth (cm) | Mean Water Equival. (mm) | Years of Data | 1975-1976 Snow Depth (cm) | 1975-1976 Water Equival. (mm) | 1976-1977 Snow Depth (cm) | 1976-1977 Water Equival. (mm) |
|---|---|---|---|---|---|---|---|
| Grouse Mountain | 316 | 1325 | 38 | 494 | 1325 | 165 | 625 |
| Hollyburn Mountain | 393 | 1621 | 30 | 630 | 2870 | 214 | 853 |
| Whistler Mountain | 226 | 888 | 7 | 265 | 848 | 89 | 292 |

Source of data: Province of British Columbia, Water Resources Service, Water Investigations Branch. Snow survey bulletin. Reports for 1936 to 1977 inclusive.

# APPENDIX 3

## Brief Soil Descriptions

## Hygric Site Soil Descriptions

| Pit 1 | | | Pit 2 | | |
|---|---|---|---|---|---|
| Horizon | Depth (cm) | Color | Horizon | Depth (cm) | Color |
| LFH | 4 - 0 | | LFH | 6 - 0 | |
| Ae | 0 - 6 | 7.5Yr 4/2 | Ahe | 0 - 6 | 2.5Yr 2.5/0 |
| Bhf | 7 - 20 | 5 Yr 3/2 | Bhf | 7 - 14 | 7.5Yr 3/2 |
| Bf | 21 - 40 | 5 Yr 3/4 | Bf | 15 - 22 | 5 Yr 3/3 |
| BC | 41 - 70 | 7.5Yr 4/4 | BC | 23 - 55 | 5 Yr 3/2 |
| C | 71 - | | C | 55 - | |

Mesic Site Soil Descriptions

| Pit 1 | | | Pit 2 | | |
|---|---|---|---|---|---|
| Horizon | Depth (cm) | Color | Horizon | Depth (cm) | Color |
| LFH | 15 - 0 | | LFH | 20 - 0 | |
| Bhf | 0 - 15 | 5Yr 2.5/2 | Ah | 0 - 8 | 5 Yr 2.5/1 |
| R | | | Ae | 9 - 18 | 7.5Yr 4/2 |
| | | | Bhf | 19 - 38 | 2.5Yr 3/4 |
| | | | BC | 39 - | |

Xeric Site Soil Descriptions

| Pit 1 | | | Pit 2 | | |
|---|---|---|---|---|---|
| Horizon | Depth (cm) | Color | Horizon | Depth (cm) | Color |
| LF | 0 - 3 | | LFH | 12 - 0 | |
| H | 4 - 48 | 2.5Yr 2.5/0 | Ae | 0 - 4 | 5Yr 4/1 |
| R | 48 - | | Bhf | 5 - 7 | 5Yr 5/6 |
| | | | Bf | 6 - 22 | 5Yr 3/4 |
| | | | C | 23 | |

# APPENDIX 4

## Overstory Biomass and Nutrient Standing Crop by Species for the Three Mt. Hemlock Study Sites

Overstory Biomass ($g/m^2$) by Component for Three Plant Associations of the Mt. Hemlock Biogeoclimatic Zone

| Component and Species | Ecosystem Type | | |
|---|---|---|---|
| | Streptopo - Abietetum amabilis | Abieto - Tsugetum mertensianae | Vaccinio - Tsugetum mertensianae |
| Wood | | | |
| M. h. | 1.42 | 2.58 | 13.74 |
| P. s. f. | 40.67 | 36.07 | 4.83 |
| Y. c. | | | 1.39 |
| Total | 42.09 | 38.65 | 19.96 |
| Bark | | | |
| M. h. | 0.37 | 0.80 | 4.94 |
| P. s. f. | 9.00 | 7.25 | 1.47 |
| Y. c. | | | 0.58 |
| Total | 9.37 | 8.05 | 6.99 |
| Big Branches | | | |
| M. h. | 0.13 | 0.28 | 1.98 |
| P. s. f. | 4.68 | 3.95 | 0.93 |
| Y. c. | | | 0.25 |
| Total | 4.81 | 4.23 | 3.16 |
| Small Branches | | | |
| M. h. | 0.15 | 0.22 | 1.14 |
| P. s. f. | 1.09 | 1.34 | 0.32 |
| Y. c. | | | 0.06 |
| Total | 1.24 | 1.56 | 1.52 |
| Twigs and Foliage | | | |
| M. h. | 0.71 | 0.17 | 1.33 |
| P. s. f. | 2.66 | 3.02 | 0.55 |
| Y. c. | | | 0.54 |
| Total | 3.37 | 3.19 | 2.42 |
| Totals | | | |
| M. h. | 2.78 | 4.05 | 23.13 |
| P. s. f. | 58.10 | 51.63 | 8.10 |
| Y. c. | | | 2.82 |
| Total | 60.88 | 55.68 | 34.05 |

M. h. = Mountain hemlock
P. s. f. = Pacific silver fir
Y. c. = Alaska yellow cedar

Nutrient Standing Crop ($g \cdot m^{-2}$) for Five Nutrients in the Streptopo - Abietetum amabilis Plant Association

| Component and Species | Nutrient N | P | K | Ca | Mg |
|---|---|---|---|---|---|
| **Wood** | | | | | |
| M. h. | 0.71 | 0.28 | 0.99 | 0.99 | 0.28 |
| P. s. f. | 20.34 | 4.07 | 24.40 | 24.40 | 4.07 |
| Total | 21.05 | 4.35 | 25.39 | 4.35 | 19.33 |
| **Bark** | | | | | |
| M. h. | 0.75 | 0.22 | 0.41 | 1.12 | 0.07 |
| P. s. f. | 24.30 | 4.50 | 13.50 | 43.20 | 2.70 |
| Total | 25.05 | 4.72 | 13.91 | 44.32 | 2.77 |
| **Big Branches** | | | | | |
| M. h. | 0.16 | 0.04 | 0.09 | 0.21 | 0.03 |
| P. s. f. | 7.02 | 0.94 | 4.21 | 14.51 | 0.94 |
| Total | 7.18 | 0.98 | 4.30 | 14.72 | 0.97 |
| **Small Branches** | | | | | |
| M. h. | 0.25 | 0.06 | 0.13 | 0.27 | 0.04 |
| P. s. f. | 2.40 | 0.33 | 1.31 | 3.16 | 0.33 |
| Total | 2.65 | 0.39 | 1.44 | 3.43 | 0.37 |
| **Twigs and Foliage** | | | | | |
| M. h. | 5.25 | 0.71 | 2.34 | 1.99 | 0.50 |
| P. s. f. | 19.68 | 2.66 | 8.78 | 11.70 | 1.86 |
| Total | 24.93 | 3.37 | 11.12 | 13.69 | 2.36 |
| **Totals** | | | | | |
| M. h. | 7.12 | 1.31 | 3.96 | 4.58 | 0.92 |
| P. s. f. | 73.74 | 12.5 | 52.20 | 96.97 | 9.90 |
| Total | 80.86 | 13.81 | 56.16 | 101.6 | 10.82 |

M. h. = Mountain hemlock
P. s. f. = Pacific silver fir

Nutrient Standing Crop ($g \cdot m^{-2}$) for Five Nutrients in the Abieto - Tsugetum mertensianae Plant Association

| Component and Species | Nutrient | | | | |
|---|---|---|---|---|---|
| | N | P | K | Ca | Mg |
| Wood | | | | | |
| M. h. | 1.29 | 0.52 | 1.81 | 1.81 | 0.52 |
| P. s. f. | 18.04 | 3.61 | 21.64 | 21.64 | 3.61 |
| Total | 19.33 | 4.13 | 23.45 | 23.45 | 4.13 |
| Bark | | | | | |
| M. h. | 1.60 | 0.48 | 0.88 | 2.40 | 0.16 |
| P. s. f. | 19.58 | 3.63 | 10.88 | 34.80 | 2.18 |
| Total | 21.18 | 4.11 | 11.76 | 37.20 | 2.34 |
| Big Branches | | | | | |
| M. h. | 0.34 | 0.08 | 0.20 | 0.45 | 0.06 |
| P. s. f. | 5.93 | 0.79 | 3.56 | 12.25 | 0.79 |
| Total | 6.27 | 0.87 | 3.76 | 12.70 | 0.85 |
| Small Branches | | | | | |
| M. h. | 0.37 | 0.09 | 0.20 | 0.40 | 0.07 |
| P. s. f. | 2.95 | 0.40 | 1.61 | 3.89 | 0.40 |
| Total | 3.32 | 0.49 | 1.81 | 4.29 | 0.47 |
| Twigs and Foliage | | | | | |
| M. h. | 1.26 | 0.17 | 0.56 | 0.48 | 0.12 |
| P. s. f. | 22.35 | 3.02 | 9.97 | 13.29 | 2.11 |
| Total | 23.61 | 3.19 | 10.53 | 13.77 | 2.23 |
| Totals | | | | | |
| M. h. | 4.86 | 1.34 | 3.65 | 5.54 | 0.93 |
| P. s. f. | 68.85 | 11.45 | 47.66 | 85.87 | 9.09 |
| Total | 73.71 | 12.79 | 51.31 | 91.41 | 10.02 |

M. h. = Mountain hemlock
P. s. f. = Pacific silver fir

Nutrient Standing Crop ($g \cdot m^{-2}$) for Five Nutrients in the Vaccinio - Tsugetum mertensianae Plant Association

| Component and Species | N | P | K | Ca | Mg |
|---|---|---|---|---|---|
| Wood | | | | | |
| M. h. | 6.87 | 2.75 | 9.62 | 9.62 | 2.75 |
| P. s. f. | 2.42 | 0.48 | 2.90 | 2.90 | 0.48 |
| Y. c. | 0.83 | 0.14 | 0.70 | 1.67 | 0.14 |
| Total | 10.12 | 3.37 | 13.22 | 14.19 | 3.37 |
| Bark | | | | | |
| M. h. | 9.88 | 2.96 | 5.43 | 14.82 | 0.99 |
| P. s. f. | 3.97 | 0.74 | 2.21 | 7.06 | 0.44 |
| Y. c. | 1.86 | 0.41 | 1.45 | 3.36 | 0.29 |
| Total | 15.71 | 4.11 | 9.09 | 25.24 | 1.72 |
| Big Branches | | | | | |
| M. h. | 2.38 | 0.59 | 1.39 | 3.17 | 0.40 |
| P. s. f. | 1.40 | 0.19 | 0.84 | 2.88 | 0.19 |
| Y. c. | 0.38 | 0.05 | 0.23 | 1.60 | 0.05 |
| Total | 4.16 | 0.83 | 2.46 | 7.65 | 0.64 |
| Small Branches | | | | | |
| M. h. | 1.94 | 0.46 | 1.03 | 2.05 | 0.34 |
| P. s. f. | 0.70 | 0.10 | 0.38 | 0.93 | 0.10 |
| Y. c. | 0.14 | 0.02 | 0.08 | 0.49 | 0.02 |
| Total | 2.78 | 0.58 | 1.49 | 3.47 | 0.46 |
| Twigs and Foliage | | | | | |
| M. h. | 9.84 | 1.33 | 4.39 | 3.72 | 0.93 |
| P. s. f. | 4.07 | 0.55 | 1.82 | 2.42 | 0.39 |
| Y. c. | 4.00 | 0.43 | 1.89 | 2.00 | 0.38 |
| Total | 17.91 | 2.31 | 8.10 | 8.14 | 1.70 |
| Totals | | | | | |
| M. h. | 30.91 | 8.09 | 21.86 | 33.38 | 5.41 |
| P. s. f. | 12.56 | 2.06 | 8.15 | 16.19 | 1.60 |
| Y. c. | 7.21 | 1.05 | 4.35 | 9.12 | 0.88 |
| Total | 50.68 | 11.20 | 34.36 | 58.69 | 7.89 |

M. h. = Mountain hemlock
P. s. f. = Pacific silver fir
Y. c. = Alaska yellow cedar

# APPENDIX 5

## Understory Biomass and Productivity Relationships for Various Ecosystems Reported in the Literature

Understory Biomass and Productivity Relationships for Forest Type IA9A

| Species | Type | Country | Age | Layer | Biomass | | Productivity | | | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $g \cdot m^{-2}$ | Percent of Overstory Biomass | $g \cdot m^{-2} \cdot yr^{-1}$ | Percent of Understory Biomass | Percent of Overstory Productivity | |
| Pseudotsuga menziesii | N | USA | 30 | 7 | 1100.0 | 29.60 | | | | (1) |
| Pseudotsuga menziesii | N | USA | 32 | 7 | 320.0 | 9.60 | | | | (1) |
| Pseudotsuga menziesii | N | USA | 38 | 7 | 130.0 | 1.50 | | | | (1) |
| Pseudotsuga menziesii | N | USA | 38 | 7 | 180.0 | 1.20 | | | | (1) |
| Pseudotsuga menziesii | N | USA | 22 | 1 | 764.0 | 11.80 | | | | (2) |
| Pseudotsuga menziesii | N | USA | 30 | 1 | 507.0 | 6.60 | | | | (2) |
| Pseudotsuga menziesii | N | USA | 42 | 1 | 424.0 | 3.30 | | | | (2) |
| Pseudotsuga menziesii | N | USA | 73 | 1 | 275.0 | 1.30 | | | | (2) |
| Pseudotsuga menziesii | N | USA | 95 | 1 | 120.0 | | | | | (2) |
| Pseudotsuga menziesii | P | USA | 42 | 1 | 339.0 | | | | | (2) |
| Sequoia sempervirens-flat | N | USA | N | 2 | 0.3 | | | 13.30 | | (3) |
| | | | | 3 | 9.0 | | 9.0 | 100.00 | 0.60 | |
| | | | | 6 | 6.0 | | | | | |
| | | | | 1 | 15.3 | 0.01 | | | | |

IA9A (Cont'd.)

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Sequoia sempervirens-slope | N | USA | N | 2 | 15.0 | 0.01 | 1.2 | 8.00 | 0.10 | (3) |
| | | | | 3 | 30.0 | 0.03 | 30.0 | 100.00 | 2.40 | |
| | | | | 1 | 45.0 | 0.04 | 31.2 | 69.30 | 2.50 | |
| Pseudotsuga-menziesii-Tsuga heterophylla | N | USA | 100 | 2 | 619.0 | 0.80 | | | | (37) |
| | | | | 3 | 136.0 | 0.20 | | | | |
| | | | | 1 | 755.0 | 1.00 | | | | |
| Abies procera-Pseudotsuga menziesii | N | USA | 115 | 2 | 150.0 | 0.20 | | | | (37) |
| | | | | 3 | 2.0 | | | | | |
| | | | | 1 | 152.0 | 0.20 | | | | |
| Pseudotsuga menziesii | N | Canada | 17 | 1 | 391.3 | 6.03 | | | | (38) |

## Understory Biomass and Productivity Relationships for Forest Type IA9B

| Species | Type | Country | Age | Layer | Biomass g·m$^{-2}$ | Biomass Percent of Overstory Biomass | Productivity g·m$^{-2}$·yr$^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Pine forest (10) | N | USA | N | 2 | 140.0 | 0.80 | 47.0 | 33.60 | 5.70 | (4) |
| | | | | 4 | 11.8 | 0.10 | | | | |
| | | | | 1 | 151.8 | 0.90 | | | | |
| Pinus taeda-P. ellottii | P | USA | 4-5 | 1 | 190.0 | 27.10 | 180.0 | 94.70 | 29.10 | (5) |
| Pinus taeda-P. ellottii | P | USA | 6-7 | 1 | 190.0 | 15.10 | 90.0 | 47.40 | 7.00 | (5) |
| Pinus taeda | P | USA | 8 | 1 | 20.0 | 1.00 | 20.0 | 100.00 | 1.70 | (5) |
| Pinus taeda | P | USA | 10 | 1 | 20.0 | 0.30 | 20.0 | 100.00 | 1.00 | (5) |
| Pinus taeda | P | USA | 11 | 1 | 20.0 | 0.20 | 20.0 | 100.00 | 1.30 | (5) |
| Pinus radiata | N | AUSTRL. | 3 | 1 | 510.0 | | | | | (6) |
| Pinus radiata | N | AUSTRL. | 12 | 1 | 400.0 | | | | | (6) |
| Pinus sylvestris | N | AUSTRL. | 28 | 1 | 200.0 | | | | | (7) |
| Pinus sylvestris | N | AUSTRL. | 28 | 1 | 100.0 | | | | | (8) |
| Pinus sylvestris | N | AUSTRL. | 47 | 1 | 700.0 | | | | | (9) |
| Pinus nigra | N | AUSTRL. | 46 | 1 | 680.0 | | | | | (9) |
| Pinus sylvestris | N | FINLAND | 28 | 2 | 110.0 | 6.10 | 32.0 | 29.10 | 13.10 | (10) |
| | | | | 3 | 1.0 | | 1.0 | 100.00 | 0.40 | |
| | | | | 8 | 166.0 | 9.30 | 56.0 | 33.70 | 22.90 | |
| | | | | 1 | 277.0 | 15.40 | 89.0 | 32.10 | 36.30 | |
| Pinus sylvestris | N | FINLAND | 47 | 2 | 170.0 | 4.10 | 37.0 | 21.80 | 9.10 | (10) |
| | | | | 8 | 141.0 | 3.40 | 44.0 | 31.20 | 10.80 | |
| | | | | 1 | 311.0 | 7.50 | 81.0 | 26.00 | 19.90 | |
| Pinus sylvestris | N | FINLAND | 45 | 2 | 63.0 | 0.80 | 21.0 | 33.30 | 4.10 | (10) |
| | | | | 3 | 9.0 | 0.10 | 9.0 | 100.00 | 1.80 | |
| | | | | 8 | 261.0 | 3.40 | 94.0 | 36.00 | 18.40 | |
| | | | | 1 | 333.0 | 4.40 | 124.0 | 37.20 | 24.30 | |
| Pinus sylvestris (+C) | N | SWEDEN | 17 | 2 | 309.0 | | 89.0 | 28.80 | | (11) |
| | | | | 6 | 154.0 | | | | | |
| | | | | 1 | 463.0 | | | | | |

| Species | Type | Country | Age | Layer | Biomass: $g \cdot m^{-2}$ | Biomass: Percent of Overstory Biomass | Productivity: $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity: Percent of Understory Biomass | Productivity: Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Pinus sylvestris (-C) | N | SWEDEN | 17 | 2 | 55.0 | | 13.0 | 23.60 | | (11) |
| | | | | 6 | 93.0 | | | | | |
| | | | | 1 | 154.0 | | | | | |
| Pinus sylvestris | N | SWEDEN | 135 | 2 | 196.0 | | 137.0 | 69.90 | | (11) |
| | | | | 6 | 251.0 | | | | | |
| | | | | 1 | 447.0 | | | | | |
| Vaccinio-pinetum typicum | N | POLAND | V | 1 | 263.1 | | 118.9 | 45.20 | | (12) |
| Vaccinio-pinetum +CD | N | POLAND | V | 1 | 223.4 | | 86.2 | 38.60 | | (12) |
| Pine Forest (11) | N | USA | N | 2 | 120.0 | 0.90 | 40.0 | 33.30 | 4.20 | (4) |
| | | | | 3 | 1.7 | | | | | |
| | | | | 6 | 2.3 | | | | | |
| | | | | 1 | 124.0 | 1.00 | | | | |
| Pine heath (12) | N | USA | N | 2 | 580.0 | 11.00 | 173.0 | 30.40 | 82.40 | (4) |
| | | | | 3 | 17.1 | 0.70 | | | | |
| | | | | 6 | 1.5 | 0.10 | | | | |
| | | | | 1 | 598.6 | 11.80 | | | | |
| Pinus muricata-Rhododendron | N | USA | 90 | 2 | 1470.0 | 3.70 | 161.0 | 11.00 | 17.80 | (3) |
| | | | | 3 | 22.0 | 0.10 | 22.0 | 100.00 | 2.40 | |
| | | | | 1 | 1492.0 | 3.80 | 183.0 | 12.30 | 20.20 | |
| Pinus ponderosa | | | | | | | | | | |
| | N | USA | 95 | 2 | 10.0 | 0.06 | 1.8 | 18.00 | 0.30 | (13) |
| P. syrobiformis | | | | 3 | 3.9 | 0.02 | 4.2 | 107.70 | 0.70 | |
| | | | | 6 | 2.8 | 0.01 | | | | |
| | | | | 1 | 16.7 | 0.10 | | | | |

IA9B (Cont'd.)

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Pinus Ponderosa | N | USA | 140 | 2 | 2.5 | 0.01 | 0.3 | 15.20 | 0.07 | (13) |
| | | | | 3 | 4.5 | 0.02 | 4.5 | 100.00 | 0.80 | |
| | | | | 1 | 7.0 | 0.03 | 4.8 | 69.70 | 0.87 | |
| Pinus ponderosa-Quercus | N | USA | 145 | 2 | 36.0 | 0.20 | 4.4 | 12.20 | 0.90 | (13) |
| | | | | 3 | 0.4 | | 0.4 | 100.00 | 0.09 | |
| | | | | 1 | 36.4 | 0.20 | 4.8 | 12.30 | 0.99 | |

Understory Biomass and Productivity Relationships for Forest Type IA9C

| Species | Type | Country | Age | Layer | Biomass: $g \cdot m^{-2}$ | Biomass: Percent of Overstory Biomass | Productivity: $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity: Percent of Understory Biomass | Productivity: Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Picea-Abies | N | USSR | 24 | 2 | 890.0 | 12.90 | | | | (14) |
| Picea-Abies | N | USSR | 93 | 3 | 100.0 | 0.40 | | | | (14) |
| Picea-Abies | P | JAPAN | 46 | 2 | 20.0 | | | | | (15) |
| | | | | 3 | 120.0 | | | | | |
| | | | | 1 | 140.0 | 1.60 | | | | |
| Picea-Abies | P | JAPAN | 46 | 2 | 20.0 | | | | | (15) |
| | | | | 3 | 160.0 | | | | | |
| | | | | 1 | 180.0 | 1.10 | | | | |
| Picea-Abies (open) | N | CANADA | 87 | 2 | 175.0 | 6.10 | | | | (16) |
| | | | | 9 | 267.0 | 9.40 | | | | |
| | | | | 1 | 442.0 | 15.50 | | | | |
| Picea-Abies (dense) | N | CANADA | 64 | 2 | 18.0 | 1.50 | | | | (16) |
| | | | | 9 | 112.0 | 9.50 | | | | |
| | | | | 1 | 130.0 | 11.00 | | | | |
| Pinus banksiana | N | USA | 50 | 2 | 437.0 | 3.70 | | | | (17) |
| Pinus banksiana | N | USA | 70 | 2 | 375.0 | 3.50 | | | | (17) |
| Pinus banksiana | N | USA | 90 | 2 | 917.0 | 7.20 | | | | (17) |
| Abies amabilis | N | USA | 175 | 10 | 177.0 | 0.40 | | | | (18) |
| | | | | 5 | 190.0 | 0.40 | | | | |
| | | | | 1 | 367.0 | 0.80 | | | | |
| Picea-Abies | N | USA | N | 2 | 96.0 | 0.30 | 22.0 | 22.90 | 2.19 | (4) |
| | | | | 3 | 22.1 | 0.10 | | | | |
| | | | | 6 | 40.4 | 0.20 | | | | |
| | | | | 1 | 158.5 | 0.60 | | | | |
| Tsuga-Fagus (cove) | N | USA | N | 2 | 2300.0 | 13.50 | 231.0 | 10.00 | 21.00 | (19) & (4) |
| | | | | 3 | 2.1 | | | | | |
| | | | | 6 | 13.3 | 0.10 | | | | |
| | | | | 1 | 2315.4 | 13.60 | | | | |

| | | | | | Biomass | | Productivity | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Type | Country | Age | Layer | $g \cdot m^{-2}$ | Percent of Overstory Biomass | $g \cdot m^{-2} \cdot yr^{-1}$ | Percent of Understory Biomass | Percent of Overstory Productivity | Reference |
| Picea-Rhododendron | N | USA | N | 2 | 2100.0 | 7.00 | 202.0 | 9.60 | 33.10 | (4) |
| | | | | 6 | 74.9 | 0.20 | | | | |
| | | | | 1 | 2174.9 | 7.20 | | | | |
| Tsuga forest | N | USA | N | 2 | 6.0 | | 1.2 | 20.00 | 0.10 | (4) |
| | | | | 3 | 31.8 | 0.10 | | | | |
| | | | | 6 | 0.6 | | | | | |
| | | | | 1 | 38.4 | 0.10 | | | | |
| Picea-Abies forest | N | USA | N | 2 | 10.0 | | 4.0 | 40.00 | 0.40 | (4) |
| | | | | 3 | 20.0 | 0.10 | | | | |
| | | | | 6 | 22.9 | 0.10 | | | | |
| | | | | 1 | 52.9 | 0.20 | | | | |
| Tsuga-Rhododendron | N | USA | N | 2 | 2100.0 | 4.30 | 172.0 | 8.20 | 20.20 | (4) |
| | | | | 6 | 12.3 | | | | | |
| | | | | 1 | 2112.3 | 4.30 | | | | |
| Abies lasiocarpa | N | USA | 115 | 2 | 64.0 | 0.20 | 8.5 | 13.30 | 1.00 | (13) |
| | | | | 3 | | | | 100.00 | | |
| | | | | 1 | 64.0 | 0.20 | 8.5 | 13.30 | 1.00 | |
| Abies concolor | N | USA | 100 | 2 | 2.1 | 0.01 | 0.3 | 14.80 | 0.30 | (13) |
| | | | | 3 | 10.8 | 0.03 | 10.8 | 100.00 | 1.00 | |
| | | | | 6 | 3.6 | 0.01 | | | | |
| | | | | 1 | 16.5 | 0.05 | | | | |
| Pseudotsuga-menziesii-Abies concolor | N | USA | 170 | 2 | 676.0 | 0.90 | 93.0 | 13.80 | 8.70 | (13) |
| | | | | 3 | 0.6 | | 0.6 | 100.00 | 0.06 | |
| | | | | 6 | 4.5 | | | | | |
| | | | | 1 | 681.1 | 0.90 | | | | |

IA9C (Cont'd.)

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Pseudotsuga menziesii | N | USA | 225 | 2 | 59.0 | 0.10 | 7.1 | 12.00 | 0.90 | (13) |
| | | | | 3 | 0.1 | | 0.1 | 100.00 | 0.02 | |
| | | | | 6 | 0.7 | | | | | |
| | | | | 1 | 59.8 | 0.10 | | | | |
| Tsuga-Picea sitchensis | N | USA | 110 | 2 | 369.0 | | | | | (37) |
| | | | | 3 | 34.0 | | | | | |
| | | | | 1 | 403.0 | | | | | |

Understory Biomass and Productivity Relationships for Forest Type IA9D

| Species | Type | Country | Age | Layer | Biomass | | Productivity | | | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $g \cdot m^{-2}$ | Percent of Overstory Biomass | $g \cdot m^{-2} \cdot yr^{-1}$ | Percent of Understory Biomass | Percent of Overstory Productivity | |
| Picea-moss (N. Taiga) | N | USSR | 200 | 2 | 9.0 | 0.10 | | | | (20) |
| | | | | 4 | 474.0 | 1.70 | | | | |
| | | | | 1 | 483.0 | 1.80 | | | | |
| Picea-moss (For. Tundra) | N | USSR | 200+ | 2 | 280.0 | 2.50 | | | | (20) |
| | | | | 4 | 238.0 | 2.20 | | | | |
| | | | | 1 | 518.0 | 4.70 | | | | |
| Abies (North Slope) | N | USA | N | 2 | 1.0 | | 0.6 | 60.00 | 0.10 | (4) |
| | | | | 3 | 100.6 | 0.50 | | | | |
| | | | | 6 | 61.9 | 0.30 | | | | |
| | | | | 1 | 163.5 | 0.80 | | | | |
| Abies (South Slope) | N | USA | N | 2 | 10.0 | 0.10 | 2.6 | 26.00 | 0.40 | (4) |
| | | | | 3 | 12.0 | | | | | |
| | | | | 6 | 315.7 | 1.60 | | | | |
| | | | | 1 | 337.7 | 1.70 | | | | |

Understory Biomass and Productivity Relationships for Forest Type IB1A

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Quercus stellata-Q. marilandica | N | USA | 80 | 1 | 141.0 | 0.80 | 30.0 | 21.30 | 2.40 | (21) |

## Understory Biomass and Productivity Relationships for Forest Type IB2C

| Species | Type | Country | Age | Layer | Biomass | | Productivity | | | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $g \cdot m^{-2}$ | Percent of Overstory Biomass | $g \cdot m^{-2} \cdot yr^{-1}$ | Percent of Understory Biomass | Percent of Overstory Productivity | |
| Cladonio-pinetum | N | POLAND | N | 3 | 23.0 | | 18.0 | 78.0 | | (22) |
| | | | | 4 | 170.0 | | | | | |
| Circaeo-alnetum | N | POLAND | N | 3 | 107.5 | | 107.5 | 100.00 | | (23) |
| Tilio-Carpinetum stachyetosum | N | POLAND | N | 3 | 72.0 | | 72.0 | 100.00 | | (24) |
| Tilio-Carpinetum typicum | N | POLAND | N | 3 | 72.0 | | 58.0 | 80.50 | | (24) |
| Fagus grandifolia (North) | N | USA | N | 2 | 1.0 | 0.01 | 2.0 | 200.00 | 0.03 | (4) |
| | | | | 3 | 47.6 | 0.40 | | | | |
| | | | | 6 | 1.5 | 0.01 | | | | |
| | | | | 1 | 50.1 | 0.42 | | | | |
| Quercus-Pinus | N | USA | N | 2 | 159.0 | 2.50 | 60.7 | 38.30 | 7.60 | (25) |
| Quercus prinus (Heath) | N | USA | N | 2 | 2400.0 | 60.00 | 318.0 | 13.30 | 159.00 | (19) & (4) |
| | | | | 3 | 1.4 | | | | | |
| | | | | 6 | 24.5 | 0.60 | | | | |
| | | | | 1 | 2425.9 | 60.60 | | | | |
| Acer (Mixed) | N | USA | N | 2 | 1.0 | | | | | (4) |
| | | | | 3 | 34.6 | 0.10 | | | | |
| | | | | 6 | 13.2 | | | | | |
| | | | | 1 | 48.8 | 0.10 | 0.2 | 20.00 | | |
| Liriodendron (Mixed) | N | USA | N | 2 | 25.0 | 0.10 | 8.0 | 32.00 | 0.40 | (4) |
| | | | | 3 | 3.2 | | | | | |
| | | | | 6 | 8.6 | 0.05 | | | | |
| | | | | 1 | 36.8 | 0.20 | | | | |
| Quercus-Carya | N | USA | N | 2 | 5.0 | | 2.0 | 40.00 | 0.20 | (4) |
| | | | | 3 | 0.8 | | | | | |
| | | | | 1 | 5.8 | | | | | |

| Species | Type | Country | Age | Layer | Biomass: $g \cdot m^{-2}$ | Biomass: Percent of Overstory Biomass | Productivity: $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity: Percent of Understory Biomass | Productivity: Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Aesculus octandra (Cove) | N | USA | N | 2 | 7.0 | | 1.5 | 21.40 | 0.10 | (4) |
| | | | | 3 | 37.5 | 0.10 | | | | |
| | | | | 6 | 20.3 | 0.04 | | | | |
| | | | | 1 | 64.8 | 0.14 | | | | |
| Fagus grandifolia (South) | N | USA | N | 2 | 10.0 | 0.10 | 4.0 | 40.00 | 0.50 | (4) |
| | | | | 3 | 17.2 | 0.10 | | | | |
| | | | | 6 | 0.2 | | | | | |
| | | | | 1 | 27.4 | 0.20 | | | | |
| Pino-quercetum | N | POLAND | N | 3 | 53.3 | | 16.6 | 31.10 | | (26) |
| | | | | 4 | 2.7 | | 2.7 | 100.00 | | |
| | | | | 1 | 56.0 | | 19.3 | 34.40 | | |
| Vaccinio-myrtilli pinetum | N | POLAND | 42 | 3 | 31.8 | | 13.1 | 41.10 | | (26) |
| | | | | 4 | 47.5 | | 16.0 | 33.70 | | |
| | | | | 1 | 79.3 | | 29.1 | 36.70 | | |
| Tilio-Carpinetum | N | POLAND | N | 3 | 30.7 | | 16.7 | 54.50 | | (26) |
| | | | | 4 | 0.9 | | 0.3 | 33.30 | | |
| | | | | 1 | 31.6 | | 17.0 | 53.90 | | |
| Quercus-Pinus | N | USA | 125 | 2 | 17.0 | 0.10 | 6.7 | 39.40 | 1.50 | (13) |
| | | | | 3 | 3.4 | 0.03 | 4.0 | 117.60 | 0.90 | |
| | | | | 6 | 0.2 | | | | | |
| | | | | 1 | 20.6 | 0.20 | | | | |

Understory Biomass and Productivity Relationships for Forest Type IB3A

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Acer-Quercus (Dense) | N | CANADA | 67 | 2 | 49.0 | 0.90 | | | | (16) |
| | | | | 9 | 211.0 | 4.00 | | | | |
| | | | | 1 | 260.0 | 4.90 | | | | |
| Acer-Quercus (Open) | N | CANADA | 62 | 2 | 224.0 | 3.60 | | | | (16) |
| | | | | 9 | 220.0 | 3.40 | | | | |
| | | | | 1 | 435.0 | 7.00 | | | | |
| Quercus-Populus (Dense) | N | USA | 52 | 2 | 157.0 | 2.10 | | | | (16) |
| | | | | 9 | 200.0 | 2.60 | | | | |
| | | | | 1 | 357.0 | 4.70 | | | | |
| Alnus-Betula | N | ENGLAND | 45 | 1 | 122.0 | | 102.0 | 83.60 | | (27) |
| Carici-elongatae alnetum | N | POLAND | N | 3 | 98.7 | | 55.7 | 56.40 | | (26) |
| | | | | 4 | 0.7 | | 0.2 | 29.80 | | |
| | | | | 1 | 99.4 | | 55.9 | 56.30 | | |
| Ilex-Sassafras-Amelanchie | N | USA | 250 | 2 | 69.8 | 0.60 | 10.2 | 14.60 | | (28) |
| | | | | 3 | 43.0 | 0.40 | 16.9 | 39.30 | | |
| | | | | 11 | 522.0 | 4.60 | 44.1 | 8.40 | | |
| | | | | 1 | 634.8 | 5.60 | 71.2 | 11.20 | | |
| Quercus-Carya | N | USA | 40 | 2 | 2.0 | 0.02 | 1.0 | 56.70 | 0.20 | (29) |
| | | | | 3 | 16.0 | 0.20 | 16.0 | 100.00 | 2.70 | |
| | | | | 1 | 18.0 | 0.22 | 17.0 | 95.40 | 2.90 | |
| Circaeo-alnetum | N | POLAND | N | 3 | 225.0 | | 225.0 | 100.00 | | (24) |
| Liriodendron tulipifera | N | USA | N | 2 | 20.0 | 0.10 | 7.0 | 35.00 | 0.30 | (4) |
| | | | | 3 | 1.5 | | | | | |
| | | | | 6 | 4.9 | | | | | |
| | | | | 1 | 26.4 | 0.10 | | | | |

IB3A (Cont'd.)

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Fagus | N | DENMARK | 85 | 1 | 169.4 | | 160.1 | 94.50 | | (30) |
| Fagus-Betula-Acer (Lower) | N | USA | N | 2 | | | 2.4 | | | (31) |
| | | | | 3 | | | 3.7 | | | |
| Fagus-Betula-Acer (Middle) | N | USA | N | 2 | | | 2.2 | | | (31) |
| | | | | 3 | | | 4.1 | | | |
| Fagus-Betula-Acer (Upper) | N | USA | N | 2 | | | 4.3 | | | (31) |
| | | | | 3 | | | 12.8 | | | |
| Quercus prinus | N | USA | N | 2 | 250.0 | 0.60 | 64.0 | 25.60 | 4.60 | (4) |
| | | | | 3 | 0.8 | | | | | |
| | | | | 6 | 3.4 | | | | | |
| | | | | 1 | 254.2 | 0.60 | | | | |
| Populus tremuloides | N | USA | N | 2 | 6.0 | | | | | (32) |
| | | | | 3 | 88.3 | | | | | |
| | | | | 12 | 23.4 | | | | | |
| | | | | 1 | 117.7 | | | | | |
| Acer-Populus-betula | N | USA | N | 2 | 2.7 | | | | | (32) |
| | | | | 3 | 36.9 | | | | | |
| | | | | 12 | 23.4 | | | | | |
| | | | | 1 | 63.0 | | | | | |
| Betula | N | USA | N | 2 | 1.3 | | | | | (32) |
| | | | | 3 | 19.7 | | | | | |
| | | | | 12 | 30.0 | | | | | |
| | | | | 1 | 51.0 | | | | | |
| Fagus-Betula-Acer | N | USA | N | 2 | 0.6 | | | | | (32) |
| | | | | 3 | 6.3 | | | | | |
| | | | | 12 | 30.7 | | | | | |
| | | | | 1 | 37.6 | | | | | |

## Understory Biomass and Productivity Relationships for Forest Type IB3B

| Species | Type | Country | Age | Layer | Biomass $g \cdot m^{-2}$ | Biomass Percent of Overstory Biomass | Productivity $g \cdot m^{-2} \cdot yr^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Quercus robur-oxalis | N | SWEDEN | 158 | 2 | 1740.0 | 9.50 | 302.0 | 17.20 | 36.00 | (33) |
| | | | | 3 | 20.0 | 0.20 | 77.0 | 385.00 | 9.30 | |
| | | | | 1 | 1760.0 | 9.70 | 379.0 | 21.50 | 45.30 | |
| Betula | N | SWEDEN | 60 | 2 | 189.0 | | 20.6 | 10.90 | 7.30 | (35) & (34) |
| | | | | 8 | | | 142.8 | | 50.80 | |
| | | | | 1 | | | 163.4 | | 58.10 | |
| Betula (Mixed) | N | SWEDEN | 100 | 2 | 290.0 | | 158.3 | 54.60 | 37.40 | (35) & (34) |
| | | | | 8 | | | 109.2 | | 25.80 | |
| | | | | 1 | | | 267.5 | | 63.20 | |
| Quercus-Corlyus | N | SWEDEN | 100 | 2 | 653.0 | | 108.5 | 16.60 | 26.80 | (35) & (34) |
| | | | | 8 | | | 70.1 | | 17.30 | |
| | | | | 1 | | | 178.6 | | 44.10 | |
| Quercus rubra | N | USA | N | 2 | 200.0 | 1.50 | 40.0 | 20.00 | 5.30 | (4) |
| | | | | 3 | 38.5 | 0.30 | | | | |
| | | | | 6 | 0.2 | | | | | |
| | | | | 1 | 238.7 | 1.80 | | | | |
| Quercus rubra-Q. alba | N | USA | N | 2 | 1700.0 | 19.80 | 57.0 | 3.40 | 11.40 | (4) |
| | | | | 3 | 10.6 | 0.10 | | | | |
| | | | | 1 | 1710.6 | 19.90 | | | | |

Understory Biomass and Productivity Relationships for Forest Type IIA2A

| | | | | | Biomass | | Productivity | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Type | Country | Age | Layer | $g \cdot m^{-2}$ | Percent of Overstory Biomass | $g \cdot m^{-2} \cdot yr^{-1}$ | Percent of Understory Biomass | Percent of Overstory Productivity | Reference |
| Vaccinio Uliginosi-pinetum | N | POLAND | 60 | 2 | 157.8 | | 97.5 | 61.80 | | (36) |
| | | | | 3 | 11.4 | | 5.9 | 51.80 | | |

Understory Biomass and Productivity Relationships for Forest Type IIB3A

| Species | Type | Country | Age | Layer | Biomass g·m$^{-2}$ | Biomass Percent of Overstory Biomass | Productivity g·m$^{-2}$·yr$^{-1}$ | Productivity Percent of Understory Biomass | Productivity Percent of Overstory Productivity | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| Frangulo-Salicetum | N | POLAND | N | 3 | 210.0 | | 210.0 | 100.00 | | (24) |

References: (1) Heilman, 1961; (2) Long and Turner, 1975; (3) Westman and Whittaker, 1975; (4) Whittaker, 1966; (5) Nemeth, 1973; (6) Forrest and Ovington, 1970; (7) Ovington, 1959; (8) Ovington and Madgwick, 1959; (9) Ovington, 1962; (10) Malkonen, 1974; (11) Persson, 1975a; (12) Traczyk et al., 1973; (13) Whittaker and Niering, 1975; (14) Sonn, 1960; (15) Satoo, 1962; (16) Telfer, 1972; (17) Tappeiner and John, 1973; (18) Turner and Singer, 1976; (19) Whittaker, 1963; (20) Marchenko and Karlov, 1962; (21) Johnson and Risser, 1974; (22) Wojcik, 1970; (23) Aulak, 1970; (24) Traczyk, 1971; (25) Whittaker and Woodwell, 1969; (26) Traczyk, 1967; (27) Hughes, 1971; (28) Art, 1971; (29) Rochow, 1974; (30) Hughes, 1975; (31) Siccama et al., 1970; (32) Zavitkovski, 1976; (33) Andersson, 1970; (34) Hyttenborn, 1975; (35) Persson, 1975b; (36) Andersson, 1970; (37) Fujimori et al., 1976; (38) Weber, 1977.

# TABLE ABBREVIATIONS

Type

N - natural stand

P - plantation

Country

AUSTR. - Australia

Age

N - not available

Layer

1 - Total Aboveground Understory

2 - Shrub Layer

3 - Herb Layer

4 - Mosses

5 - Lichens

6 - Cryptogams

7 - Shrub and herbs

8 - Field Layer

9 - Ferns, Grasses, Mosses, and Lichens

10 - Shrubs, Herbs, and Mosses

11 - Lianas

12 - Sedges, Rushes, and Grasses

# APPENDIX 6

## Elemental Concentration Data for Sampled Species by Component in Three Mt. Hemlock Ecosystems at Various Sampling Dates Throughout the Study Period

Nutrient Concentrations of all Sampled Species in the Streptopo - Abietetum amabilis Plant Association Sampled During the Summer of 1975

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentration | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | N | P | Ca | Mg | K | Mn | Zn | Cu |
| | | | | ---------- | ---------- | ---------- | % | ---------- | ---------- | -- ppm | -- |
| ARLA | All | 10 | 14.89 (1.45)+ | 3.65 (0.37) | 0.38 (0.06) | 0.80 (0.12) | 0.24 (0.03) | 5.57 (0.77) | 0.03 (0.01) | 50 (7) | 21 (5) |
| ATFF | All | 2 | 13.54 (0.93) | 4.13 (0.03) | 0.50 (0.07) | 0.24 (0.01) | 0.37 (0.00)# | 5.12 (0.38) | 0.01 (0.00) | 58 (5) | 25 (6) |
| GYDR | All | 6/9* | 10.26 (0.32) | 3.65 (0.44) | 0.33 (0.07) | 0.24 (0.01) | 0.37 (0.04) | 3.81 (0.12) | 0.03 (0.00) | 30 (3) | 13 (3) |
| OSCH | All | 5/6 | 16.06 (1.05) | 3.69 (0.21) | 0.37 (0.03) | 1.31 (0.19) | 0.26 (0.02) | 5.40 (0.33) | 0.04 (0.00) | 36 (3) | 18 (4) |
| RUPE | All | 5/1 | 7.88 | 3.20 (0.41) | 0.33 (0.06) | 0.38 | 0.42 | 2.30 | 0.08) | 67 | 14 |
| STAM | All | 7/4 | 16.17 (1.78) | 3.03 (0.19) | 0.35 (0.05) | 0.92 (0.24) | 0.20 (0.04) | 4.87 (1.69) | 0.02 (0.00) | 69 (13) | 16 (6) |
| STRO | All | 10 | 16.12 (1.08) | 3.14 (0.24) | 0.39 (0.06) | 0.93 (0.16) | 0.23 (0.03) | 5.90 (0.58) | 0.02 (0.01) | 59 (8) | 11 (3) |
| STST | All | 1 | 13.39 | 3.11 | 0.40 | 0.67 | 0.19 | 5.14 | 0.04 | 92 | 18 |
| TIUN | All | 10/5 | 11.26 (0.65) | 3.45 (0.43) | 0.35 (0.06) | 0.93 (0.10) | 0.29 (0.03) | 3.44 (0.27) | 0.04 (0.01) | 58 (6) | 16 (4) |
| VEVI | All | 10 | 13.10 (0.74) | 3.63 (0.54) | 0.38 (0.05) | 0.71 (0.16) | 0.18 (0.03) | 5.04 (0.33) | 0.01 (0.00) | 62 (16) | 24 (7) |
| VASI | All | 9/8 | 13.59 (0.79) | 3.53 (0.41) | 0.37 (0.03) | 0.72 (0.09) | 0.22 (0.02) | 5.29 (0.30) | 0.02 (0.00) | 40 (4) | 13 (3) |
| VIGL | All | 5/4 | 14.79 (1.50) | 4.06 (0.28) | 0.34 (0.02) | 0.60 (0.17) | 0.38 (0.04) | 5.77 (0.95) | 0.03 (0.01) | 55 (6) | 12 (2) |
| VASP | Leaf | 1 | 5.48 | 4.25 | 0.39 | 0.52 | 0.30 | 1.62 | 0.24 | 87 | 15 |

(Cont'd.)

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Elemental Concentration | | | | | | | |
| | | | | -------- % -------- | | | | | | -- ppm -- | |
| RUSP | Leaf | 3 | 5.61 (2.19) | 4.53 (0.05) | 0.40 (0.04) | 0.65 (0.02) | 0.36 (0.03) | 2.40 (0.38) | 0.08 (0.02) | 53 (5) | 20 (2) |
| VAPA | Leaf | 1 | 5.83 | 3.25 | 0.22 | 0.43 | 0.24 | 1.49 | 0.35 | 27 | 13 |
| VAAL | Leaf | 2 | 6.14 (0.06) | 3.94 (0.28) | 0.27 (0.02) | 0.73 (0.05) | 0.31 (0.02) | 1.46 (0.01) | 0.43 (0.10) | 21 (3) | 9 (1) |
| VASP | Stem | 1 | 2.19 | 0.94 | 0.11 | 0.18 | 0.06 | 0.40 | 0.13 | nd | nd |
| RUSP | Stem | 3 | 2.43 (0.71) | 0.96 (0.27) | 0.11 (0.04) | 0.27 (0.06) | 0.09 (0.02) | 0.56 (0.19) | 0.03 (0.02) | 42 (7) | 12 (2) |
| VAPA | Stem | 1 | 1.76 | 0.93 | 0.08 | 0.18 | 0.04 | 0.29 | 0.20 | 44 | 15 |
| VAAL | Stem | 2 | 1.13 (0.06) | 0.54 (0.02) | 0.05 (0.01) | 0.13 (0.01) | 0.04 (0.00) | 0.19 (0.01) | 0.15 (0.00) | 41 (4) | 7 (1) |

+ Standard deviation
* No. of samples for N and P/cations and % ash
nd Concentration not determined
# A standard deviation less than 0.01% or 1 ppm.

Nutrient Concentrations of all Sampled Species in the Streptopo - Abietetum amabilis Plant Association Sampled During the Summer of 1976

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | % | | | | | | ppm | |
| ARLA | All | 1 | 11.53 | 3.81 | 0.35 | 0.83 | 0.18 | 4.57 | 0.02 | 45 | 20 |
| ATFF | All | 3 | 12.36 | 4.13 | 0.38 | 0.41 | 0.41 | 5.10 | 0.02 | 45 | 17 |
| | | | (0.41)+ | (0.26) | (0.05) | (0.06) | (0.07) | (0.29) | (0.01) | (4) | (2) |
| GYDR | All | 2 | 9.75 | 4.10 | 0.29 | 0.27 | 0.30 | 4.30 | 0.02 | 35 | 15 |
| | | | (0.35) | (0.20) | (0.03) | (0.02) | (0.01) | (0.30) | (0.00)* | (0) | (0) |
| OSCH | All | 1 | 11.83 | 4.14 | 0.35 | 1.39 | 0.26 | 4.27 | 0.04 | 35 | 10 |
| RUPE | All | 1 | 6.61 | 3.28 | 0.28 | 0.39 | 0.33 | 2.20 | 0.11 | 60 | 15 |
| STAM | All | 1 | 13.18 | 3.79 | 0.26 | 0.83 | 0.19 | 5.44 | 0.02 | 72 | 3 |
| STRO | All | 2 | 14.61 | 3.11 | 0.37 | 0.92 | 0.21 | 5.68 | 0.02 | 70 | 20 |
| | | | (0.96) | (0.45) | (0.02) | (0.00) | (0.01) | (0.50) | (0.01) | (0) | (5) |
| TIUN | All | 2 | 9.02 | 3.89 | 0.31 | 0.97 | 0.27 | 3.31 | 0.03 | 50 | 13 |
| | | | (0.38) | (0.08) | (0.01) | (0.01) | (0.04) | (0.34) | (0.01) | (5) | (3) |
| VEVI | All | 3 | 20.77 | 3.94 | 0.35 | 0.52 | 0.12 | 5.11 | 0.01 | 47 | 14 |
| | | | (4.42) | (0.42) | (0.05) | (0.14) | (0.02) | (0.50) | (0.00) | (9) | (4) |
| VASI | All | 1 | 10.92 | 2.83 | 0.24 | 0.87 | 0.18 | 4.31 | 0.02 | 35 | 12 |
| VIGL | All | 1 | 13.76 | 4.52 | 0.29 | 0.69 | 0.33 | 5.58 | 0.03 | 60 | 7 |
| ARLA | Leaf | 1 | 12.77 | 5.80 | 0.37 | 1.18 | 0.28 | 4.79 | 0.03 | 50 | 25 |
| STRO | Leaf | 1 | 17.10 | 4.16 | 0.34 | 1.07 | 0.25 | 5.57 | 0.02 | 45 | 15 |

(Cont'd.)

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentration | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | N | P | Ca | Mg | K | Mn | Zn | Cu |
| | | | | % | | | | | | ppm | |
| TIUN | Leaf | 1 | 8.91 | 4.26 | 0.33 | 1.00 | 0.30 | 3.00 | 0.03 | 55 | 15 |
| VASI | Leaf | 1 | 9.29 | 6.14 | 0.37 | 0.84 | 0.24 | 3.40 | 0.02 | 55 | 12 |
| VEVI | Leaf | 2 | 10.40 | 6.27 | 0.37 | 0.95 | 0.19 | 3.40 | 0.02 | 45 | 28 |
| | | | (1.41) | (0.15) | (0.01) | (0.04) | (0.02) | (0.10) | (0.00) | (5) | (3) |
| ARLA | Stem | 1 | 16.63 | 1.88 | 0.22 | 0.79 | 0.11 | 6.87 | 0.02 | 50 | 17 |
| STRO | Stem | 1 | 17.79 | 1.45 | 0.27 | 0.42 | 0.10 | 6.66 | 0.01 | 90 | 12 |
| TIUN | Stem | 1 | 10.31 | 2.00 | 0.27 | 0.98 | 0.25 | 3.90 | 0.04 | 55 | 12 |
| VASI | Stem | 1 | 12.63 | 1.87 | 0.22 | 0.79 | 0.11 | 5.27 | 0.01 | 35 | 15 |
| VEVI | Stem | 2 | 31.96 | 2.04 | 0.23 | 0.40 | 0.06 | 5.14 | 0.01 | 50 | 15 |
| | | | (1.71) | (0.38) | (0.00) | (0.00) | (0.00) | (0.07) | (0.00) | (5) | (0) |
| LICO | All | 1 | | 4.18 | 0.38 | | | | | | |

\+ Standard deviation
* A standard deviation less than 0.01% or 1 ppm.

Nutrient Concentrations of all Sampled Species in the Abieto - Tsugetum mertensianae Plant Association Sampled During the Summer of 1975

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Elemental Concentration | | | | | | | |
| | | | | % | | | | | | ppm | |
| GYDR | All | 2/1* | 10.69 | 2.41 | 0.21 | 0.30 | 0.36 | 3.80 | 0.02 | 25 | 10 |
| | | | | (0.15)+ | (0.02) | | | | | | |
| RUPE | All | 9/1 | | 2.28 | 0.24 | 0.41 | 0.41 | 1.98 | 0.08 | 50 | 12 |
| | | | | (0.17) | (0.05) | | | | | | |
| STRO | All | 4/2 | 13.88 | 2.59 | 0.27 | 0.48 | 0.32 | 5.53 | 0.01 | 59 | 12 |
| | | | (0.43) | (0.13) | (0.03) | (0.12) | (0.04) | (0.41) | (0.00)# | (16) | (7) |
| STST | All | 4 | 14.05 | 2.41 | 0.32 | 0.51 | 0.18 | 5.73 | 0.03 | 69 | 5 |
| | | | (0.72) | (0.18) | (0.04) | (0.07) | (0.02) | (0.35) | (0.00) | (1) | (0) |
| TIUN | All | 2/1 | 9.65 | 2.25 | 0.23 | 0.85 | 0.34 | 3.25 | 0.07) | nd | nd |
| | | | | (0.13) | (0.00) | | | | | | |
| VEVI | All | 1 | 15.57 | 2.27 | 0.29 | 0.26 | 0.30 | 6.79 | 0.01 | nd | nd |
| SOSI | Leaf | 1 | 7.66 | 3.51 | 0.29 | 0.72 | 0.47 | 2.30 | 0.04 | 30 | 6 |
| VAAL | Leaf | 9 | 6.07 | 3.24 | 0.24 | 0.71 | 0.35 | 1.38 | 0.14 | 21 | 13 |
| | | | (0.41) | (0.14) | (0.01) | (0.09) | (0.04) | (0.20) | (0.05) | (2) | (2) |
| VAOV | Leaf | 8 | 6.03 | 3.41 | 0.25 | 0.76 | 0.38 | 1.21 | 0.14 | 21 | 9 |
| | | | (0.39) | (0.22) | (0.02) | (0.11) | (0.04) | (0.18) | (0.06) | (4) | (2) |
| VAME | Leaf | 4 | 5.51 | 3.05 | 0.23 | 0.64 | 0.33 | 1.17 | 0.10 | 20 | 10 |
| | | | (0.54) | (0.12) | (0.01) | (0.05) | (0.03) | (0.13) | (0.02) | (3) | (1) |
| VAPA | Leaf | 1 | 6.88 | 2.97 | 0.26 | 0.75 | 0.35 | 1.53 | 0.18 | 23 | 14 |
| SOSI | Stem | 1 | 1.86 | 0.62 | 0.10 | 0.33 | 0.10 | 0.35 | 0.09 | nd | nd |
| VAAL | Stem | 9/1 | | 0.65 | 0.07 | 0.13 | 0.06 | 0.23 | 0.09 | 44 | 6 |
| | | | | (0.12) | (0.01) | | | | | | |
| VAOV | Stem | 8 | 1.32 | 0.58 | 0.06 | 0.12 | 0.06 | 0.19 | 0.09 | 37 | 8 |

(Cont'd.)

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Elemental Concentration | | | | | | | |
| | | | | % | | | | | | ppm | |
| | | | (0.21) | (0.10) | (0.01) | (0.04) | (0.02) | (0.03) | (0.04) | (13) | (3) |
| VAME | Stem | 4/1 | | 0.65 | 0.07 | 0.11 | 0.06 | 0.23 | 0.09 | 46 | 6 |
| | | | | (0.09) | (0.01) | | | | | | |
| VAPA | Stem | 2/1 | | 0.77 | 0.07 | 0.12 | 0.06 | 0.22 | 0.10 | 53 | 9 |
| | | | | (0.03) | (0.00) | | | | | | |

\+ No. of samples for N and P/% ash and cations

\+ Standard deviation

# Standard deviation less than 0.03% or 1 ppm.

Nutrient Concentrations of all Sampled Species in the Abieto - Tsugetum mertensianae

Plant Association Sampled During the Summer of 1976

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentrations | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | N | P | Ca | Mg | K | Mn | Zn | Cu |
| | | | | % | | | | | | ppm | |
| LYPO | All | 1 | 5.54 | 1.06 | 0.12 | 0.09 | 0.07 | 2.03 | 0.01 | 34 | 8 |
| RUPE | All | 3 | 7.26 | 2.93 | 0.28 | 0.42 | 0.34 | 2.47 | 0.08 | 47 | 6 |
| | | | (0.54)* | (0.29) | (0.02) | (0.01) | (0.03) | (0.26) | (0.01) | (2) | (1) |
| STRO | All | 1 | 11.74 | 2.76 | 0.21 | 0.85 | 0.29 | 4.21 | 0.02 | 60 | 7 |
| STST | All | 1 | 15.92 | 3.05 | 0.31 | 0.66 | 0.13 | 5.71 | 0.03 | 70 | 10 |
| TIUN | All | 1 | 9.96 | 2.66 | 0.28 | 0.74 | 0.28 | 4.08 | 0.05 | 60 | 10 |
| VEVI | All | 1 | 11.71 | 2.95 | 0.28 | 0.65 | 0.18 | 3.47 | 0.005 | 25 | 10 |

* Standard deviation

Nutrient Concentrations of all Sampled Species in the Vaccinio - Tsugetum mertensianae Plant Association Sampled During the Summer of 1975

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Elemental Concentration | | | | | | | |
| | | | | ---------- % ---------- | | | | | | -- ppm -- | |
| CANI | All | 1 | 6.02 | 2.89 | 0.27 | 0.19 | 0.17 | 1.94 | 0.02 | 56 | 14 |
| CAME | All | 3 | 2.10 | 1.05 | 0.11 | 0.20 | 0.11 | 0.47 | 0.01 | 29 | 8 |
| | | | (0.24)+ | (0.04) | (0.02) | (0.00)* | (0.01) | (0.12) | (0.00) | (4) | (2) |
| PHEM | All | 6 | 2.00 | 0.97 | 0.10 | 0.15 | 0.13 | 0.48 | 0.04 | 35 | 6 |
| | | | (0.17) | (0.09) | (0.01) | (0.02) | (0.01) | (0.07) | (0.01) | (6) | (2) |
| RUPE | All | 2 | 7.32 | 2.05 | 0.25 | 0.48 | 0.45 | 2.26 | 0.04 | 56 | 10 |
| | | | (0.20) | (0.18) | (0.03) | (0.07) | (0.03) | (0.19) | (0.00) | (5) | (0) |
| ROAL | Leaf | 8 | 5.88 | 2.51 | 0.25 | 0.69 | 0.41 | 1.48 | 0.02 | 42 | 9 |
| | | | (0.83) | (0.38) | (0.05) | (0.12) | (0.04) | (0.30) | (0.01) | (6) | (3) |
| VAOV | Leaf | 4 | 5.62 | 3.23 | 0.26 | 0.73 | 0.39 | 1.11 | 0.04 | 25 | 15 |
| | | | (0.81) | (0.22) | (0.02) | (0.17) | (0.05) | (0.08) | (0.01) | (5) | (4) |
| VASP | Leaf | 9 | 5.52 | 2.94 | 0.25 | 0.65 | 0.34 | 1.21 | 0.07 | 25 | 16 |
| | | | (1.01) | (0.35) | (0.05) | (0.13) | (0.05) | (0.30) | (0.02) | (4) | (2) |
| VAAL | Leaf | 7 | 5.41 | 2.99 | 0.24 | 0.67 | 0.33 | 1.21 | 0.06 | 25 | 11 |
| | | | (0.72) | (0.30) | (0.03) | (0.10) | (0.04) | (0.22) | (0.03) | (6) | (2) |
| VAME | Leaf | 10 | 5.45 | 3.05 | 0.25 | 0.68 | 0.35 | 1.19 | 0.05 | 24 | 10 |
| | | | (0.55) | (0.32) | (0.02) | (0.06) | (0.04) | (0.26) | (0.02) | (4) | (3) |
| ROAL | Stem | 8 | 1.15 | 0.34 | 0.04 | 0.13 | 0.05 | 0.10 | 0.03 | 15 | 5 |
| | | | (0.09) | (0.06) | (0.00) | (0.01) | (0.01) | (0.02) | (0.01) | (3) | (0) |
| VAOV | Stem | 4 | 1.18 | 0.52 | 0.06 | 0.12 | 0.05 | 0.15 | 0.03 | 30 | 5 |
| | | | (0.13) | (0.04) | (0.01) | (0.03) | (0.01) | (0.02) | (0.01) | (9) | (0) |
| VASP | Stem | 9 | 1.39 | 0.61 | 0.07 | 0.14 | 0.06 | 0.18 | 0.06 | 38 | 6 |
| | | | (0.34) | (0.13) | (0.02) | (0.05) | (0.01) | (0.07) | (0.03) | (9) | (3) |
| VAAL | Stem | 7 | 1.00 | 0.49 | 0.05 | 0.12 | 0.04 | 0.14 | 0.04 | 24 | 3 |
| | | | (0.19) | (0.07) | (0.01) | (0.03) | (0.01) | (0.03) | (0.01) | (2) | (2) |
| VAME | Stem | 10 | 1.22 | 0.51 | 0.06 | 0.13 | 0.04 | 0.15 | 0.04 | 27 | 5 |
| | | | (0.11) | (0.06) | (0.01) | (0.02) | (0.01) | (0.04) | (0.01) | (6) | (1) |

+ Standard deviation

* A standard deviation less than 0.01% or 1 ppm.

Nutrient Concentrations of all Sampled Species on the Vaccinio - Tsugetum mertensianae Plant Association Sampled During the Summer of 1976

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentration N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | % | % | % | % | % | % | ppm | ppm |
| CANI | All | 2 | 5.29 | 2.85 | 0.20 | 0.13 | 0.18 | 1.94 | 0.01 | 55 | 17 |
| | | | (0.18)* | (0.04) | (0.03) | (0.02) | (0.03) | (0.14) | (0.00)+ | (1) | (0) |
| CAME | All | 4 | 2.20 | 1.17 | 0.10 | 0.25 | 0.12 | 0.45 | 0.02 | 26 | 8 |
| | | | (0.28) | (0.10) | (0.01) | (0.04) | (0.01) | (0.05) | (0.01) | (4) | (2) |
| LUPE | All | 1 | 2.80 | 1.70 | 0.16 | 0.23 | 0.12 | 0.86 | 0.01 | 62 | 16 |
| PHEM | All | 4 | 1.53 | 0.90 | 0.09 | 0.12 | 0.11 | 0.39 | 0.03 | 33 | 12 |
| | | | (0.20) | (0.08) | (0.01) | (0.02) | (0.01) | (0.06) | (0.01) | (3) | (2) |
| RUPE | All | 1 | 6.08 | 1.97 | 0.19 | 0.50 | 0.39 | 1.94 | 0.04 | 40 | 10 |

* Standard deviation

\+ Standard deviation less than 0.01% or 1 ppm.

Elemental Concentrations for the Shrub Components Sampled During the Summer of 1976

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentrations N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | % | % | % | % | % | % | ppm | ppm |
| RUSP | Leaf | 5 | 6.54 (0.24)* | 5.19 (0.50) | 0.31 (.05) | 0.70 (0.24) | 0.48 (0.03) | 1.86 (0.46) | 0.10 (0.02) | 40 (3) | 15 (3) |
| RUSP | Stem | 5 | 0.98 (0.19) | 0.83 (0.04) | 0.07 (0.01) | 0.17 (0.02) | 0.07 (0.01) | 0.28 (0.06) | 0.03 (0.02) | 34 (4) | 11 (3) |
| RUSP | Twig | 4 | 3.93 (0.51) | 1.34 (0.13) | 0.17 (0.05) | 0.35 (0.07) | 0.16 (0.00)+ | 1.51 (0.30) | 0.02 (0.00) | 51 (4) | 17 (3) |
| RUSP | Mort. | 1 | 1.19 | 1.05 | 0.06 | 0.31 | 0.06 | 0.14 | 0.07 | 40 | 17 |
| RUSP | Flfr | 1 | | 2.80 | 0.34 | | | | | | |
| RUSP | Pet. | 2 | 9.97 (0.29) | 1.52 (0.03) | 0.21 (0.04) | 0.53 (0.05) | 0.28 (0.02) | 4.34 (0.54) | 0.04 (0.01) | 55 (5) | 17 (4) |
| ROAL | Leaf | 5 | 5.63 (0.56) | 3.29 (0.20) | 0.24 (0.02) | 0.66 (0.08) | 0.37 (0.05) | 1.61 (0.20) | 0.01 (0.00) | 44 (4) | 9 (2) |
| ROAL | Stem | 5 | 0.88 (0.04) | 0.39 (0.04) | 0.04 (0.01) | 0.12 (0.01) | 0.05 (0.00) | 0.19 (0.02) | 0.01 (0.00) | 15 (3) | 5 (3) |
| ROAL | Twig | 2 | 3.34 (0.16) | 1.82 (0.00) | 0.21 (0.00) | 0.35 (0.02) | 0.17 (0.00) | 0.94 (0.04) | 0.01 (0.00) | 42 (2) | 17 (3) |
| ROAL | Mort. | 1 | 1.20 | 0.57 | 0.04 | 0.29 | 0.05 | 0.07 | 0.03 | 45 | 5 |
| ROAL | Flfr | 1 | 5.17 | 2.80 | 0.34 | 0.27 | 0.18 | 1.69 | 0.003 | 45 | 15 |
| VASP | Leaf | 6 | 5.77 (0.48) | 3.83 (0.26) | 0.25 (0.01) | 0.72 (0.06) | 0.29 (0.03) | 1.50 (0.17) | 0.20 (0.17) | 21 (5) | 15 (5) |
| VASP | Stem | 6 | 1.01 (0.29) | 0.52 (0.09) | 0.06 (0.01) | 0.12 (0.02) | 0.04 (0.01) | 0.21 (0.04) | 0.10 (0.08) | 33 (9) | 8 (5) |
| VASP | Twig | 3 | 3.31 (0.37) | 1.66 (0.20) | 0.19 (0.02) | 0.54 (0.02) | 0.13 (0.01) | 0.82 (0.07) | 0.25 (0.19) | 74 (19) | 19 (4) |
| VASP | Mort. | 3 | 0.63 (0.21) | 0.64 (0.11) | 0.05 (0.01) | 0.17 (0.03) | 0.02 (0.01) | 0.07 (0.03) | 0.05 (0.03) | 35 (14) | 14 (1) |

* Standard deviation
\+ A standard deviation less than 0.01% or 1 ppm.

Elemental Concentrations of Sampled Species in the Streptopo - Abietetum amabilis Site at the End of September, 1976

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Elemental Concentration | | | | | | | |
| | | | | ---------- | ---------- | % | ---------- | ---------- | ------- | ppm | ------- |
| ATFF | All | 2 | 12.99 | 3.81 | 0.24 | 0.56 | 0.37 | 5.50 | 244.9 | 48 | 19 |
| | | | (0.07)* | (0.04) | (0.04) | (0.10) | (0.05) | (0.01) | (6) | (2) | (2) |
| GYDR | All | 2 | 9.85 | 3.03 | 0.16 | 0.44 | 0.38 | 3.93 | 530.0 | 25 | 9 |
| | | | (0.15) | (0.11) | (0.00)+ | (0.03) | (0.03) | (0.08) | (10) | (0) | (0) |
| OSCH | All | 1 | 13.65 | 3.07 | 0.26 | 1.79 | 0.24 | 4.97 | 592.4 | 30 | 13 |
| RUPE | All | 2 | 6.42 | 2.80 | 0.23 | 0.47 | 0.39 | 2.24 | 1773.0 | 65 | 9 |
| | | | (0.23) | (0.25) | (0.01) | (0.02) | (0.04) | (0.14) | (622) | (15) | (4) |
| STRO | All | 1 | 11.33 | 2.17 | 0.19 | 1.26 | 0.19 | 4.51 | 381.1 | 60 | 11 |
| TIUN | All | 2 | 10.14 | 3.18 | 0.25 | 1.39 | 0.30 | 3.35 | 339.7 | 57 | 13 |
| | | | | (0.13) | (0.01) | (0.31) | (0.04) | (0.15) | (60) | (3) | (3) |
| VASI | All | 1 | 10.35 | 2.95 | 0.25 | 1.48 | 0.24 | 3.28 | 218.9 | 30 | 10 |
| VEVI | All | 2 | 16.83 | 2.43 | 0.17 | 1.09 | 0.14 | 4.44 | 184.6 | 33 | 9 |
| | | | (3.81) | (0.01) | (0.01) | (0.20) | (0.01) | (0.74) | (85) | (3) | (2) |
| VIGL | All | 1 | 18.02 | 3.62 | 0.21 | 1.46 | 0.51 | 7.41 | 630.6 | 80 | 15 |
| ARLA | Leaf | 1 | 13.17 | 4.09 | 0.27 | 1.56 | 0.32 | 5.39 | 628.7 | 45 | 15 |
| STAM | Leaf | 1 | 8.18 | 4.19 | 0.24 | 0.45 | 0.11 | 3.94 | 49.9 | 95 | 12 |
| STRO | Leaf | 1 | 13.70 | 3.25 | 0.23 | 1.51 | 0.23 | 5.56 | 486.6 | 45 | 14 |
| TIUN | Leaf | 1 | 11.16 | 3.96 | 0.25 | 1.37 | 0.44 | 3.92 | 291.5 | 50 | 10 |

(Cont'd.)

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentration N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | ---------- % | | | | ---------- | ------ ppm | | ------- |
| VASI | Leaf | 1 | 10.79 | 3.68 | 0.26 | 1.40 | 0.21 | 3.70 | 359.6 | 40 | 10 |
| VEVI | Leaf | 2 | 10.99 | 3.26 | 0.17 | 2.15 | 0.13 | 2.97 | 149.7 | 20 | 14 |
| | | | (0.35) | (0.23) | (0.00) | (0.26) | (0.00) | (0.04) | (29) | (0) | (1) |
| ARLA | Stem | 1 | 11.64 | 1.73 | 0.19 | 0.78 | 0.11 | 5.62 | 467.7 | 45 | 10 |
| STAM | Stem | 1 | 13.20 | 1.07 | 0.11 | 1.82 | 0.30 | 4.60 | 240.0 | 40 | 15 |
| STRO | Stem | 1 | 12.35 | 1.60 | 0.20 | 0.59 | 0.12 | 5.81 | 326.9 | 91 | 15 |
| TIUN | Stem | 1 | 11.27 | 1.80 | 0.21 | 1.14 | 0.27 | 4.59 | 608.2 | 60 | 6 |
| VASI | Stem | 1 | 9.45 | 1.69 | 0.18 | 1.11 | 0.15 | 3.68 | 318.4 | 35 | 5 |
| VEVI | Stem | 2 | 17.48 | 1.01 | 0.11 | 0.81 | 0.10 | 3.75 | 165.1 | 58 | 10 |
| | | | (6.17) | (0.18) | (0.03) | (0.12) | (0.03) | (0.94) | (95) | (18) | (0) |

* Standard deviation

\+ A standard deviation less than 0.01% or 1 ppm.

Elemental Concentrations of Sampled Species in the Streptopo - Abietetum amabilis Site at the End of October, 1976

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentration N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | % | % | % | % | % | ppm | ppm | ppm |
| ARLA | All | 1 | 14.45 | 2.84 | 0.21 | 2.51 | 0.31 | 3.19 | 394 | 47 | 17 |
| ATFF | All | 3 | 11.86 | 2.53 | 0.15 | 0.66 | 0.34 | 4.35 | 341 | 50 | 13 |
| | | | (3.70)* | (0.18) | (0.03) | (0.14) | (0.10) | (1.22) | (199) | (4) | (2) |
| GYDR | All | 1 | 9.70 | 2.33 | 0.13 | 0.74 | 0.37 | 3.00 | 480 | 30 | 10 |
| OSCH | All | 1 | 14.41 | 2.98 | 0.25 | 2.07 | 0.22 | 4.03 | 663 | 29 | 20 |
| RUPE | All | 1 | 7.21 | 2.69 | 0.27 | 0.62 | 0.37 | 2.20 | 1222 | 45 | 5 |
| STRO | All | 1 | 11.97 | 1.47 | 0.11 | 1.56 | 0.18 | 4.19 | 359 | 50 | 11 |
| TIUN | All | 2 | 11.27 | 2.83 | 0.22 | 1.61 | 0.40 | 3.34 | 314 | 50 | 5 |
| | | | (0.39) | (0.03) | (0.01) | (0.09) | (0.03) | (0.15) | (15) | (0)+ | (2) |
| VASI | All | 1 | 12.01 | 2.39 | 0.21 | 1.38 | 0.24 | 4.10 | 471 | 40 | 10 |
| VEVI | All | 1 | 13.04 | 1.49 | 0.09 | 1.75 | 0.20 | 4.18 | 508 | 45 | 2 |
| VEVI | Leaf | 1 | 12.29 | 2.11 | 0.12 | 2.64 | 0.15 | 2.30 | 380 | 20 | 10 |
| VEVI | Stem | 1 | 10.17 | 0.70 | 0.05 | 1.50 | 0.08 | 2.69 | 199 | 95 | 5 |
| STST | All | 1 | | 1.83 | 0.14 | | | | | | |

* Standard deviation
\+ A standard deviation of less than 0.01% or 1 ppm.

Elemental Concentrations of Sampled Species on the Abieto - Tsugetum mertensianae Site at the End of September, 1976

| Species Code | Component | No. of Samples | % Ash Content | Elemental Concentration | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | N | P | Ca | Mg | K | Mn | Zn | Cu |
| | | | | % | | | | | ppm | | |
| LYPO | All | 1 | 6.30 | 1.61 | 0.17 | 0.18 | 0.07 | 2.34 | 90 | 45 | 27 |
| RUPE | All | 4 | 6.98 (0.54)* | 2.63 (0.27) | 0.25 (0.02) | 0.44 (0.05) | 0.42 (0.05) | 2.34 (0.16) | 1038 (48) | 43 (3) | 8 (3) |
| STRO | All | 1 | 7.69 | 1.76 | 0.14 | 1.39 | 0.34 | 1.85 | 330 | 90 | 17 |
| STST | All | 1 | 11.84 | 2.31 | 0.23 | 0.91 | 0.17 | 3.27 | 407 | 74 | 19 |
| TIUN | All | 1 | 10.35 | 2.12 | 0.24 | 1.01 | 0.45 | 3.66 | 589 | 58 | 12 |

* Standard deviation

Elemental Concentrations of Sampled Species in the Vaccinio - Tsugetum mertensianae Site at the End of September, 1976

| Species Code | Component | No. of Samples | % Ash Content | N | P | Ca | Mg | K | Mn | Zn | Cu |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Elemental Concentration | | | | | | | |
| | | | | % | | | | | ppm | | |
| CAME | All | 3 | 2.46 | 1.07 | 0.10 | 0.24 | 0.14 | 0.54 | 120 | 28 | 13 |
| | | | (0.17)* | (0.03) | (0.01) | (0.03) | (0.01) | (0.07) | (42) | (6) | (2) |
| CANI | All | 3 | 5.12 | 2.27 | 0.15 | 0.16 | 0.18 | 2.15 | 140 | 50 | 15 |
| | | | (0.27) | (0.24) | (0.01) | (0.04) | (0.04) | (0.16) | (44) | (7) | (0)+ |
| LUPE | All | 1 | 3.38 | 1.53 | 0.15 | 0.20 | 0.15 | 0.89 | 159 | 50 | 11 |
| PHEM | All | 5 | 2.00 | 1.02 | 0.10 | 0.13 | 0.12 | 0.42 | 362 | 24 | 9 |
| | | | (0.29) | (0.14) | (0.01) | (0.02) | (0.02) | (0.07) | (127) | (6) | (2) |
| RUPE | All | 1 | 6.51 | 1.93 | 0.18 | 0.47 | 0.47 | 2.30 | 341 | 55 | 5 |

* Standard deviation
\+ A standard deviation less than 0.01% or 1 ppm.