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Dry Matter and Nutrient Dynamics in Red Spruce-Fraser Fir and Yellow Birch Ecosystems in the Balsam Mountains, Western North Carolina

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I am submitting herewith a dissertation written by George T. Weaver entitled "Dry Matter and Nutrient Dynamics in Red Spruce-Fraser Fir and Yellow Birch Ecosystems in the Balsam Mountains, Western North Carolina." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

H. R. DeSelm, Major Professor

We have read this dissertation and recommend its acceptance:

F. H. Norris, M. E. Springer, G. E. Hunt

Accepted for the Council:

Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)
March 2, 1972

To the Graduate Council:

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[Signature]

Major Professor

We have read this dissertation and recommend its acceptance:

[Signature]

[Signature]

Accepted for the Council:

[Signature]

Vice Chancellor for Graduate Studies and Research
DRY MATTER AND NUTRIENT DYNAMICS IN RED SPRUCE-FRASER FIR
AND YELLOW BIRCH ECOSYSTEMS IN THE BALSAM MOUNTAINS,
WESTERN NORTH CAROLINA

A Dissertation
Presented to
the Graduate Council of
The University of Tennessee

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

by
George T. Weaver
June 1972
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ABSTRACT

The relative importance of dry-matter sinks in 40-50 year old immature spruce-fir and yellow birch ecosystems (elevation 1585-1951 m) and a >100 year old mature yellow birch ecosystem (elevation 1570-1580 m) were soil (S) > vegetation (V) > forest floor (FF). The relative importance of calcium sinks in the spruce-fir ecosystem were V > FF > S but V = FF > S in both yellow birch ecosystems. The relative importance of potassium, Mg and P sinks were FF > V > S in spruce-fir but FF > V = S in yellow birch ecosystems. Coarse texture, low pH and low nutrient status, except for K, characterized all soils.

Above-ground biomass was 180 t/ha, 154 t/ha, and 103 t/ha in spruce-fir, mature yellow birch, and immature yellow birch. Estimates were based on allometric every-tree summation of woody plants > 0.5 m tall and quadrat samples of other strata. Larger proportions of biomass were in foliage and boles in spruce-fir and in branches in yellow birch. Leaf area index was 21, 8, and 5 in spruce-fir, immature yellow birch, and mature yellow birch. Understory strata constituted < 3 per cent of the biomass, but contained up to 6 per cent of the vegetational nutrient pool in immature ecosystems, and in mature yellow birch.
30 per cent of the pool and up to 89 per cent of annual accumulation of nutrients in above-ground perennial components of vegetation.

Bole volume increment was significantly highest in spruce-fir of three ecosystems. Dry-matter production ranged from 5-10 t/ha/yr and tended to decrease in the order spruce-fir > immature yellow birch > mature yellow birch, but the differences were not significant due to the great specific gravity of yellow birch wood.

Net production of understory strata was < 8 per cent of total ecosystem production in immature stands but was 25 per cent in mature yellow birch stands; there, assuming net production equalled one-third of biomass, bryophytes alone contributed 20 per cent of total production. In the tree-tall shrub stratum, boles and foliage constituted one-third and one-half of production in immature ecosystems, respectively, and foliage constituted three-fourths of net production in mature yellow birch. Branch and reproductive structure production in immature yellow birch and spruce-fir, respectively, were relatively large. Annual litterfall was a good predictor of above-ground net production in immature ecosystems. Biomass and net production were correlated with few soil-site factors but multiple correlation coefficients between net production and certain stand structural parameters were highly significant.
Net assimilation rates (NAR) of bole and branch production decreased curvilinearly with increased leaf area index and net production was more or less constant across the range of stand basal area and biomass sampled in the spruce-fir ecosystem. The ratio of photosynthetic:nonphotosynthetic tissue of spruce-fir increased as stand density increased and mean tree size decreased; net production was significantly correlated to stand density. NAR were independent of foliage biomass in immature yellow birch; stand basal area, density, and biomass; leaf area, and foliage biomass were positively correlated with each other and with net production in these stands. Net production in mature yellow birch was positively correlated with stand density. NAR by ecosystem were immature yellow birch > spruce-fir > mature yellow birch. NAR in spruce-fir stands were more highly correlated with net production than leaf efficiency.

Annual input of Ca, K, and Mg via gross precipitation was equivalent to quantities of each which accumulated in above-ground perennial vegetation components. Interception of precipitation was 20 per cent and 25 per cent in yellow birch and spruce-fir ecosystems, but throughfall contained larger quantities of nutrients than precipitation in the open. Litterfall was the major transfer pathway explored for Ca, Mg, and P but throughfall and litterfall contained similar quantities of K. Stemflow was equivalent to < 6 per
cent of precipitation in the open and contained < 6 per cent of the nutrients in precipitation beneath the canopy of each ecosystem.

Increasing order of intensity of cycling rates was Ca < K < Mg < P among nutrients and mature yellow birch < spruce fir < immature yellow birch among ecosystems. These ecosystems were better differentiated by distribution of dry matter, nutrients, and net production and by nutrient cycling rates than by absolute quantities of dry matter and nutrients.
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I. INTRODUCTION

The present study seeks to estimate and compare rates of annual net primary production and flux of four macronutrients in contrasting high elevation *Picea rubens*-*Abies fraseri* (spruce-fir) and *Betula lutea* (yellow birch) ecosystems and to relate variations of net production and nutrient flux to certain site and stand structural parameters. The study was conducted at elevations between 1524 and 1954 meters in the Balsam Mountains of Western North Carolina. Biomass and pools of calcium, potassium, magnesium, and phosphorus were determined in each of five vegetational strata, the forest floor, and the solum. Net production of dry matter and nutrient flux through annual litterfall, annual nutrient uptake by vegetation, accumulation in perennial components, and precipitation input and transfers of nutrients leached from trees were estimated.

Intensified forest utilization resulting from seemingly inevitable population growth over the next several generations (Miles, 1971) and declining forest resources (Melekhov, 1970) will require increased production from existing forest lands and perhaps utilization of proportions of trees which now remain in forests after harvesting. Management of forests for maximum and sustained yield of particular products has long been a fundamental tenet of forestry.
The relation of productivity to environment and stand structure is complex and poorly understood. Research studies which have examined these relations especially between stand productivity and stand structure have often led to contradictory conclusions (Möller, 1954; Assmann, 1950, as cited by Baskerville, 1965; Baskerville, 1965) and the biological basis of productivity remains obscure (Ellenberg, 1971).

One approach to increased productivity is to convert forest lands to softwood production on shortened rotations (Ovington, 1968). However as production increases, whether by changing rotations, other silvicultural practices, or tree improvement, greater nutrient demands are exerted on sites and nutrient depletion due to harvesting is likely to be of significance over the long period on all sites (Rennie, 1955). Utilization of whole trees wherein the emphasis would be on fiber rather than bole production has also been advocated as an approach to increase yields from forests (Young, 1964). If technological developments permit extensive use of bark and larger branches or even whole trees, then site deterioration due to nutrient depletion will become of immediate concern, especially on poorer sites (Rennie, 1955). Shifting from bole to fiber production may affect cycles of elements differently. Removal of boles has greatest implications in calcium and magnesium cycles (Ovington, 1965) whereas greater utilization of bark could have important
implications in potassium and phosphorus cycles; evaluating the effects of various management practices on ecosystem integrity requires an understanding of the characteristics of specific nutrient cycles.

It has become increasingly apparent that in order to successfully manage natural ecosystems for sustained yield, an understanding of fundamental vegetational and environmental relationships which regulate ecosystem processes is essential; it is hoped that analyses of three specific forest ecosystems through the present study will contribute to an understanding of these relationships.
II. REVIEW OF LITERATURE

Estimation of Biomass

Biomass of forest ecosystems itself is not a reliable indicator of annual net primary production (Ovington, 1962; Satoo, 1970) but its profound influence over dry-matter distribution, nutrient dynamics, and forest management compels its accurate estimation. The multilayered structure of forests as it includes many growth forms requires a variety of methods of biomass estimation. Biomass of ground vegetation including herbs, bryophytes, and tree and shrub seedlings has been estimated from harvested quadrats (Tamm, 1953; Whittaker, 1961; 1966,; Baskerville, 1966; Forman, 1969; Traczyk, 1967; Weetman and Timmer, 1967; Damman, 1971). Estimation of arboreal biomass is particularly difficult and direct measurement or weighing is impractical or undesirable in many studies (Kira and Shidei, 1967). Indirect methods have involved destructive harvesting of sample trees to determine biomass of components with the results being extrapolated to entire stands (Newbould, 1967). Various methods of selecting sample trees and applying results to stands have been compared (Ovington and Madgwick, 1959a; Baskerville, 1965; Attiwill, 1966; Ovington, et al., 1967; Satoo, 1966, 1970; Kira and Shidei, 1967; Attiwill and Ovington, 1968; Crow, 1971); currently the allometric method
is widely accepted (Kira and Shidei, 1967) particularly where stand structure is complex (Crow, 1971). Weight (W) of tree components is expressed as a function of tree stem diameter (D), usually at breast height. The relation may be expressed in the form:

$$\text{Log } W = a + b \text{ (Log } D)$$

where (a) is the y-intercept and (b) is the slope of a regression line (Madgwick, 1970). Sample trees representing the range of sizes, species, and stand and site characteristics encountered in the study are harvested and regressions calculated. Coupled with non-destructive sampling, component weights of each tree in the stand are estimated and stand weights obtained by summing. Shrub biomass is estimated by similar methods (Newbould, 1967). This method may yield over estimates of biomass under some circumstances (Madgwick, 1970).

Expressing foliage weights as a function of stem diameter was originally proposed by Kittredge in 1944 or perhaps as early as 1934 in Russia, according to Utkin (1969). In the past two decades numerous investigations such as those cited previously have confirmed that weights of other components including roots, stems, branches, cones, surface area, volume, and increment of stems and branches can also be expressed as a function of stem diameter. Tree crown weight may be more closely related to stem diameter at
the base of the living crown (Attiwill, 1966a) but difficulties of making measurements under field conditions have generally precluded its use.

General agreement is lacking on the validity of combining data from trees harvested from a number of stands for developing regression equations to estimate biomass. Satoo (1966, 1970) has emphasized that the constants in regression equations are dependent on competition (stand density) within stands and Kira and Shidei (1967) have reported variations in leaf biomass in relation to stand age and stand structure. In these and other studies (Madgwick, 1970) involving birch, pines, and Cryptomeria japonica errors were especially large for estimates of foliage biomass. However, Baskerville (1965) found total dry-weight of branches and foliage to be highly correlated with tree stem diameter at breast height and independent of stand density and crown position for Abies balsamea, Picea glauca, and Betula papyifera. These apparent contradictions show that the nature of the relationship varies among species and suggests at least for pine, fir, and spruce that light tolerance and perhaps needle longevity may affect crown structure. Factors related to the apparent insensitivity of Betula papyrifera to stand density are not apparent.

Estimation of Net Primary Production

Net ecosystem production is the sum production by tree,
shrub, and ground strata (Whittaker and Woodwell, 1968). Annual production by bryophytes has been estimated as the sum of weights of shoots of specific ages for species in which ages of segments could be determined (Tamm, 1953); in other species one-half, one-third, or one-fourth of the biomass has been assumed to equal annual production (Romell, 1939; Tamm, 1953; Traczyk, 1967; Damman, 1971). Herb production has been estimated from above-ground clippings which were repeated several times during the growing season to include species of different phenological development (Whittaker, 1966; Traczyk, 1967; Shanks, et al., 1961). Production is underestimated by this method if loss of components occurs prior to harvest, when correction is not made for insect consumption (Newbould, 1967; Milner and Hughes, 1968), and by excluding root production. Exclusion of roots results in greater underestimation of production by herbs than trees and by perennial herbs than annuals (Bray, 1963).

Production by woody seedlings and small shrubs has been estimated from clipping weights of current year's tissues (Traczyk, 1967; Siccama, et al., 1970). These weights alone underestimate shoot production by disregarding weight increment of evergreen leaves, branches, and stems. Whittaker (1961, 1962) studied production relations among components of several shrubs and developed ratios of shoot production to clipping weights of current tissues. In the
first year, current tissues were 100 per cent of aerial production; with increasing age, the proportion decreased to 55-67 per cent of shoot production in most young and small shrubs. Shifts in production were more closely related to size than age (Whittaker, 1962). These results suggest that use of clipping weights of current tissues as estimates of seedling and small shrub production would result in relatively small underestimates.

Aerial production by trees and other shrubs is the sum of production of stems, branches, foliage, and reproductive components (Newbould, 1967). Study of root production is difficult (Newbould, 1968) and has been limited. Similar methods may be used in estimates of tree and shrub production (Newbould, 1967) although some modification for shrubs may be required if growth increment is small and stand variability high (Gimingham and Miller, 1968). In studies in the Great Smoky Mountains, shrubs were treated as small trees (Whittaker, 1961, 1962). Estimates involve determining biomass change and may take several forms (Newbould, 1967). These include successive remeasurements of permanent plots over a period of several years and analysis of radial increment based on destructive samples or increment cores.

Stemwood production has been estimated from some measure of radial increment from which volume and subsequently biomass increment can be inferred (Baskerville, 1965; Whittaker, 1966; Whittaker and Woodwell, 1968; Newbould, 1967).
Estimates based on the most recent annual radial increment represent current annual increments; current periodic annual increment is estimated when estimates are based on the mean radial increments over the last five or ten years (Art and Marks, 1971). The ratio of biomass to stand age is the mean annual increment which usually underestimates current woody production (Art and Marks, 1971). Branch production is difficult to measure and estimates are limited (Satoo, 1966) but methods relating branch dry-weight to branch age have been reported (Baskerville, 1965; Whittaker, 1965, 1963, 1961). Baskerville's (1965) estimates for Abies balsamea and Picea glauca were obtained by calculating and summing the mean annual increment (whorl weight/whorl age) of branch whorls from sample trees. These estimates were applied to stands. Branch increments of Betula papyrifera were obtained by dividing total crown weight by mean age at mid-crown.

Branch increment has also been estimated by using allometric equations relating branch biomass to stem diameter (Kira and Shidei, 1967; Madgwick, 1970). Branch increment was the difference between two estimates of biomass, one at sampling time and the other at some previous time. Stem diameter a few years prior to sampling was determined from radial increment analysis. The same allometric equations were applied to this diameter and biomass estimated. The assumption is that the relation of stem and branch
dimensions remains constant over the time interval (Madgwick, 1970; Satoo, 1970). This assumption has been questioned (Satoo, 1970) but Madgwick (1970) concluded that for an interval of a few years the method might give reasonable estimates of branch production.

Foliage production may be estimated as the difference between maximum and minimum leaf weights of trees during the year (Newbould, 1967). In deciduous stands, biomass of foliage near the end of the growing season approximates this difference and has been used as an estimate of foliage production in a number of studies (Baskerville, 1965--Betula papyrifera; Whittaker and Woodwell, 1968; Whittaker, 1966; Madgwick, 1970). Current foliage as a per cent of total foliage has been measured for some conifers (Baskerville, 1965; Clark, 1961) and the proportions applied to foliage biomass of trees in stands. Foliage production has also been estimated from leaf litterfall (Heller, 1971; Kira and Shidei, 1967; Madgwick, 1970; Duvigneaud and Denaeyer-DeSmet, 1970). Leaf biomass divided by years of leaf persistence and ratios of leaf biomass to stemwood production also have been used as indices of foliage production (Whittaker, 1966).

Common errors associated with most of these methods which cause underestimation of foliage production include failure to correct for litter losses prior to foliage estimates and insect consumption, decline in leaf weight toward
end of growing season, and year to year fluctuations in foliage production (Bray and Gorham, 1964; Madgwick, 1970; Satoo, 1970). Insect consumption of foliage in some forests ranges from 3.2 - 15.0 per cent of the foliage and may represent ca. 1 per cent of the primary production (Bray, 1961).

Failure to include reproductive components may result in serious underestimation of production by forests (Ovington, 1963). Standing crop of flowers, fruits, and cones has been used as an estimation of production of these components (Baskerville, 1965; Whittaker, 1962; Whittaker and Woodwell, 1968; Newbould, 1967). Ratio of fruits to current twigs (Whittaker, et al., 1963) and separation of reproductive components from annual litterfall also serve as estimates of production (Newbould, 1967).

**Biomass and Production of Temperate Forests**

Biomass and dry-matter production of major world forest types have been reviewed by Ovington (1962, 1965) and Art and Marks (1971) and Rodin and Basilevic (1967, 1968), who also included other major vegetation types. Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific have been summarized by Kira and Shidei (1967). More recently biological productivity of forests outside the U.S.S.R. (Utkin, 1969) and in the U.S.S.R. (Utkin, 1970) have been reviewed. Westlake (1963)
compared productivity of plants in several aquatic and terrestrial ecosystems, including forests.

**Biomass**

Biomass of most temperate zone forest ecosystems varies from 50 to 400 metric tons per hectare (t/ha) based on these reviews. Forest biomass generally increases from north to south with maximum values characterizing tropical forests (Rodin and Basilevic, 1968; Utkin, 1968). Kira and Shidei (1967) found no correlation of biomass with geographic location in the Western Pacific however, and concluded that biomass of tropical forests was not necessarily greater than biomass of well-developed forests elsewhere. Especially high biomass was indicated for cove forests in the Great Smoky Mountains (up to 610 t/ha) and coastal redwood forests (Whittaker, 1966). Biomass increased from low to intermediate elevations and decreased toward higher elevations in some mountains (Kira and Shidei, 1967) although the relation was complicated by replacement of deciduous forests by coniferous forests and by environmental changes associated with increasing elevation (Whittaker, 1966). Biomass also increased from poor to well-drained sites (Rodin and Basilevic, 1967), from xeric to mesic sites (Whittaker, 1966), as stand density and basal area increased (Baskerville, 1965), with increasing stand age, at least up to maturity (Ovington and Madgwick, 1959a; Ovington, 1962; Kira
and Shidei, 1967), and with increasing net primary production (Whittaker, 1966; Rodin and Basilevic, 1968).


Temperate zone deciduous forests biomasses typically ranged between 150 and 300 t/ha (Ovington, 1962, 1965; Rodin and Basilevic, 1967; Utkin, 1969, 1970; Kira and Shidei, 1967) although European beech and oak and U. S. maple forests varied upward to 370 - 507 t/ha (Rodin and Basilevic, 1968; Zedler, 1969). Canadian and U. S. aspen stands varied from 60 to 230 t/ha (Bray and Dudkiewicz, 1963; Peterson, et al., 1970). High elevation beech (Shanks, et al., 1961; Whittaker, 1966) and oak forests (Whittaker, 1966) in the Great Smoky Mountains ranged from 86 to 170 t/ha. Comparable northern hardwood forests in the Northeastern United States have not been studied. Differences between coniferous and deciduous forests are not readily apparent from these studies, supporting Ovington's (1962) conclusion that regionally, maximum biomass on good sites
may be uniform among various forest types.

General patterns characterize the distribution of biomass within forests. Biomass of understory plants was minor as compared with trees (Ovington, 1962; Utkin, 1969, 1970) and often represented only 1.5 to 2.0 per cent of total biomass (Ovington, 1965). Shrub biomass was 2 per cent or less of tree biomass in high elevation deciduous forests and less than 0.1 per cent in most spruce-fir forests in the Great Smoky Mountains (Whittaker, 1966). In dense balsam fir stands, shrubs may be absent (Baskerville, 1966). Herbs and mosses frequently represent 0.5 per cent or less of total biomass (Whittaker, 1966; Ovington, et al., 1963; Baskerville, 1966). Herb and moss biomass varied inversely with tree biomass (Heilman and Gessel, 1963) or density (Ovington, 1962; Tamm, 1953). Mosses were more important contributors to total biomass in coniferous forests (Forman, 1969) and became increasingly important in northern open and waterlogged spruce forests (Rodin and Basilevic, 1967). Herbs and mosses respond to higher light intensities beneath less dense forests (Anderson, et al., 1970) but root competition from overstory vegetation (Ovington, 1962), quantity of nutrients leached from tree crowns (Tamm, 1953), and variation in precipitation throughfall related to canopy density (Anderson, et al., 1970) were also related to variations in understory development.
The distribution of biomass among components of trees varies in relation to forest type and environmental factors. In spruce stands on waterlogged sites where root development was impeded, up to 41 per cent of the biomass was in leaves, 48 per cent in boles and branches, and 11 per cent in roots (Rodin and Basilevic, 1967); in secondary forests which have been burned repeatedly, roots may account for 56 per cent of the total biomass of trees (Woodwell and Whittaker, 1968). Ovington (1965) summarized the distribution of biomass in trees in several spruce and birch stands; in spruce stands leaves and branches each made up approximately 6.5 per cent, boles 63.5 per cent, and roots 23.5 per cent of the biomass in trees. In birch stands, leaves were less than 2 per cent, branches 9 per cent, boles 66.1 per cent, and roots 23.3 per cent of the tree biomass. In balsam fir stands of lowest density, percentage of tree biomass was: foliage 2.7, branches 13.8, boles 51.3, and roots 21.8. As stand density and basal area increased, biomass of all components increased but crowns were relatively smaller and a lower percentage of biomass was in leaves and branches (Baskerville, 1963).

Proportions of biomass may increase in both boles and roots in comparison with proportions in foliage as stand density increases (Baskerville, 1965). Distribution of biomass among tree components also changes with stand age. Foliage was a larger proportion of biomass of young stands
(Ovington, 1962), and increased at least until canopy closure occurred (Kira and Shidei, 1967; Satoo, 1966). Beyond this stage, foliage biomass became fairly independent of stand biomass (Rodin and Basilevic, 1967) to some constant level (Kira and Shidei, 1967). As woody tissues accumulated with age, foliage decreased as a percent of total biomass.

Upper limits of foliage biomass seem to exist (Möller, 1947; Satoo, 1970; Kira and Shidei, 1967) although absolute quantities vary among species or among ecologically similar groups of species and with stand structure (Kira and Shidei, 1967). The effect of site conditions on leaf biomass is unresolved and seems to differ among species. Möller (1947) concluded that leaf biomass was unrelated to site quality while others found larger biomasses associated with better sites (Heilman and Gessel, 1963; Switzer, et al., 1966; Satoo, 1970). Foliage biomass also varied directly with solar intensity and decreased with increasing distance from the equator in Western Pacific Forests (Kira and Shidei, 1967). Foliage biomass increased with leaf longevity and consequently was lowest in deciduous stands, higher in pine stands and highest in spruce and fir stands (Kira and Shidei, 1967). Absolute quantities of foliage ranged between 2 to 4 t/ha in temperate zone deciduous forests, 7 to 9 t/ha in pine stands, and between 6 and 30 t/ha in spruce and fir forests (Kira and Shidei, 1967; Satoo, 1970).
An additional common method of expressing the magnitude of photosynthetic system of an ecosystem is leaf area index (LAI) which is the surface area of foliage per unit surface area of ground (Newbould, 1967). Leaf area indices of 4 to 6 characterize many deciduous forests world wide (Tadaki, 1966) or frequently vary within a narrow range near LAI 7 (Satoo, 1970). Leaf area indices from 1 to 11 in birch stands and as high as 15.8 in beech stands have been reported however (Utkin, 1969, 1970). Comparatively low LAI of 3 has been reported in beech forests in the Smokies (Whittaker, 1966). Understory species may contribute more to stand leaf area than stand biomass (Satoo, 1970), a trend in agreement with the general increase in leaf blade area to dry weight ratio from sun to shade leaves (Jackson, 1967; Monk, et al., 1970) and from trees in the canopy to advanced regeneration (Gulidova, 1959).

The larger leaf biomass of coniferous forests (Satoo, 1970) is reflected in a larger leaf area index. Black spruce stands in Canada with LAI 8.9 and spruce-fir stands in the Great Smoky Mountains with LAI 12-15 have been reported (Weetman and Harland, 1953; Whittaker, 1966).

Higher ratios characterized some coniferous stands including: LAI 17-28, Norway spruce (Tadaki, et al., 1965; Droste zu Hulshoff, 1970); LAI 38, Norway spruce (Utkin, 1969); and Abies alba, LAI 17 (Tadaki, et al., 1965).
Net Primary Production

Dry-matter production of forests has been studied less frequently than forest biomass and often production estimates were limited to particular strata within the ecosystem. Annual net production of many subarctic and subalpine coniferous forests varies from 10 to 15 t/ha (Whittaker, 1966; Kira and Shidei, 1967; Satoo, 1970). Spruce and fir forests of the middle and southern taiga in Europe and U.S.S.R. are lower varying from 5 to 10 t/ha (Utkin, 1969, 1970; Rodin and Basilevic, 1967, 1968). Mean annual production over a 65-year period was only 1.7 t/ha in an upland black spruce stand in Canada (Weetman and Harland, 1963); balsam fir stands in eastern Canada ranged from 9.4 to 12.6 t/ha (Baskerville, 1965). Spruce-fir stands in the Great Smoky Mountains were similar to other subalpine forests except Fraser fir stands in which production ranged from 5.7 to 6.5 t/ha (Whittaker, 1966). Unusually high production by both fir stands (exceeding 25 t/ha/yr) and Cryptomeria japonica plantations (40-45 t/ha/yr) has been reported in the Western Pacific (Kira and Shidei, 1967).

Annual production in temperate deciduous forests may be 25 to 30 t/ha (Whittaker, 1966; Kira and Shidei, 1967) but rates of 5 to 10 t/ha are typical (Utkin, 1969, 1970; Satoo, 1966, 1970; Rodin and Basilevic, 1967; Ovington, et al., 1963; Tadaki, et al., 1965; Bray and Dudkiewcz, 1963).
Production in various high elevation deciduous forests in the Great Smoky Mountains was from 5.7 to 11.0 t/ha/yr (Whittaker, 1966). From 82 to 95 per cent of net primary production was attributed to trees (Whittaker, 1962, 1963, 1966; Ovington, et al., 1963; Utkin, 1969). Shrub and herb production was generally low but varied seasonally (Ovington, 1955; Whittaker, 1966; Traczyk, 1967), with forest type (Whittaker, 1966; Siccam, et al., 1970), and with variation in forest structure (Rodin and Basilevic, 1967). Increased herb production may be related to increased light intensity associated with more open stands (Good, 1963; Anderson, et al., 1970), reduced root competition (Ovington, 1962), with increased precipitation throughfall resulting from variation in overstory canopy density (Anderson, et al., 1970), and with increased moisture (Whittaker, 1966). In some stands, herb production was 30 to 40 per cent of tree production (Bray and Dukiewicz, 1963; Satoo, 1966), and increased toward higher elevations (Whittaker, 1966; Siccam, et al., 1970).

Production by bryophytes while generally low (Whittaker, 1966) may equal wood production by trees (Romell, 1939; Damman, 1971; Scott, 1955; Weetman and Timmer, 1967). Bryophytes become more important on waterlogged sites (Rodin and Basilevic, 1967), possibly in relation to increased light intensities associated with reduced canopy cover on
these sites. Bryophyte productivity increases with increasing light intensity up to a maximum which is less than full sunlight (Tamm, 1953; Weetman and Timmer, 1967). Where light is not limiting, productivity varies with nutrient contents of throughfall (Tamm, 1953, 1964) and throughfall precipitation (Weetman and Timmer, 1967). Bryophyte productivity is also higher in coniferous than deciduous stands (Whittaker, 1966).

Distribution of net primary production among tree components shows considerable variability among stands but certain trends are suggested (Utkin, 1969, 1970; Satoo, 1966; Bray and Dudkiewicz, 1963; Ovington, et al., 1963; Baskerville, 1965). In many spruce and fir stands, production of boles was approximately 50 per cent of the net production, but proportions varied from 45 per cent to 65 per cent. Leaf production was from 23 per cent to 45 per cent of net primary production but more generally varied from 30 to 40 per cent. Usually 10 to 15 per cent of net production was in branches, although proportions as low as 5 per cent or up to 23 per cent occurred. The distribution of production was more variable in birch than in spruce and fir stands, and differed between trees and shrubs. Shrub stemwood and branchwood production were similar and each was less than 30 per cent of total production. Current twigs and leaves were from 33 to 60 per cent of total production (Whittaker, 1962).
Lower bole production has been reported in balsam fir stands where proportions varied from 34 to 42 per cent, from 15.1 to 16 per cent and 43 to 50 per cent of net production was distributed among branches and leaves, respectively (Baskerville, 1965). Site quality, age, and tolerance (light) possibly were related to these departures from conditions in other stands (Wegge, 1966; Satoo, 1966). Baskerville's (1965) data showed that as stand density increased (either as measured by basal area or stems per unit land area), stem production increased and branch and leaf production decreased relatively. In smaller trees, which characterized denser stands, a larger proportion of net production went into stemwood and less into foliage. Smaller trees had a greater proportion of shade foliage which was more efficient due to a very low light saturation point. Similar trends have been noted elsewhere (Satoo, 1966).

Numerous factors have been shown to affect total net primary production. In agricultural crops, leaf area and its pattern of development during the growing season are principal factors regulating dry-matter production (Watson, 1952). In some forests a direct, linear relation of dry-matter production to leaf area index (LAI) occurred (Satoo, 1970). The relationship is complex however and in some forests where leaf biomass and presumably LAI remained relatively constant, dry-matter production varied directly
with site quality. As total production declines, important changes may occur in the distribution of dry-matter (Sato, 1966). On poorer sites, production of crown components seemed to be maintained at the expense of stemwood production and stemwood production decreased more than branch and leaf production.

Net production and volume increment also vary with stand structure but various conclusions concerning the nature of the relationship have been reached. Principal models proposed include: (1) an optimum basal area for maximum increment exists for each site and increment declines at greater and lesser densities (Assmann, 1950, cited by Møller, 1954); and (2) increments are more or less constant over a broad range of densities (Møller, 1954). More recently, studies have shown that in at least some stands, volume increment and aerial net production increased directly with and over a broad range of stand densities (Baskerville, 1965; Sjolte-Jorgensen, 1967; Safford, 1968). Wegge (1966) reviewed several studies in which apparent contradictions concerning density and increment occurred and concluded that the effect of density on volume and presumably dry-matter increment varied with the particular combination of species (light tolerant and intolerant species), site quality, and age which characterized a stand.

Broad, regional patterns of productivity exist
(Westlake, 1963; Rodin and Basilevic, 1967; Ovington, 1968; Reichle, 1970; cf. front piece after Leith) which have been related to temperature (Paterson, 1956), solar radiation levels (Jordan, 1971), length of growing season (Westlake, 1963; Paterson, 1956; Brunig, 1967), precipitation (Westlake, 1963; Paterson, 1956; Jordan, 1971), and actual evapotranspiration (Rosenzweig, 1968). Within regions or zones, variations in forest ecosystem productivity are superimposed upon the broad, zonal patterns in relation to numerous environmental parameters. Tree growth rates together with net primary production are affected by microclimatic conditions (Coile, 1952; Ralston, 1964; Ovington, 1965). Efforts to relate forest productivity to nutrient levels of soils have been less successful than to physical properties (Coile, 1952; Ralston, 1964) but this apparently reflects difficulties of sampling heterogeneous forest soils (Ovington, 1965), inappropriate analytical techniques (Ralston, 1964; Ovington, 1965) and inadequate understanding of forest tree nutrition.

Although not thoroughly investigated, feeding activities of insects which reduce leaf area or produce other deleterious physiological effects also reduce foliage and wood production (Rafes, 1970).

Forest Floor

The forest floor consisting of 01 and 02 horizons
(Soil Conservation Service, 1962) has attracted much interest due to its relation to moisture availability (Trimble and Lull, 1956; Helvey, 1964), forest regeneration (Bakuzis and Hansen, 1965; Gilbert, 1960; Long, 1940), soil properties (Lutz and Chandler, 1946), and site quality (Lutz and Chandler, 1946). More recently it has become apparent that an appreciable portion of the dry matter and nutrients in forest ecosystems is in the forest floor (Rodin and Basilevic, 1967; Ovington, 1968). Roots of many forest species including various spruces and firs (Coile, 1939; Korstian, 1937, Weetman and Timmer, 1967) and herbs (Kirikova, 1970) are largely restricted to humus layers. This together with mycorrhizal relationships of many tree-fungi associations (Trappe, 1957, 1960, 1962) and possible direct nutrient transfer from litter to trees via fungi (Went and Stark, 1968) further accentuates the significance of litter in forest ecosystems.

In the Northeastern United States, accumulations of dry matter on the forest floor ranged from 27 to 48 t/ha in red spruce-balsam fir (Lyford and MacLean, 1966), 113 t/ha in spruce-hardwood (Lunt, 1932), from 144 to 233 t/ha in red spruce-yellow birch (McFee and Stone, 1965), and 87 and 65 t/ha in Canadian black spruce and balsam fir stands, respectively (Damman, 1971). Accumulations were in the same range in Southern Appalachian spruce-fir (98 t/ha)
(McGinnis, 1958) and in Canadian black spruce stands (118-155 t/ha) (Weetman and Timmer, 1967). These weights are higher than characteristic of most European and Russian spruce forests (Rodin and Basilevic, 1967). Forest floor weights are usually lower in deciduous forests (Alway and Harmer, 1927; Bourn and Brown, 1971; Ovington, 1962; Rodin and Basilevic, 1967, 1968) although weights of 105 t/ha occurred in some northern hardwoods (Lunt, 1932). Weights of 20 t/ha or less are more typical (Alway and Kittredge, 1933; Blow, 1955; Ovington, 1962). Forest floor weight was 6.7 t/ha in Southern Appalachian beech gap forest (McGinnis, 1958) where the "H" layer was not developed. In a nearby spruce-fir stand, 79 per cent of the dry matter was concentrated in the well-developed "H" layer. Poorly developed H-layers have been reported in other deciduous and some coniferous stands (Bourn and Brown, 1971; Metz, et al., 1970), but in northern deciduous and coniferous stands, both "F" and "H" layers were often well-developed and H-horizon accounted for a large per cent of forest floor weight (Stoeckeler, 1961; Mader and Lull, 1968; McFee and Stone, 1965; Stottlemyer and Ralston, 1970).

Variability of forest floor weight characterizes many forest types (Aldon, 1968; Gregory, 1960; Kittredge, 1940; Moer and Grier, 1969; Youngberg, 1966). Although there are exceptions (Scott, 1955), the relation of litter
production and storage is often inverse and is an expression of decay rates (Olson, 1963). In the Northeastern United States, the ratio of annual litterfall to forest floor weight is 0.25 or less (Olson, 1963). Decay rates decrease toward the north and litter accumulates (Rodin and Basilevic, 1968). Decay rates also decrease with elevation (Shanks and Olson, 1961) and the litterfall:forest floor ratio may be 0.01 or less in subalpine forests (Olson, 1963).

Decay rates vary among litter production by different tree species (Kucera, 1959) and with litter composition (Ovington, 1954; Broadfoot and Pierre, 1939; Coile, 1937). Ash was higher in litter from most deciduous trees (Scott, 1959) and forest litter tended to decrease as deciduous trees and grasses increased in coniferous stands (Rodin and Basilevic, 1967). While waterlogging and higher forest floor weights are directly related (Rodin and Basilevic, 1967), the relation to other side factors such as slope, steepness, aspect, and topographic position varies (Knighton, 1970; Hart, 1961). Variations of the forest floor were related to microrelief and affected regeneration success in many northeastern stands (Hart, et al., 1962; Lyford and MacLean, 1966; Youngberg, 1966).

Reductions of the forest floor from fires may remain evident for many years (Korstian, 1937; Coile, 1939; Blow, 1955). Weights also decrease after logging or thinning
(Wright, 1957; Coile, 1939; Blow, 1955), apparently reflecting increased decay rates (Wright, 1957).

Stand structural characteristics associated with increased forest floor weight include older age of stands (Aldon, 1968; Williston, 1966; Gregory, 1960) and higher stand basal area (Williston, 1966; Aldon, 1969; Boyer and Fahnestock, 1966; Ffolliott, et al., 1968) but not number of trees per unit land area (Aldon, 1968; Moer and Grier, 1969).

**Annual Litterfall**

Annually tissues shed by forest plants result in substantial additions of dry matter to the forest floor. Because of the quantity and high ratio of non-woody to woody tissues, litterfall is a major pathway along which energy and nutrients are transferred in forest ecosystems. In this and subsequent discussions, the Russian concepts of litterfall and leaf litterfall (Rodin and Basilevic, 1967) have been adopted. Leaf litterfall denotes the leaves, reproductive tissues, small twigs, and bark shed annually. Litterfall refers to the total dry matter shed annually and includes tree boles, large branches, and leaf litterfall.

In U. S. and Canadian coniferous forests, annual leaf litterfall ranged from 1.1 to 3.0 t/ha in black spruce stands (Weetman and Timmer, 1967; Damman, 1971) and from 2.5 to 3.2 t/ha in balsam fir stands (Chandler, 1944) as compared with 5.25 t/ha in a Southern Appalachian red spruce-
Fras er fir forest (Shanks, et al., 1961). These values are in the range of many eastern and western U. S. coniferous forests (Tarrant, et al., 1951; Reukema, 1964; Alway and Zon, 1930; Sims, 1932; Morgan and Lunt, 1931; Chandler, 1944; Scott, 1955) excepting _Sequoia gigantea_ forests where leaf litterfall was 9.0 to 9.4 t/ha/yr (Biswell and Gibbens, 1966). Litter production in forests on a world basis has been reviewed by Bray and Gorham (1964) and Rodin and Basilevic (1967) and in the western Pacific by Kira and Shidei (1967) who indicate leaf litterfall in temperate zone coniferous forests generally is between 2 and 5 t/ha annually, in close agreement with northern U. S. and Canadian studies.

Annual leaf litterfall in deciduous forests in the United States and Canada was 2.1 and 3.1 t/ha in north-eastern mixed hardwoods (Chandler, 1944; Scott, 1955), 3.4 to 6.3 t/ha (mean 4.3 t/ha,) in a Canadian maple-oak forest (Bray and Gorham, 1964), and 1.3 to 4.5 in Southern Appalachian hardwoods (Hursch, 1928; Blow, 1955). Leaf litterfall of 5.5 t/ha in high elevation beech forests in the Great Smoky Mountains (Shanks, et al., 1961) was higher than most U. S. deciduous forests and near the maximum of the 3 to 5 t/ha/yr range reported in most cool temperate deciduous forests (Bray and Gorham, 1964; Rodin and Basilevic, 1967).
Leaf litter makes up a larger proportion of litter-fall than tree boles and large branches in most forests although the relation between the two varies. In deciduous stands less than 20 years of age, leaf litter was 75 to 85 per cent of total litter; with increased stand age, bole and branch litterfall also increased until in older forests leaf litter was from 40 to 65 per cent of total litter (Rodin and Basilevic, 1967). A similar shift occurred with age in coniferous forests which produced up to 40 per cent more non-leaf litter than deciduous forests (Bray and Gorham, 1964); older coniferous forests, leaf litter was from 30 to 66 per cent of total litter production (Rodin and Basilevic, 1967).

Litter production varies in relation to numerous structural and environmental parameters. Litter production generally increased from north to south (Bray and Gorham, 1964; Rodin and Basilevic, 1967), parallel to increasing temperatures and increasing forest productivity. Greatest litterfall in mountainous regions was in intermediate elevation forests and declined with increasing elevation (Kittredge, 1948; Bray and Gorham, 1964). Gymnosperms produce approximately one-sixth more litter than angiosperms and consequently within climatic zones, litter production is greatest in coniferous forests (Bray and Gorham, 1964). Litter production, however, was greatest in some mixed
coniferous-hardwood forests (Rodin and Basilevic, 1967), possibly in relation to somewhat higher soil nutrient levels and production rates. Litter production varied among tree species (Scott, 1955), and generally increased with stand basal area although stand density had little apparent effect (Bray and Gorham, 1964). The relation of litterfall to stand age is more complex (Kittredge, 1948; Alway and Zon, 1930; Scott, 1955; Bray and Gorham, 1964; Rodin and Basilevic, 1967). Litterfall increases with age until maximum net primary production is reached, perhaps between 30 and 60 years depending on the forest, and declines with increasing age. Litterfall increases with increasing site quality (Kittredge, 1948; Chandler, 1941; Scott, 1955; Bray and Gorham, 1964), from southwest to northeast aspects and from xeric to mesic sites (Bray and Gorham, 1964).

Litter production also varies from year to year within forests (Scott, 1955; Alway and Zon, 1930; Kittredge, 1948; Damman, 1971; Reukema, 1964). Ratios of maximum: minimum leaf litterfall may be up to 1.8 in deciduous, 2.4 in some spruce forests (Bray and Gorham, 1964), 3 in douglas fir forests (Reukema, 1964), and 1.3 to 1.4 in black spruce and balsam fir forests, respectively (Damman, 1971).

The composition of leaf litter differs between deciduous and coniferous forests although some trends are evident within each type (Rodin and Basilevic, 1967; Bray
and Gorham, 1964). Leaves made up from 80 to 90 per cent of the litter in deciduous stands, twigs and bark from 4 to 12 per cent, and reproductive components from 1 to 7 per cent. The ranges were greater in coniferous stands where leaves were 53 to 90 per cent of leaf litter; twigs and bark, and reproductive components often formed a larger percentage and ranged from 9 to 35 per cent and 1 to 22 per cent, respectively. The proportion of bark in litter also was greater in stands of trees with loose, exfoliating bark. The proportion of needles in litter decreased and proportion of branches increased as stands aged. The greatest proportion of leaf litter was produced by trees and ranged from 85 to 95 per cent in high elevation stands in the Southern Appalachians (Shanks, et al., 1961). There shrubs produced less than 3 per cent and herbs from 4 to 12 per cent of the leaf litter; in the northeast in mixed hardwoods and pine stands, the understory produced 15 per cent of the leaf litter (Scott, 1955).

The relationship of litter production and net primary production suggests that litterfall or leaf litterfall may be useful indices of net primary production of forests. Rodin and Basilevic (1967) found that the ratio of litterfall to net primary production was fairly consistent in taiga spruce stands. Ratios were between 0.65 and 0.78 although decreases occurred from north to south. In birch forests,
ratios were more consistent and ranged from 0.65 to 0.72. Bray and Gorham (1964) noted that a difficulty in using leaf litterfall as an index was the varying proportion of leaf to non-leaf tissue between coniferous and deciduous stands.

**Nutrient Cycling**

The fundamental relation of nutrient dynamics to productivity in forest ecosystems has been widely recognized (Rennie, 1955; Ovington, 1968; Duvigneaud and Denaeyer-Desmet, 1970; Switzer, et al., 1968; Heilman and Gessel, 1963; Curlin, 1970; Kornev, 1959). Recent reviews (Basilevic and Rodin, 1964; Rodin, 1964; Rodin and Basilevic, 1967) of major world vegetation types have shown that significant variations in nutrient dynamics differentiate ecosystems and suggest that understanding the characteristics of cycles is basic to manipulation of systems for maximum dry-matter production.

Nutrient flux in ecosystems is polycyclic including sub-annual cycles which cover hours, days, or longer periods, annual cycles, long-term cycles consisting of successive annual cycles (Remezov, 1959), or cycles measured in geologic time (Ovington, 1968). Nutrient cycles may be "open" or "closed" although the distinction is somewhat arbitrary since it is not possible to sharply delimit the boundaries of ecosystems (Evans, 1956). From a practical point of view, it is necessary to establish ecosystem boundaries across which nutrient flux occurs and consequently open cycles of
elements must be considered. Closed cycles refer to nutrients transferred among components within the defined boundaries of ecosystems.

**Nutrient Inputs and Outputs**

Nutrient flux across ecosystem boundaries involves meteorological, geological, and biological processes (Bormann and Likens, 1967; Ovington, 1968). Annually, input into ecosystems of Ca, K, Mg, and P along with other nutrients occurs via precipitation. Concentrations of several ions in bulk precipitation in North Carolina have been determined by Junge and Fisher (1958) and Gambell and Fisher (1966). Calcium concentrations ranged from 0.2 to 1.4 ppm; K, 0.1 to 0.3 ppm; and Mg, 0.1 to .2 ppm. In the northeastern United States and Canada, Ca ranged from 0.29 to 3.9 ppm; K, .008 to 3.83 ppm; Mg, .007 to .156 ppm; and P, 0.08 ppm (Fisher, et al., 1968; Likens, et al., 1967; Weetman and Timmer, 1967). Month to month and seasonal variations were apparent in these data and calcium frequently showed spring and summer maxima in association with spring and summer road and agricultural dust maxima (Gambell and Fisher, 1966). Magnesium had a winter maximum, reflecting the influence of maritime air masses although both variability and concentration decreased inward from sea coasts (Gambell and Fisher, 1966). Cation ion content of precipitation also varies during storms and with storm size
Major sources of nutrients vary with the ion. Calcium originates chiefly from road or agricultural dust and is present in higher concentrations in arid regions (Gambell and Fisher, 1966; Gorham, 1961; Junge and Werby, 1958; Tamm and Troedsson, 1955; White and Turner, 1970). Potassium also originates from soil dust but sea spray may be of greater importance than in the supply of Ca (Gorham, 1961; Gambell and Fisher, 1966; Junge and Werby, 1958; White and Turner, 1970). Magnesium originates primarily from sea spray (Gambell and Fisher, 1966; White and Turner, 1970). Air pollutants are also sources of most ions (Gorham, 1961).

In New Hampshire, annual input was: Ca, 3.0 kg/ha; K, 2.5 kg/ha; and Mg, 0.7 kg/ha (Likens, et al., 1967). These levels are within input rates generally reported in the temperate zone where Ca ranges from 3-19 kg/ha; K, 1-10 kg/ha; Mg, 4-11 kg/ha; and P, 0.2-0.6 kg/ha (Ovington, 1968). Attempts to quantify nutrient budgets of temperate forest ecosystems indicate that nutrient inputs via precipitation may be of appreciable significance. The ratio of nutrients in annual leaf litterfall to precipitation in some coniferous and deciduous forests varies from ca 3 to 10, depending on the element (Gorham, 1961; citing Viro, 1955). Quantities supplied via precipitation may nearly equal annual accumulation in harvestable boles of Ca, K, and Mg, but not P.
Precipitation inputs of nutrients may approximate from 0.3 to 0.4 of annual losses from ecosystems via leaching; potassium input may exceed losses in some ecosystems (Likens, et al., 1967).

Changes in the nutrient capital of ecosystems through migrations of animals is difficult to measure. Where systems selected for study were more or less homogeneous and contained no special attractions or deterrents for animal migrations, equal biological input and output have been assumed (Bormann and Likens, 1967). Removal of tree boles may result in significant loss of nutrients from forest ecosystems, irrespective of site fertility (Rennie, 1955).

Changes in nutrient status can also occur from loss of nutrients through mass movement of soils, through erosion and leaching, and with subsequent removal in streamflow and deep seepage (Bormann and Likens, 1967). Leaching losses have been estimated through use of lysimeters (Cole and Gessel, 1968) and where bedrock geology permits, through analysis of stream water discharge from small watersheds (Likens, et al., 1967; Nelson and Curlin, 1968; Stottlemeyer and Ralston, 1970). Annual losses from some forests ranged from approximately 4 to 18 kg/ha of Ca; 1 to 5 kg/ha of K; 2 to 4 kg/ha of Mg; and less than 0.1 kg/ha of P (Likens, et al., 1967; Cole and Gessel, 1968).
Nutrient input also occurs through chemical weathering of soil and bedrock minerals which has been estimated in forests of the Northeastern United States as equal to net losses from the ecosystem as measured in stream water discharge (Likens, et al., 1967; Johnson, et al., 1968). Ecosystem nutrient dynamics also may be altered through manipulation including clearcutting and herbicide treatments (Gessel and Cole, 1965; Likens, et al., 1970; Likens, et al., 1969).

The circulation of nutrients within forest ecosystems involves uptake, retention and restitution of nutrients over intervals of time of varying lengths (Duvigneaud and Denaeyer-DeSmet, 1970). The concentration of nutrients within components together with rates of dry-matter production and factors which affect ecosystem structure interact and result in distribution patterns and transfer rates which may vary from system to system. Chemical analysis of plants from deciduous and coniferous forests of the eastern United States and Canada show that significant differences exist among species and often may be the most important factor affecting stand to stand differences (Scott, 1955; Bard, 1945; Fraser and McGuire, 1969; Likens and Bormann, 1970; Beaton, et al., 1965; Young and Carpenter, 1967; Young, et al., 1965).

Large variations in nutrient concentrations occur among tissues and organs within species also. Published
analyses (Likens and Bormann, 1970; Scott, 1955; Young and Guinn, 1966) of red spruce, balsam fir, yellow birch, and several other northern hardwoods showed appreciable differences in concentrations of specific nutrients among components and that relative concentrations among different nutrients varied from component to component. Frequently potassium was the most abundant nutrient in foliage. Calcium was often the most abundant ash element in other tissues although K concentrations in bark of some species was greater. Magnesium and P concentrations were relatively low. Among tissues, foliage and current tissues often contained highest concentrations of nutrients although bark, particularly of branches of some species, contained higher concentrations. Wood was lowest in nutrients of all tissues.

Nutrient concentrations also vary among life forms. Foliage K levels of herbs were high relative to foliage K of trees. Foliage K also was high relative to other elements within herbs (Scott, 1955; Likens and Bormann, 1970; Bard, 1945; Bard, 1949; Shanks, et al., 1961). Concentrations of Ca and Mg were highest in herbs, second highest in shrubs, and lowest in mosses (Gagnon, et al., 1958). Concentrations of ash elements also were higher in shrubs than in trees (Kornev, 1959; Scott 1955). Patterns varied, however, among nutrients. Potassium levels of herbs and mosses were similar and exceeded concentrations in shrubs; phosphorus concentrations of herbs and shrubs were similar and exceeded
concentrations of mosses (Gagnon, et al., 1958). Concentration of nutrients of foliage varies with age of many species (Beaton, et al., 1965; Lowry and Avard, 1965; Fraser and McGuire, 1969; Fraser, et al., 1964) including yellow birch (Hoyle, 1965) and red spruce (Safford and Young, 1968). Concentrations of yellow birch foliage varied during the season (Hoyle, 1965, 1969) similar to trends in other species (Guha and Mitchell, 1966; Mitchell 1936; Wells, 1969; Lavender and Carmichael, 1966; Lowry and Avard, 1969; Likens and Bormann, 1970) and even from hour to hour during the day (Lowry and Avard, 1965). Variations in nutrient concentrations have been related to temperature patterns prior to foliage sampling (Miller, 1966), to soil drainage (Hoyle, 1969), and to elevational changes (Likens and Bormann, 1970), and to soil moisture conditions (Broadfoot and Farmer, 1969).

Foliar analysis has shown varying results concerning the relation between nutrient concentrations and soil nutrient status. Differences in phosphorus and potassium concentrations in red spruce foliage (Safford and Young, 1968) and calcium, potassium and phosphorus (but not magnesium) concentrations of foliage of a number of other northeastern trees (Bard, 1945; Scott, 1955) have been related to soil nutrient levels. Other studies (Metz, et al., 1966; Ovington, 1954), however, have shown little relation
between soil and foliage nutrient concentrations and Crocker (1959) concluded that a relation was apparent only when soil nutrient levels are extreme.

Nutrient concentrations of foliage also vary in relation to position of leaves (needles) within the crown of many species (Lavender and Carmichael, 1966; Lowry and Avard, 1965) including red spruce (Young, et al., 1967) and yellow birch (Hoyle, 1965), crown class of tree (Lowry and Avard, 1968; Wells, 1969), and between sun and shade leaves (Hoyle, 1965; Likens and Bormann, 1970).

The significance of component in determining nutrient mass depends on relative biomass as well as nutrient concentrations. Of the calcium and potassium in aerial components of coniferous trees (excepting pines), 34 to 36 per cent may be in boles, 31 to 34 per cent in branches, and 30 to 34 per cent in foliage (Rennie, 1955). Distribution of phosphorus differs wherein boles contain 25 per cent, branches, 29 per cent, and foliage, 46 per cent (Rennie, 1955).

Distribution patterns differ between hardwoods and conifers also. Boles contain 63 per cent calcium, 48 per cent of the total potassium, and 43 per cent of the total phosphorus. Branches contain 25 per cent of total calcium, 29 per cent of total potassium, and 32 per cent of total phosphorus. Foliage contains smaller proportions of total nutrients approximately 13 per cent of total calcium, 23 per
cent of total potassium, and 25 per cent of total phosphorus (Rennie, 1955).

**Nutrient Sinks**

Major nutrient sinks in forest ecosystems are vegetation, forest floor, and soil. Nutrients also accumulate in fauna but the limited data available (Grimshaw, et al., 1958) indicate that absolute quantities are less than one gram per hectare of each of several macronutrients. In the Great Smoky Mountains, absolute quantities (kg/ha) of calcium, potassium, magnesium, and phosphorus were, respectively, 543, 221, 74, and 49 in trees of a spruce-fir stand and 416, 189, 61, and 46 in trees of an adjacent beech stand (Shanks, et al., 1961). Herbs contained less than 0.8 kg/ha of each of these nutrients in the coniferous stand but 6.6 kg/ha - Ca, 20.1 kg/ha - K, 2.4 kg/ha - Mg, and 1.7 kg/ha - P indicating not only greater absolute but greater relative quantities of nutrients of the herb stratum of deciduous stands. Calcium and potassium weights in the forest floor were, respectively, 361 and 88 kg/ha in the coniferous stand and 38 and 6 kg/ha in the beech stand (McGinnis, 1958). Relatively large quantities of calcium and potassium (860 and 988 kg/ha, respectively) were indicated in the soil of the coniferous stand (McGinnis, 1958).

The distribution and quantities of nutrients in these Southern Appalachian forest ecosystems, in general, are
similar to the other temperate zone coniferous and deciduous forests (Ovington, 1962; Rennie, 1955; Rodin and Basilevic, 1967; Wooldridge, 1970; Gessel and Balci, 1965; Weetman and Timmer, 1967; Cole et al., 1967). These studies and reviews indicated that above ground vegetation in spruce and fir forests may contain from 200 to 500 kg/ha - Ca, 75 to 300 kg/ha - K, and 25 to 100 kg/ha each of Mg and P. Birch spp. and beech spp. stands contained between 75 and 300 kg/ha - Ca, 75 and 200 kg/ha - K, 25 and 150 kg/ha - Mg, and 50 kg/ha - P or less.

Nutrient weights in the forest floor are more variable. In spruce and fir forests, most quantities ranged between 50 and 300 kg/ha - Ca, 25 and 300 kg/ha - K, 10 and 100 kg/ha - Mg, and 10 and 150 kg/ha - P. In birch and beech forests, weights usually ranged from 25 to 500 kg/ha - Ca, 10 to 100 kg/ha - K, 10 to 75 kg/ha - Mg, and 10 to 50 kg/ha - P. Studies in which soil nutrients and other nutrient weights have been determined are limited but in spruce and fir forests levels of exchangeable or available soil nutrients were usually 150 to 500 kg/ha - Ca, 150 to 300 kg/ha - K, 200 to 400 kg/ha - Mg, and 100 to 400 kg/ha - P. In stands of birch and beech, weights ranged from 100 to 400 kg/ha for each of these nutrients.

The forest floor contains an appreciable proportion of the nutrients in temperate zone forests (Ovington, 1968) where most accumulate in the humus layer (H or O2) (Rodin
and Basilevic, 1967); in many coniferous forests, quantities of nutrients in the forest floor may exceed quantities in the vegetation. In deciduous forests, the forest floor contains a smaller weight of nutrients than the vegetation (Rodin and Basilevic, 1967). The absolute weight of nutrients in the forest floor is only slightly less than in coniferous stands, however, reflecting higher concentrations of most nutrients in deciduous litter. Relative abundance of nutrients changes during decay and Fe, Si, and Al, all relative minor components of vegetation, are among the principal nutrients of the forest floor (Rodin and Basilevic, 1967).

In both coniferous and deciduous forests, the absolute quantity of nutrients in the vegetation is directly related to biomass and increases with it (Rodin and Basilevic, 1967; Curlin, 1970). Consequently, as stands age, the absolute quantity of nutrients in the vegetation increases but the rates of accumulation vary among specific nutrients (Ovington and Madgwick, 1959b). Nutrient quantities are less on poorer sites and vary with climatic conditions but this probably reflects lower rates of net primary production and differences in species composition more than lower concentrations in plant tissues of nutrients (Rennie, 1955; Rodin and Basilevic, 1967; Ovington, 1968).

In spruce, fir, and birch forests, nutrients accumulate
in the biomass in the order Ca > K > Mg > P (Rodin and Basilevic, 1967). Larger absolute quantities generally characterize deciduous stands, although beech and birch stands are exceptions. In these forests, nutrient concentrations are lower and nutrient cycles less intense and are more like coniferous than many deciduous forests (Rodin and Basilevic, 1967). The presence of deciduous trees in coniferous stands increases the nutrients in biomass. In pure spruce stands, nitrogen exceeds calcium but the reverse is true of mixed stands. Also, the abundance of magnesium and phosphorus relative to other nutrients is greater in deciduous than coniferous forests.

The total accumulation of nutrients is generally small in understory plants as compared with trees (Ovington, 1962) although exceptions occur such as in spruce stands with well-developed moss ground cover (Weetman and Timmer, 1967) and some deciduous stands with well-developed herbaceous strata (Shanks, et al., 1961).

Comparisons of nutrients in the forest floor and vegetation with soil nutrients indicate that absolute quantities of calcium and potassium are of the same order of magnitude as in the forest floor and plant biomass.

Data which allow comparison of absolute quantities of nutrients in soil with nutrients in the forest floor and plant biomass suggest that soil accumulations are generally
larger although the differences are not always great especially when calcium quantities in the soil and plant biomass of spruce and fir stands are compared (Ovington, 1962).

**Annual Nutrient Flux**

Nutrient transfers among compartments within forest ecosystems occur through uptake from soil and forest floor by plants, litterfall involving plant tissues, and leaching and wash off from plants surfaces by precipitation. Transfers from roots to soil are poorly understood (Ovington, 1968) and transfer through animal litter is minor relative to plant litter as suggested by the small nutrient quantities in animal biomass (Grimshaw, *et al.*, 1958). Annual uptake by forests is closely related to biomass increment (Curlin, 1970) and is maximum when net primary production is greatest (Rodin and Basilevic, 1967). Uptake is usually in the order of Ca > K > Mg > P (Rodin and Basilevic, 1967) although the absolute quantities of specific nutrients vary among species (Duvigneaud and Denaeyer-DeSmet, 1970). In most coniferous and deciduous stands, photosynthetic tissues take up from 70 to 80 per cent of the nutrients (Rodin and Basilevic, 1967); from 23 to 53 per cent of the annual uptake may be by mosses in some spruce stands (Weetman and Timmer, 1967).

Nutrient requirements for the production of merchantable wood as determined by Ljameborsaj (1968) was ca 2.5 kg/cu m; K 1.8 kg/cu m; P 1.1 kg/cu m; for Norway
spruce; requirements of birch were only slightly greater for calcium and slightly lower for potassium and phosphorus. Data from several studies (Weetman and Timmer, 1967; Cole, et al., 1967; Remezov, 1956; Sonn, 1960, cited by Ovington, 1968; Rodin and Basilevic, 1967) indicated ranges of annual nutrient uptake by spruce forests were Ca-17 to 52 kg/ha; K-5 to 40 kg/ha; Mg-2 to 15 kg/ha; and P-2 to 10 kg/ha. Similar ranges were indicated for birch excepting for calcium where some annual rates exceeded 100 kg/ha (Smirnova and Gorodentseva, 1958, cited by Ovington, 1968).

Annual litterfall is the most significant mode of nutrient transfer between vegetation and forest floor in many forests (Curlin, 1970). Quantities in leaf litterfall in spruce-fir vegetation in the Great Smoky Mountains were Ca-18.4 kg/ha; K-14.4 kg/ha; Mg-5.9 kg/ha; and P-4.0 kg/ha; quantities were higher in a beech forest, especially for Ca and K which exceeded values in the spruce stand by factors of 2 and 2.3, respectively (Shanks, et al., 1961). The relatively large values in the deciduous stand reflects in the importance of shrubs and herbs which contributed from 20 to 63 per cent of the total leaf litterfall nutrients. Understory plants have been shown to contribute a greater proportion of nutrients than dry matter to litterfall in other forests (Scott, 1955) or to contain more nutrients than needle litter of some spruce and fir stands.
(Damman, 1971; Weetman and Timmer, 1967). Some Canadian spruce and fir stands produce lesser quantities of litter nutrients annually than spruce-fir stands in the Great Smoky Mountains (Damman, 1971; Weetman and Timmer, 1967). Litter in some northeastern U. S. deciduous forests in comparison with Great Smoky Mountains beech forests contained less potassium and phosphorus; calcium and magnesium weights in beech litter were intermediate as compared with the northeastern stands (Chandler, 1941, 1944; Scott, 1955). These studies showed that a larger quantity of nutrients was in deciduous than coniferous litter.

Rodin and Basilevic (1967) concluded that nutrients in annual litterfall represented from 3 to 5 per cent of nutrients in the plant biomass of spruce forests and from 8 to 10 per cent of the nutrients in deciduous stands. These differences would reflect the higher nutrient concentrations of deciduous litter (Scott, 1955; Lutz and Chandler, 1946) and the nearly complete annual turnover of foliage in deciduous stands; leaf litter is especially important in nutrient transfers to the forest floor in all forests and accounts for from 55 to 90 per cent of total litterfall nutrients (Rodin and Basilevic, 1967). Litterfall nutrients reach maximum rates of return between 50 and 70 years but may decrease thereafter (Rodin and Basilevic, 1967).

Studies in numerous forest types indicate that relative to litterfall, a large proportion of nutrients may be
transferred from vegetation to the forest floor annually through precipitation (Cole, et al., 1967; Will, 1955, 1965; Tamm, 1953; Madgwick and Ovington, 1959; Carlisle, et al., 1967; Voigt, 1960). Quantities transferred annually range from 6 to 21 kg/ha calcium, 5 to 25 kg/ha potassium, 1.4 to 6.8 kg/ha magnesium and 0.3 to 0.9 kg/ha phosphorus (Weetman and Timmer, 1967; Cole, et al., 1967; Carlisle, et al., 1967; Madgwick and Ovington, 1959). These ranges characterize numerous deciduous and coniferous stands and with exception of one oak stand with high values, little difference is apparent among forest types.

The sources of nutrients in precipitation beneath forests include leachates from plant tissues, plant exudates, and dry aerosols which are washed off plant surfaces (Attiwill, 1966b; Nihlgard, 1970; White and Turner, 1970). Nutrients are susceptible to leaching from living tissues in the order K > Ca > Mg (Tukey, et al., 1958); susceptibility also increases from living to dead tissues, and with senescences (Nihlgard, 1970; Mina, 1965; Attiwill, 1966b; Moore, 1966). Concentrations of nutrients in throughfall may not be closely correlated with foliage concentrations but variations have been related to foliage weight, branch weight, leaf morphology, relative mobility of various nutrients, variations in structure of tree crowns, leaf arrangement, length of time precipitation was in contact with plant
surfaces, rainfall intensity, and duration of dry periods preceding storms (Madgwick and Ovington, 1959; Mina, 1965).

Highest nutrient concentrations characterize stem-flow precipitation (Nihlgard, 1970; Bollen, et al., 1968; Mina, 1965; Tarrant, et al., 1968). Concentrations in stemflow reflect nutrient concentrations of bark (Kaul and Billings, 1965) and generally increase with increasing bark roughness of trees and increased acidity of stemflow water (Mina, 1965; Nihlgard, 1970). High concentrations of nutrients in stemflow water of spruce relative to birch have been reported which were related to bark texture and water pH (Nihlgard, 1970; Mina, 1965).

Despite higher concentrations, stemflow is relatively insignificant in the total quantity of nutrients transferred via precipitation (Bollen, et al., 1968; Mina, 1965; Carlisle, et al., 1967; Tarrant, et al., 1968), reflecting its minor role in the hydrologic cycle of most forests (Helvey and Patric, 1965; Zinke, 1967). Concentration of stemflow about the base of trees results in accumulation of nutrients over a period of years (Mina, 1965) which may affect soil properties (Mina, 1965; Gersper and Holowaychuk, 1971). Stemflow may also be of significance in the nutrient dynamics of epiphytes (Carlisle, et al., 1967; Mina, 1965; Tamm, 1964b).
Annual Nutrient Retention

Nutrients taken up by net production of perennial tissues enter longer cycles such that the annual return of nutrients to the forest floor is less than annual uptake. In many forests retention as compared with annual return is small (Rodin and Basilevic, 1967) although nutrients in litterfall and retention may be nearly equal in some beech forests (Duvigneaud and Denaeyer-DeSmet, 1970). Retention tends to follow the pattern of net primary production, increasing with age to maximum rates at 20 to 30 in coniferous stands or somewhat later in deciduous stands (Rodin and Basilevic, 1967). The absolute quantities of nutrients retained in perennial components annually is generally less than 15 kg/ha of calcium and potassium and 5 kg/ha or less of magnesium and phosphorus in coniferous stands; quantities are higher in mixed and deciduous stands (Rodin and Basilevic, 1967). Patterns of retention of specific nutrients differ from quantities in litterfall and uptake (Rodin and Basilevic, 1967). Potassium is retained in greatest quantities, followed in order by calcium, phosphorus, and magnesium.

Riekerk (1968) compared patterns of transfer within an ecosystem and found that nutrients were characterized by different rates and types of cycles. The major pathway of calcium which tended to remain in the forest floor was
through litterfall and lesser quantities were transferred by leaching. Small quantities of phosphorus were transferred through leaching as compared with litterfall and movement was from upper soil layers to specific sites lower in mineral soil. Madgwick and Ovington (1959) reported large quantities of potassium were transferred through precipitation; other studies (Witherspoon, 1964; Riekerk, 1968) showed that potassium tended to move in rapid subannual cycles.
III. THE STUDY AREA

Location and Topography

The study area lies within the Southern section of the Blue Ridge Province of the Appalachian Highlands (Fenneman, 1938) along the crest of the Balsam Mountains in Haywood and Jackson counties, North Carolina, between $35^\circ\ 15'\ N - W\ 82^\circ\ 55'$ and $35^\circ\ 25'\ N - W\ 83^\circ\ 3'$. Stands were sampled between Wolf Bald (elevation ca. 1768 m, 5800 ft), Sam Knob quadrangle and Wesner Bald (elevation ca. 1695 m, 5550 ft), Hazelwood quadrangle. These peaks are adjacent to mile 425.5 and mile 439.0, respectively, of the Blue Ridge Parkway which traverses the crest of these mountains. The range extends from southeast where contact occurs with Pisgah Ridge, for approximately 46 km (28.5 miles) toward the northwest where it is connected with the Great Smoky Mountains (Wright, 1931). Areas above 1676 m (5500 ft) occupy approximately 28.5 km² (11 square miles) of which 1.4 km² (0.6 square miles) are in the Balsam Mountains; more extensive Southern Appalachian land areas above the 1676 m occur only in the Great Smoky Mountains (Ramsaur, 1960). Maximum elevation is 1954 m (6410 ft) on Richland Balsam.

Surface drainage within the study area is via the
West Fork of the Pigeon River and its tributaries along northeast slopes and the tributaries of the Tuckasegee River along southwest slopes (Goldston, et al., 1948; Goldston, et al., 1954). Within 12 km these tributaries with headwaters often above 1676 m fall to elevations of 823 m and 670 m, respectively, in valley floors along northeast and southwest slopes (Goldston, et al., 1948; Goldston, et al., 1954; Ramseur, 1960). Slopes of 30 to 60 per cent steepness prevail over much of the mountain land (Goldston, et al., 1954).

**Climate**

Abundant and well distributed precipitation throughout the year is indicated by records from a precipitation station maintained at Beech Gap (TVA, 1970; Station #190), elevation 1646 m, 3 km southeast of the study area. Normal precipitation was 193.3 cm./yr. during the 36-year period ending in 1970. Precipitation of this magnitude apparently is typical throughout the study area (TVA, 1963). During the 1963-1970 period, a precipitation minimum of 150.7 cm (59.3 in) occurred in 1963 (TVA, 1963) and a maximum precipitation of 281.8 cm (110.9 in) occurred in 1964 (TVA, 1964). During the remaining years, quantities were below normal only in 1966.

Seasonal variations include maxima during late winter--early spring and during the summer. Minima occur in May and
in the autumn. This pattern is similar to that reported in
the Great Smoky Mountains (Stephens, 1969). This does not
imply that a distinct dry period occurs however; monthly
mean precipitation varied only 4.1 cm between March and May
when the highest and lowest rates, respectively, occurred
(TVA, 1970). Normally, 58 per cent of the precipitation
occurs during the April through October period.

During the 1947-1950 period, precipitation occurred
on the average between 9.5 and 18.2 days per month at 1524 m
elevation in the Smokies (Stephens, 1969). At 1920 m pre-
cipitation occurred from 10.2 to 18.0 days per month. Mean
number of consecutive days per month between periods of pre-
cipitation ranged from 2.0 to 4.1 days at 1524 m and 2.1 to
4.5 days per month to 1920 m. These data indicate the
uniform distribution of precipitation typical of all months
in the Smokies; similar conditions probably exist in the
study area. Snowfall was recorded on 25 to 26 days per year
at both elevations in the Smokies (Stephens, 1969). The
greatest number of snow days was recorded during March; snow
occurred as late as April and as early as October at each
station. Snow cover persisted for approximately 50 days
per year and 13 days for each February and March at both ele-
vations. Total snowfall generally increases with elevation
with a curvilinear relation (Dickson, 1959). In the study
area, snow may accumulate to a depth of a few feet, but is
variable from year to year (James Fleetwood, Personal Communication, 1969). In the Smokies, Shanks (1954) classified the climate as perhumid at 1524 m and above.

Climatic gradients in relation to elevation would be expected (Geiger, 1966) and apparently characterize the Southern Appalachian region. Precipitation generally increases with elevation (Smallshaw, 1953; Dickson, 1959) but important variations are related to topography. Along crests, more precipitation occurs in the mountain passes (known as "gaps" in the Southern Appalachians) than on nearby peaks (Stephens, 1969). Weather systems, especially those associated with cyclonic storms in winter, apparently are compressed in coves and funneled through gaps. In addition, updrafts may carry precipitation across sharp crests (Smallshaw, 1953; Dickson, 1959). Consequently, precipitation is often reduced on windward slopes and crests and may be only 70 per cent of that received on north slopes a short distance below (Smallshaw, 1953).

Temperature data are not available from the study area, but cool summers and cold, but not severe, winters seem normal. Generally, annual January and July monthly mean temperatures decrease with increasing elevation (Dickson, 1959). Soil temperature patterns also parallel this trend (Shanks, 1956). Soil temperature relations show that the nature of vegetation is important in affecting
microclimates, especially in the seedling environment (Shanks, 1956). In the Smokies at high elevations, soil temperatures were much more variable under a deciduous forest than under adjacent spruce-fir forests. Contrast was especially great in the spring prior to canopy closure and was equivalent to more than a 305 m (1000 ft) elevational differential. In the Smokies, February, the coolest month, air temperatures averaged \(-0.7^\circ\) C (\(30.7^\circ\) F) and \(-1.8^\circ\) C (\(28.7^\circ\) F), respectively, at 1524 m and 1920 m. Comparable July means were \(14^\circ\) C (\(57.2^\circ\) F) and \(13.6^\circ\) C (\(56.5^\circ\) F). Absolute winter minima were \(-22.2^\circ\) C (\(-8^\circ\) F) and \(-24.4^\circ\) C \((-12^\circ\) F) (Stephens, 1969). Absolute summer maxima were \(31.6^\circ\) C (\(89^\circ\) F) and \(26.6^\circ\) C (\(80^\circ\) F). Over much of the Southern Appalachians, mean daily temperature ranges, both in winter and summer, tend to decrease toward higher elevations in association with increased wind and cloudiness (Dickson, 1959).

The degree of cloudiness affects radiation flux at the earth's surface (Reifsnyder and Lull, 1965) and therefore is an important parameter regulating ecosystem processes such as evapotranspiration and primary productivity. Both cloudiness and fog increase with increasing elevations in the Southern Appalachians (Dickson, 1959; Stephens, 1969).

Shanks (1954) classified the climate in the Smokies as mesothermal at 1524 m (after Thornthwaite, 1948) and as microthermal at 1920 m. The boundary between these climates
approximates the lower limit of continuous spruce-fir forest. It was noted, however, that Southern Appalachian spruce-fir forests are wetter than their Taiga counterparts.

In association with altitudinal-temperature relations, frost-free period decreases with increasing elevation (Dickson, 1959). Interpolation from graphs presented by Dickson (1959) indicates frost-free periods of ca 155 days at 1524 m and ca 130 days at 1920 m. In the Smokies, periods between 0°C temperatures in spring and autumn were 148 days at 1524 m and 152 days at 1920 m. The latter seems anomalous, especially since this period was 152 days at 1173 m (3850 ft) and 156 days at 445 m (1460 ft). The deviations from Dickson's (1959) results emphasize the significance of cold air drainage as related to topography. Geiger (1965) has noted that cold air drainage may cause lower elevations to have lower minima than higher elevations. Cold air drainage proved to be so important that separate regressions were necessary to predict length of growing season in valleys and on adjacent summits in the Southern Appalachians (Dickson, 1959). At comparable elevations, the frost-free period of summits was several days longer than in valleys. Topographic position would be an important factor influencing precipitation and temperature throughout the Southern Appalachians, including the study area.

Ultimately moisture available to plants is a function
of the interaction of gross precipitation, interception by vegetation and the forest floor, soil properties, and evapotranspiration. Low vapor pressure deficits were typical throughout the year and, as would be expected, potential evapotranspiration decreases with increasing elevation (Shanks, 1954; Dickson, 1959; Stephens, 1969). Potential evapotranspiration ranging from ca 6-9 cm characterizes high elevations of both the Smokies (Stephens, 1969) and the Mt. Mitchell area (Dickson, 1959). Values were only slightly higher at the 1524 m elevation in the Smokies. At both Smoky Mountain elevations, precipitation exceeded potential evapotranspiration by a factor of nearly four annually and by a factor of more than two from April to October inclusive. Stephens (1969) calculated high soil moisture levels in the Smokies; he concluded that soil moisture stress was infrequent at higher elevations due to the combination of high soil moisture, frequent precipitation, and low vapor pressure deficit. Soil moisture measurements made by Helvey and Hewlett (1962) 50 km southwest of the Balsam Mountains in an area with soils of similar texture but at lower elevations and with less organic matter support Stephens' (1969) conclusions. They found that soils consistently remained above soil moisture tensions of 15 atmospheres through the growing season and concluded that vegetation on deep soils throughout the high rainfall belt of the Southern Appalachians seldom,
if ever, suffers from true drought.

Geology

The southeastern one-half of the study area is included in the Pisgah Quadrangle which was mapped and described by Keith (1907). The remaining northeast one-half has been considered in varying degrees of detail by Pratt and Lewis (1905); Wright (1927, 1928, 1931); and Olson, et al., (1946). The area is almost entirely underlain by Carolina gneiss. This is a Precambrian metasedimentary and much metamorphosed Series. It apparently underwent metamorphism and invasion by granitic materials during Precambrian and again during Paleozoic periods (Hadley and Goldsmith, 1963). The Series consists of a heterogenous assemblage of layered micaceous and hornblendic gneisses, mica schist, and amphibolite (Hadley and Goldsmith, 1963). Mica gneisses and mica schists predominate in the study area (Keith, 1907). Mica gneiss is a broad compositional group including biotite gneiss, two-mica gneisses and mica schist, mica-feldsparquartz gneiss, hornblende-biotite gneiss, and calc-silicate granofels (Hadley and Goldsmith, 1963). Keith (1907) noted an abundance of cyanite gneiss, garnet gneiss and pegmatite in the Balsam Mountains. Small areas of Roan gneiss consisting of larger quantities of hornblende-gneiss were differentiated by Keith (1907) in the present study area.
In a more modern treatment (Hadley and Goldsmith, 1963) these rocks were considered as a lithologic variant of Carolina gneiss in which they were included. Other features of this Series include numerous enclosed bodies of intrusive granite (Keith, 1907) and numerous faults and joints (Olsen, 1946).

The presence of pegmatite containing microcline and biotites which yield potassium upon weathering (Voigt, 1965) may be of significance in the present study. Also, Keith (1907) noted that the cyanite and garnet gneisses with abundant quartz and mica weather producing coarse textured soils.

Certain other surficial features attributual to the geology of the area are of importance in the ecology of the forests. The cyanite and garnet gneisses often form large cliffs and rocky slopes (Keith, 1907). This would reduce effective soil volume in which vegetation may root, but at the same time, introduce fresh rock near the surface from which nutrient inputs to the soils may occur via geologic weathering. Keith (1907) suggests that site productivity is lowest where schists predominate, higher where cyanite and garnet gneisses are important and highest where other gneisses occur.

Block fields may also occur above 1524 m on steep slopes and in headwater basins of streams (Hadley and Goldsmith, 1963). Blocks may be up to 6 m in length and resemble talus due to the removal of interstitial material by surface
runoff. These are not talus since cliffs are usually not present (Hadley and Goldsmith, 1963). Such block fields are colluvial in origin and were formed by mechanical weathering of massive bedrock on higher slopes. Hadley and Goldsmith (1963) noted that there is no evidence of recent accumulation by falling or sliding and that little change in character of the slopes seems to have occurred in recent times. Further, they felt the presence of large trees would retard further development of these fields. They suggested that their origin may have been similar to that of block fields in the northern Appalachians, i.e., by frost action and solifluction during the waning stage of glaciation. Furthermore, the formation would have been augmented by the absence of trees; Hadley and Goldsmith (1963) suggest that a timberline may have existed in the Smokies at 1524 m (5000 ft) or perhaps as low as 914 m (3000 ft) during the Pleistocene.

The contrast between the geology of the study area and the Great Smoky Mountains where extensive areas of spruce-fir forest also occur may be of importance in nutrient dynamics of the Balsam Mountain forests. Much of the Smokies is underlain by late Precambrian aged variably metamorphased sandstone, conglomerate, and siltstone of the Ocoee Series (Hadley and Goldsmith, 1963). Carolina gneiss and associated plutonic rocks are much older than the Ocoee Series
and form a basement complex beneath it. No sharp boundary exists between the two, but the Ocoee from the northwest and Carolina gneiss from the southeast intermingle immediately north of the study area in the Hazelwood and Dellwood Quadrangles (King, et al., 1958).

Soils

Soils of three Series have been mapped in the study area (Goldston, et al., 1948; Goldston, et al., 1954). Ashe stony loam, 30 to 60 per cent slope, covers the northwest one-half of the area extending from Wesner Bald to beyond Lone Bald. The remainder of the area is mapped as stony rough land which has been considered as either a complex of Porters and Ashe soils or a complex of Porters and Ramsey soils. The occurrence of Ramsey soils in the immediate study area is doubtful since it develops from shale, quartzite, sandstone, or conglomerate parent materials which are not present at high elevations in the Balsam Mountains. Ashe soils develop from parent material higher in siliceous materials, are lighter in color, and lower in plant nutrients than Porters soils. Both are generally shallow, usually being 75 cm or less to bedrock. Cambic rather than Argillic subsurface horizons are present in both. Throughout the area, shallow rocky soils with frequent rock outcrops are typical (Holmes, 1911; Korstian, 1937; Coile, 1939; Goldston, et al., 1948; Goldston, et al., 1954).
Locally, the soil consists of organic material several centimeters thick directly over bedrock.

These Series have been classified as Gray-Brown Podzolic soils, but their immature profiles have been noted (Goldston, et al., 1954). More recently, similar soils have been described at high elevations in the Great Smoky Mountains and classified as Sols Bruns Acides (McCracken, et al., 1962; Wolfe, 1967) or the equivalent Umbric Dystrochrepts (Wolfe, 1967).

These soils are characterized by duff mull, low pH, low base status, high exchangeable aluminum and decreasing amounts of organic carbon with increasing depth (McCracken, et al., 1962). Soil pH may range from 2.9 - 4.3 under spruce and 3.7 - 5.0 under beech and yellow birch (Cain, 1931; McCracken, et al., 1962). Acidity decreases with increasing depth to approximately pH 4.5 in the C horizon under both spruce-fir and beech (McCracken, et al., 1962). Acidity also increases with increasing elevations (Cain, 1931). Exchangeable cations decrease with depth beneath spruce-fir ranging downward from 1.3 meq/100 g of soil in the Al horizon. Base status is similar beneath beech although slightly higher in the B horizon than beneath spruce-fir (McCracken, et al., 1962). Additional characteristics of soils under Southern Appalachian spruce-fir include lesser quantities of detritus on the forest floor as compared with
northern spruce-fir stands (Oosting and Billings, 1951; McGinnis, 1958); gradual transition from organic to mineral horizons (Oosting and Billings, 1951; McGinnis, 1958; McCracken, et al., 1962; Wolfe, 1968); well developed Al horizons (Oosting and Billings, 1951; McCracken, et al., 1962; Wolfe, 1967); Oosting and Billings, 1951; McCracken, et al., 1962; Wolfe, 1967); and textures including loam, sandy loam, and sandy clay loam (Holmes, 1911; Coile, 1938; McCracken, et al., 1962).

Podzols have also been described at various locations in Southern Appalachian spruce-fir forests (Coile, 1938; Oosting and Billings, 1952; Wolfe, 1967), including Haywood and Transylvania counties adjacent to and possibly within the present study area (Coile, 1938). In the southern part of the region considered by Coile (1938) (which includes the present study area), Podzols were less well-developed than farther north in West Virginia. Podzols classified as Entic Normorthods described by Wolfe (1967) in the Great Smoky Mountains occurred locally in association with coarser textured parent materials such as sandstone and at crests of higher peaks where slopes were less steep. Wolfe (1967) suggested that development of Spodic and Albic horizons is retarded on steeper slopes where lateral translocation of free iron oxides may occur.

The properties of Podzols may be further affected by
the nature of the vegetation. Coile (1938) found a zone of iron accumulation typical beneath spruce but not pure fir stands.

Flora and Floristic Elements

The flora of the Southern Appalachians above 1676 m elevation including the Balsam Mountains has been studied by Ramseur (1960). Three hundred ninety-one species and varieties in 214 genera and 63 families were present. Spruce-fir and non-beech deciduous forests were composed of 145 and 201 species, respectively, and shared 75 per cent of the species in common. Thirty-seven species of shrubs and 48 species of trees occurred in these two communities. Two hundred sixty-five species occurred in the Balsam Mountains exceeding the number of species of all other high elevation areas studied. Of these, 22 were trees; 33 were shrubs; and 210 were herbs.

Fraser fir (Abies fraseri), Rhododendron catawbiense, Cardamine clematitis, Stachys clingmanii, and Solidago glomerata were among 41 species of Southern Appalachian (Little, 1971) where it occurs in seven disjunct areas (Ramseur, 1960). Closely related species are Abies balsamea, widely distributed in the northeastern United States and eastern and central Canada and Abies lasiocarpa in the mountains of western United States and Canada (Bakuzis and Hansen, 1965). In Virginia, where the ranges of Fraser fir
and *Abies balsamea* are contiguous (Little, 1971), hybridization has been suggested (Fulling, 1936; Bakuzis and Hansen, 1965) but recent anatomical and morphological investigations (Robinson and Thor, 1969) negate this possibility. Two varieties of *Abies balsamea* have been described which represent ends of a cline and form a continuous population (Bakuzis and Hansen, 1965). Fraser fir is similar to *A. balsamea* var. *phanerolepis* and originally was part of the same population (Bakuzis and Hansen, 1965). Fraser fir has been isolated since the Pleistocene and is distinct from *A. balsamea* (Bakuzis and Hansen, 1965).

Species generally widespread in Canada and northern United States but limited to uplands and mountains in the Southern Appalachians include *Picea rubens*, *Betula lutea*, *Prunus pensylvanica*, *Sorbus americana*, *Acer spicatum*, *Acer pensylvanicum*, *Ribes rotundifolium*, *R. glandulosum*, *Rubus idaeus* var. *canadensis*, *R. canadensis* L., *Rhododendron maximum*, *Viburnum alnifolium*, *V. cassinoides*, *Sambucus pubens*, *Veratrum viride*, *Clintonia borealis*, *Maianthemum canadense*, *Trillium erectum*, *Claytonia caroliniana*, *Tiarella cordifolia*, *Oxalis acetosella*, *Viola blanda*, *Circaea alpina* and *Aster acuminatus* (Ramseur, 1960).

Northern species near their southern limit in the Southern Appalachians include *Lycopodium lucidulum*, *Luzula acuminata*, *Amelanchier laevis* weig. (*A. arborea* var. *laevis*),
Acer saccharum, Aesculus octandra, Impatiens pallida, and Eupatorium rugosum. Species widespread in the Eastern United States form the largest single element of the flora comprising 36.8 per cent of the species (Ramseur, 1960).

**Classification of High Elevation Forests**

At higher elevations in the Southern Appalachians, forests of northern hardwoods, spruce, and fir are characteristic (Braun, 1950). Northern hardwood forests occur above elevations of 1372 m (4500 ft) where the principal species include sugar maple, yellow birch, beech, and buckeye. Within gaps, beech frequently dominates stands on south slopes (Whittaker, 1956), while yellow birch may dominate north and northeast slopes (Crandall, 1958).

These high elevation forests have been variously classified in broad vegetational treatments. Shantz and Zon (1924) considered the deciduous forests of beech, yellow birch, maple, and hemlock as part of the Northeastern hardwood forest; similarly, spruce and fir forests have been considered a southern extension of the northern coniferous forest (Shantz and Zon, 1924; Korstian, 1937). Although these forests share many elements with New England forests, Braun (1950) notes the occurrence of a number of endemic species not the least of which is *Abies fraseri* which suggests an antiquity of these forests predating the Pleistocene.
Hence, the spruce-fir forests restricted to higher elevations within the oak chestnut forest region are considered as distinct from the northern coniferous forests (Braun, 1950). Oosting and Billings (1951) compared Southern Appalachian spruce-fir stands with northern stands. On the basis of physiognomy and composition, they concluded that the southern stands are part of the Boreal Forest Formation but should be recognized as a phase distinct from northern forests in that floristic and ecological differences occur. More recently (Küchler, 1964), these forests were classified as the Southeastern spruce-fir forest and differentiated from the Northeastern spruce-fir forest. Forests of elevations just below the coniferous forest were classified as Northern Hardwoods.

**Forest Extent**

The original area of spruce-fir forests in the Southern Appalachians was estimated as one million acres (Korstian, 1937). Possibly from 40,500 ha (100,000 acres) to 60,700 ha (150,000 acres) were in Western North Carolina (Holmes, 1911) of which some of the most extensive and heaviest were in the Balsam Mountains (Pinchot and Ashe, 1897; Harshberger, 1911). In recent surveys (Tennessee Valley Authority, 1959; Tennessee Valley Authority, 1962), spruce-fir forests occupied 2350 ha (5000 acres) or 3 per cent of the commercial forest land within National forest land but outside the Great
Smoky Mountains National Park in Haywood County, North Carolina. Comparable data were not available from Jackson County, although in the two-county area, spruce and fir comprised ca 2.8 per cent of the volume in trees 15.2 cm dbh and larger. Northern hardwoods occupied ca 3520 ha (8700 acres) or 4 per cent of the forest area in Haywood County and 7975 ha (19,700 acres) or 8 per cent of the forest area in Jackson County. Over the two-county area, 1.9 per cent of the volume in trees 15.2 cm dbh and larger was in yellow birch.

**Characteristics of Dominants**

At this southern location, red spruce grows more rapidly and to larger sizes than elsewhere within its range. Red spruce 57 in dbh (145 cm) and 162 ft tall (49 m) has been reported (Korstian, 1937). Trees with up to 359 annual rings are reported but 200-250 years seems to be an average maximum age; during this time trees in the south may attain sizes exceeding 20 in dbh as compared with only 15-20 in dbh in the north (Oosting and Billings, 1951). Fraser fir is a smaller tree, the maximum diameter reported being 29 in dbh (ca 73.5 cm) and usually less than 80 ft (24 m) tall (Crandall, 1958). Maximum age reported is 168 years, while 150 years is probably more typical (Oosting and Billings, 1951). Growth rates of Fraser fir exceed both that of red spruce in the south and balsam fir in the north.
(Oosting and Billings, 1951). At 100 years, Fraser fir may exceed the diameter of red spruce in the south by ca 15 percent and balsam fir in the north by one-third (Oosting and Billings, 1951).

Few data are available concerning growth rates or longevity of yellow birch in the Southern Appalachians; however, growth rates of young yellow birch may exceed that of young spruce and fir (Korstian, 1937) and maximum age probably equals or exceeds fir (Oosting and Billings, 1951).

Characteristics of red spruce and fir seedlings also differ. Red spruce seedlings have exceptionally slow-growing, fibrous, shallow root systems (Hart, 1959), and establishment is suppressed by hardwood litter (Korstian, 1937) or thick litter layers in general wherein susceptibility to drying is high (Hart, 1959a). Balsam fir, and presumably Fraser fir, is more prolific and less susceptible to desiccation than red spruce (Hart, 1959b).

**High Elevation Vegetation of the Great Smoky Mountains and Adjacent Areas**

At the lower limit of high elevation forests, red spruce with limited Fraser fir forms stands on open slopes, alternating with deciduous forests of the coves and gaps (Whittaker, 1956). With increasing elevation, coniferous forests occupy an increasing portion of the sites. Red spruce forests reach maximum development between 1372 m
(4500 ft) and 1676 m (5500 ft). Deciduous trees important in these stands include yellow birch, beech, *Acer spicatum*, *Acer pensylvanicum*, and *Amelanchier laevis*. Between 1676 m and 1829 m (6000 ft) red spruce and Fraser fir share dominance. Toward higher elevations and especially on northern slopes, Fraser fir increasingly dominates stands, and above 1890 m (6200 ft) on upper slopes and summits of the highest peaks may form nearly pure stands. *Sorbus americana* may be the only deciduous species in the extreme developments of this forest type; elsewhere red spruce, yellow birch and a few other species occur in small numbers (Pinchot and Ashe, 1897; Korstian, 1937; Braun, 1950; Whittaker, 1956). On extremely exposed sites at high elevations, spruce and fir forests contact health balds (Whittaker, 1956) while along the lower elevational limits, spruce stands contact northern hardwood forests in sheltered situations or, on more exposed sites and southern aspects, red oak dominated forests (Braun, 1950; Whittaker, 1956).

Variations in undergrowth related to site conditions occur. Whittaker (1956) recognized five site-related subtypes in spruce forests and four within Fraser fir forests of the Smokies. Crandall (1958) considered the relation of ground vegetation to site and forest types more intensively and found variations in understory strata related to forest structure, elevation, slope steepness, aspect, and apparent
moisture conditions of sites. Based on frequency and coverage of shrubs, herbs, ferns, and mosses, eight site types were recognized in spruce-fir forests, and three in each spruce-hardwood forests and beech-birch gap forests. Several of these site types corresponded with those described in the Adirondack region (Crandall, 1958). In the balsam fir forests of the northeast, various site types based on herbs and mosses (Heimburger, 1934; Linteau, 1955; Rowe, 1959) are associated with site quality classes, soil moisture regimes, and soil nutrient status (Bakuzis and Hansen, 1965), suggesting that variations in ground cover may reflect variations in the potential of different sites to support forest growth.

Specific attention has been directed to bryophytic communities within subalpine forests of the Smokies by Cain and Sharp (1938) who demonstrated that mosses and liverworts were integral components of humid stands; coverage of surfaces frequently was 100 per cent with the composition of the bryophytic community varying with forest type, with nature of substrata, with stage of successional development, and with site conditions. Within Fraser fir forests, eight distinct bryophytic communities were described, of which one occurred on soil and small boulders, four on fallen logs, and three on tree trunks. The communities on fallen logs showed successional relationships which terminated in a
community similar to the predominant terrestrial community. The fourth was highly site restricted, occurring only on fallen logs on steep north slopes frequently moistened by flowing water. Communities on the trunks were extensively developed and floristically diverse. Development of similar extensive terrestrial communities occurred in red spruce stands. Fallen logs were characterized by only three communities in these stands; the terminal *Hylocomium splendens* community which developed on fallen logs in fir stands was absent in red spruce stands. Lower humidity in red spruce stands was cited as a possible reason. Communities on red spruce boles were floristically impoverished, consisting of only four species as compared with 22 on fir trunks. Coverage was also low, rarely attaining 50 per cent.

Terrestrial, rock surface, and fallen log communities were absent or nearly so in beech forests. The extensive development of herbs and absence of boulders and deep shading accounted for these conditions. Communities on tree trunks were exceptionally well-developed, however.

**High Elevation Vegetation of the Balsam Mountains**

Eight high elevation (above 1676 m) communities recognized in the Balsam Mountains include: spruce-fir forests, fire cherry complex, grass bald, shrub bald, heath bald, beech forest, disclimax (areas disturbed by man) and transition (between spruce-fir and deciduous forests)
Spruce-fir and the fire cherry complex collectively occupied more than 90 per cent of the high mountain region (Ramseur, 1960). Fire cherry forms nearly pure stands during early successional stages, and subtle shifts in community composition develop as various shrubs and herbs invade these stands. The most widespread of these in the Balsams was the fire cherry-yellow birch phase (Ramseur, 1960). Yellow birch appeared after fire cherry. \textit{Acer spicatum}, \textit{Sorbus americana}, red spruce and Fraser fir were frequent components. This community was best expressed on gentle protected slopes or coves. Fire cherry was usually ca 10 cm (4 in) dbh while yellow birch ranged from 10 cm to 15 cm (5.9 in). Shrubs in this phase included \textit{Rubus canadensis}, \textit{Ribes rotundifolium}, \textit{R. glandulosum}, \textit{Rhododendron maximum}, \textit{R. catawbiense}, \textit{Viburnum alnifolium}, \textit{V. cassinoides}, and \textit{Sambucus pubens}. Herbs included \textit{Aster chlorolepis}, \textit{Luzula acuminata}, \textit{Eupatorium rugosum}, \textit{Impatiens pallida}, and \textit{Dryopteris austriaca} (Jacq.) Woynar [\textit{D. intermedia} (Willd.) Gray].

**Occupancy and Land Use Systems**

Prior to European settlement, various Indian tribes occupied Western North Carolina, the last of which were the Cherokees (Gersmehl, 1970). The Cherokees located their villages in the lowlands where limited agriculture was practiced and utilized the uplands for travel and hunting.
The use of fire in association with these activities may have aided in thinning the original forests (Gersmehl, 1970). Contact between Cherokees and European traders and explorers predates the Revolutionary War (Goldston, et al., 1948; Gersmehl, 1970). The new demand for barter goods intensified hunting pressure (Gersmehl, 1970) and perhaps increased the effects of Cherokee occupancy on upland forests.

European settlement began during the latter decades of the eighteenth century, especially after the Revolution (Goldston, et al., 1948; Goldston, et al., 1954); Haywood County, North Carolina, was settled by officers and soldiers who received land grants immediately following the War (Federal Writer's Project, 1939). A form of transient livestock grazing was practiced several miles in advance of permanent settlements (Gersmehl, 1970) with possible effects on forests. Earliest settlers occupied the bottomlands such as those along the Pigeon River in Haywood County and Tuckasegee River in Jackson County, while lands along smaller streams were occupied somewhat later (Goldston, et al., 1954). Lowlands were utilized for crop production and uplands for livestock grazing, a practice which was widespread and continued through much of the nineteenth century (Gersmehl, 1970). Clearing of mountain lands for grazing was initiated by Europeans and may explain the origin and maintenance of certain grassy balds at high elevations in the Balsam and surrounding mountains (Gersmehl, 1970).
Grazing declined toward the latter part of the nineteenth century as forest utilization intensified. The period between 1880 and 1930 was one of intensive logging (Gersmehl, 1970); by its close, virtually all mountain lands had been cut-over and large areas were clearcut. Utilization of forest products, however, continued (Goldston, et al., 1954) and large paper mills are presently located at Canton, Haywood County, and at Sylva, Jackson County. Lumber production continued commercially at several locations in the two-county area (Goldston, et al., 1948; Goldston, et al., 1954). Commercial deposits of several minerals, including mica, occur in the two-county area (Olson, et al., 1946). Roads to mines, some of which are at high elevations, and spoil deposited around lines have local but very intense effects on forests.

Between World Wars I and II, a transition of land use practices occurred (Gersmehl, 1970); much mountain land was abandoned and large tracts came under Government ownership (Lord, 1968). Large areas including high elevation lands were also purchased by paper companies. Currently, land along the crests of the Balsam Mountains is in the National Park System and administered by the Blue Ridge Parkway (Lord, 1968). Much of the adjacent land is in the Pisgah National Forest or is owned by Mead Paper Company.
Forest Utilization in the Balsam Mountains

Selective logging was practiced as early as the mid-1800's near streams and transportation routes (Gersmehl, 1970). By the 1880's the valuable timber species had been removed from more accessible forests and logging was extended into more remote mountain lands. High elevation forests of the Balsam Mountains were still considered non-commercial in 1897 (Pinchot and Ashe, 1897) and perhaps as late as 1907 (Trotter, 1907). Logging was in progress during 1911 near Richland Balsam (Holmes, 1911) and large areas of the spruce-fir forest had been logged by 1916 (Canby, 1916). Although some uncut stands remained near the study area on Pisgah Ridge possibly until the 1920's, cutting was widespread throughout the area by that time (Korstian, 1937). By the early 1930's, the virgin Southern Appalachian spruce-fir forest had been reduced by logging and fire to one-tenth its original extent (Korstian, 1937).

The nature of succession and present vegetation of the area depended on the particular logging method, the extensiveness of the harvest, and the ensuing fire history of sites (Korstian, 1937). Logging was typically by combined steam and animal skidding. The latter damaged residual vegetation very little, but steam skidding was particularly destructive. All trees and regeneration in and near the skidding lanes were frequently destroyed by breakage or
covered by slash. Smaller residual trees were often cut for pulp wood, which together with destructive logging practices left inadequate advanced regeneration and seed sources for re-establishment of coniferous stands. Frequently, even though a few conifers remained especially on better sites, hardwoods such as fire cherry (*Prunus pensylvanica*) and yellow birch grew at faster rates and ultimately dominated stands. Both red spruce and Fraser fir are shade tolerant and could persist for long periods (up to 50 years) after being overtopped. In such cases, where seed trees were nearby and residual conifers remained, stands tended to revert to spruce-fir within a generation. Increased exposure of sites and the build-up of deciduous litter beneath hardwoods where they became established suppressed red spruce regeneration more than relatively prolific and drought resistant fir regeneration. Under these conditions, Fraser fir would be a more important component of secondary stands than red spruce. On sites outside the seeding range of spruce and fir, several generations would be required for re-establishment of conifers.

Immediate establishment of spruce was the exception usually restricted to the poorest and rockiest sites.

Re-establishment of coniferous stands after logging was virtually non-existent on lands which burned (Korstian, 1937). Spruce-fir stands in natural condition were usually
so moist that they rarely burned (Holmes, 1918; Korstian, 1937). However, drying occurred with increased exposure after cutting which together with slash from logging created conditions such that fire was nearly inevitable (Holmes, 1918; Korstian, 1937). Frequently, logged areas burned in successive years and eliminated conifers which might have escaped earlier fires (Korstian, 1937). Fires removed litter (Korstian, 1937; Coile, 1938) and in some intense fires the "soil" (organic matter of the surface mineral layers) burned (Lord, 1968). Erosion removed much of the remaining mineral soil (Korstian, 1937) and in some cases exposed bedrock over extensive areas such as Sam Knob where well-developed spruce stands had formerly existed (Lord, 1968). Hardwoods, especially fire cherry and yellow birch, followed on areas where soil remained (Korstian, 1937). Fire cherry grew rapidly and predominated for 15-20 years. It eventually was replaced by yellow birch, other hardwoods, and shrubs including *Rhododendron* spp. Hardwoods may persist for generations on former coniferous sites (Korstian, 1937). Korstian (1937) concluded that depletion of the Southern Appalachian spruce forest was due to burning following destructive logging.
IV. MATERIALS AND METHODS

Reconnaissance of forest stands in the study area was completed during the fall of 1968 and early spring of 1969. Sought were stands dominated by yellow birch, Fraser fir and/or red spruce of several age classes, and density classes on several aspects within the 1524 m (5000 ft) -1980 m (6500 ft) elevation belt. Elevation to the nearest 6 m (20 ft) using a hand-held aneroid altimeter, azimuth using a Silva compass, horizontal slope form (concave, convex, flat), and slope gradient to the nearest 2 per cent (Suunto clinometer) were determined. Plot centers were marked with wooden stakes. Using the combination rangefinder-Bitterlich method (Lindsey, et al., 1958), density of stems 5.08 cm (2.01 in) or greater at 1.37 m (4.5 ft, dbh) within 0.04 ha (0.1 acre) circular plots was tallied by species. Plot radius was corrected according to slope gradient (Bryan, 1956). In the density tally, trees near plot perimeters were determined to be "in" or "out" using an Edscorp 6-inch Field Rangefinder. Basal area was tallied by species using a 10 factor wedge prism.

Forty 0.04 ha (0.1 acre) plots representing the range of vegetational and site parameters encountered during the preliminary survey were selected for further study.
The perimeter of each plot was delineated by rotating a radius line anchored at plot center. Trees and tall shrubs 2.54 cm diameter at 1.37 m height (dbh) within these plots were measured by dbh tape to the nearest 0.25 cm and tallied by species. One increment core was taken from the north side of ten or more trees selected to represent the species and 2.54 cm and over diameter size classes present. Increment cores were assigned an identification number and stored in plastic straws sealed with small foam rubber cubes (modified from Woods, 1951). In the laboratory, cores were soaked in water for 24 hours and radial increment from 1960-1964 and 1965-1969 measured using a stereoscopic microscope equipped with an ocular micrometer. Additional field measurements taken from each of these trees included height of tree and height to base of living crown to the nearest 0.3 m by Blume-Leiss altimeter, estimated north-south and east-west crown diameters, and crown class as defined by Baker (1950). Increment cores and field measurements were taken from 410 trees. Diameter increments and other dimensions were calculated using programs written for the IBM 360 Model 65 computer.

Vegetational attributes of inferior strata were sampled in twenty of the 0.04 ha plots. Trees and low shrubs less than 2.54 cm dbh and 0.46 m (18 in) or more in height were sampled using one circular 0.009 ha (.0229 acre)
plot nested at the center of each 0.04 ha plot. The diameter at 0.46 m height of each stem was measured to the nearest 0.1 cm with a vernier caliper. The biomass of herbaceous species was estimated from nine 1.0 m square quadrats located at random within the 0.04 ha plots. Herbs were harvested from three quadrats on May 9, June 19, and August 21. These dates coincided with flowering of major species; new plots were randomly selected for each harvest. Above ground portions were clipped, stored in plastic bags, and returned to the laboratory. Vegetation from each quadrat was sorted by species, oven-dried and weighed. Drying was done in a forced ventilation oven at 80 °C for 24 hours.

Biomass and net primary production estimates were based on the harvest date nearest the maximum weight of each species. Voucher specimens of plants excepting the most familiar trees were collected and deposited in the Herbarium, The University of Tennessee, Knoxville. Nomenclature of bryophytes follows Watson (1968); that of vascular plants follows Radford, Ahles, and Bell (1968).

Above ground portions of tree and shrub regeneration less than 0.46 m in height and within each of the three herb quadrats per 0.04 ha plot were harvested on August 21, 1969. Plants were sorted by species and the current year's twig and leaf growth was clipped from 10 or more individuals of each. Ratios of current growth to total biomass were
calculated and applied to the total biomass harvested to estimate annual above-ground production of this stratum.

Biomass of bryophytes was estimated from five 10 cm x 10 cm quadrats located at random in each of 20 0.04 ha plots. Harvesting was done in July, 1969. Mosses in each quadrat were separated from the substratum and rocks; dead branches and leaves of higher taxa were removed. Samples were air-dried and stored in paper bags. Following identification, samples were oven-dried and weighed. Net primary production was estimated as one-third of the biomass following Tamm's procedure (1953).

Biomass estimates of woody stems 0.46 m and taller were based on regression equations relating biomass to stem diameter. Regressions were calculated using both arithmetic and logarithmic ($\log_{10}X$) forms of diameter measurements and biomass estimates. Equations providing the greatest precision were selected for plot parameter estimates. A series of 75 trees representing yellow birch, red spruce, and Fraser fir was harvested during 1959 from the study area and served as the basis for regression equations used in estimating biomass of these species (H. R. DeSelm, unpublished data).

Sixty-seven additional shrubs and trees of 23 species representing additional size classes of the above and other species encountered during plot sampling were harvested
during August and September of 1969. Plants were selected adjacent to plots when possible. Otherwise, inventory was kept of plants harvested within plots for use in possible future re-measurements. Generally, a 100 per cent above ground sample was taken of plants less than 2.54 cm dbh. Plants were cut at the base and carefully lowered to avoid leaf loss. Branches with leaves and fruits intact were removed and placed in labeled paper bags. Bole diameters at 0.46 m and 1.37 m height were measured. Boles were sectioned into short lengths and bagged. Paper bags were placed inside heavy plastic bags for transport to the laboratory. Larger trees were cut at ground level and lowered as carefully as possible. The diameter of all branches on each tree was measured to the nearest 0.1 cm with a vernier caliper just above the basal swell and recorded. Three or more branches (ca 100 among all shrub and tree species) including twigs, leaves, and fruits representing the size classes and crown positions encountered were harvested from each tree. These were stored for transport as above. In some cases, where large branches were present, branches were treated as trees and second order branches were tallied by size and samples collected accordingly. Main boles and larger branches were marked into sections, usually one meter in length, and the terminal diameter and length of each recorded. Cross-sectional discs were cut from the first two
sections (nearest the ground), then from alternate sections, and from the terminal section. Bole and branch discs were stored for transport and later used for specific gravity and nutrient concentration analysis.

In the laboratory, leaves and fruits were removed from twigs. Current leaves and twigs of *Rhododendron* spp. were separated from older leaves and twigs. Leaves, usually 10 or more, were selected from each branch and silhouettes obtained from a photocopy machine. These leaves were oven-dried and weighed. Leaf area of blades of deciduous species was measured with a polar planimeter and the ratio of leaf area (one surface) to weight calculated. Leaf area of Fraser fir was similarly determined except estimates were based on two surfaces and calculated separately for needles aged 1, 2, 3, and 4 years and older. Surface area of red spruce needles were calculated for these age groups but based on four sides, the dimensions of which were measured using a stereoscopic microscope and ocular micrometer. Leaf area measurements were made from ca 2,350 blades and needles of 24 species. Remaining leaves, twigs, and fruits were oven-dried at 80°C for 24 hours. Regressions were calculated of dry weight of leaves, fruits, and twigs, each separately on branch basal diameter by species. Regressions were applied to field branch tallies to estimate crown dimensions. Bole discs were dried for 48 hours and stored.
Prior to specific gravity determinations, triangular wedges were cut from the discs for nutrient analysis. The remaining bole or branch disc was soaked in water for 96 hours or longer until saturated and specific gravity determined by immersion (U. S. Forest Service, 1956). A dissecting needle or ice pick, depending on disc size, was inserted into each sample. The needle or ice pick was placed in a buret clamp and supported on a stand. This assembly was lowered until the sample was submerged in a container of water on the pan of an automatic or triple beam balance and the apparent weight increase recorded. The increase represented the volume (cubic centimeters) of the sample. The specific gravity was calculated as the ratio oven dry weight to volume (grams/cubic centimeter). Approximately 150 determinations representing 12 species were made.

Harvesting procedures during the summer of 1959 from which data were obtained for estimating the biomass and nutrient contents of red spruce, Fraser fir and yellow birch were similar except branches on individual trees were tallied by basal diameter size classes and wood and bark of boles and branches were treated separately. Increment cores from various heights and discs from branch sections were collected and relative proportions of wood and bark and the specific gravity of each determined.

The above measurements were applied to field measurements
and laboratory weights for calculating wood and bark volumes and biomass of boles and branches. The regression of diameter of 1965 as estimated from radial increment on diameter in 1969 of yellow birch, red spruce, and Fraser fir was calculated separately for each plot. These and subsequent regressions using arithmetic and logarithmic forms of data were calculated using Biomedical Stepwise Regression Programs (Dixon, 1969) on the IBM 360 Model 65 Computer utilizing computer facilities of both The University of Tennessee and Southern Illinois University. Increment data from several plots were combined and regressions calculated in cases of minor species. The regressions were the basis of estimating diameter growth and biomass increment during the 1965-69 period. Mean net primary production of perennial bole and branch components was estimated as one-fifth of the difference between the biomass of each component in 1969 and 1965 (Newbould, 1967).

Litterfall was measured between April 24, 1969, and May 4, 1970, in 20 0.04 ha plots for purposes of estimating the net primary production of leaves (Newbould, 1967), evaluating various classes of litterfall as indexes of total stand productivity, and estimating the role of various components in the cycling of four macrometabolites. Large branch and bole litterfall was estimated from one randomly selected 1 m x 5 m quadrat in each plot. At the beginning of
the study, all branch and bole litter was cleared from each quadrat or marked for future identification. Branches exceeding 0.46 m in length falling into the quadrat were periodically harvested, oven-dried, and weighed. Boles were measured and samples collected for specific gravity determinations. Volume assuming the bole section conformed to the frustrum of a cone and weights were computed from these data. Sub-samples were collected for nutrient analysis. Leaves, reproductive parts, bark, and small twig litter were measured using two wooden baskets located at randomly selected sites in each of 20 0.04 ha plots. Baskets were constructed from one-bushel sized containers with bottoms of a fine mesh polyester fabric and supported horizontally at a height of 0.60 m using wooden stakes. Litter was collected every two weeks except the period from November 13, 1969, and April 9, 1970. Deciduous leaves, needles, reproductive components, and bark and small twigs were separated, dried, and weighed. Computer programs were written to calculate annual litterfall from these data. Samples were retained for nutrient analysis.

Dry matter of the forest floor (01 and 02 layers, Soil Conservation Service, 1962) was sampled in each of the twenty intensive study plots. Bole and branch litter 2.54 cm or larger in diameter was sampled using four 1 m x 3 m quadrats extended from plot center to perimeter along
a randomly located transect. The length and terminal diameters of each branch or bole were measured for volume estimates. Volume was calculated assuming frustrum of a cone. Samples were collected for specific gravity determination and nutrient analysis. Biomass was estimated from volume and specific gravity data. Nutrient reserves were estimated by applying nutrient concentrations to biomass estimates (Figure 1).

Dry-matter weight of the litter and humus of the forest floor were samples in 20 0.04 ha plots. Five 1 dm² quadrats were located beginning at the plot center and outward at 3 m intervals along a randomly selected transect. Harvesting was done by cutting around the perimeter of each sample with a large knife and carefully removing the surrounding litter. The limits of the 01 and 02 horizons were determined and thickness of each measured along two edges. The layers were carefully separated, placed in separate labeled paper bags, oven-dried and weighed. Volumes were estimated from thickness data and specific gravity calculated. Sub-samples from the first and second and third through fifth samples were combined and analyzed for nutrient concentrations. The thickness of each horizon was measured at 20 additional points located at 1.5 m intervals along two additional randomly selected transects. The dry-matter weight and nutrient pools of the forest floor were estimated from these and other data.
1. Sample trees felled

2. Bole measurements
   a. Diameter at base and 1.37 m
   b. Section lengths
   c. Section diameters
   d. Discs harvested

   Boles
   Volume
   Specific gravity
   Nutrient analysis
   Bole biomass
   Bole nutrient pools

   Estimates of stand parameters

3. Branch measurements
   a. Tally by basal diameter
   b. Subsamples harvested (three or more intact branches per tree)

   Branch weights
   Foliage
   Twig
   Nutrient analysis
   Estimates of crown parameters by species

4. Stand data
   (diameter tally by species)

Figure 1. Generalized procedure for estimating biomass and nutrient pools of larger woody plants. Regression equation for estimating biomass of tree components from diameter tally are given in Appendix.
Precipitation was measured during the period May 23, 1969, to June 6, 1970. Gross precipitation was measured at five locations distributed the length of the study area. Precipitation throughfall and stemflow were measured in twelve stands. Gauges for measuring gross precipitation and through fall were constructed of one-gallon plastic containers. Collecting funnels with 15.2 cm (6 in) orifices were constructed by removing the bottoms from similar containers. These were connected to storage containers with cork stoppers and copper tubing. Filters of polyester fabric were installed at the bottom of each funnel to exclude leaves and other debris. In addition, a standard 8-inch rain gauge was established according to U. S. Weather Bureau Standards (1952) at one of the open stations to calibrate the plastic gauges.

Within stands, throughfall was measured using a system of roving gauges as recommended by Helvey and Patrie (1964). Four gauges were used in each plot and were re-located at random positions each month. Precipitation was measured and samples collected at two-week intervals from spring to autumn. Because of limited access to the study area, gauges with a larger storage capacity and longer measuring intervals were used during the winter. These gauges were constructed from 20-gallon, plastic garbage bins, each with a 15.2 cm diameter orifice in the top.
One gauge was located at each of the five stations outside stands and at random locations within each of twelve stands. In the autumn one gallon of permanent antifreeze was added to each gauge to insure that snow would melt as it fell into the gauge and not overflow the collector. A small quantity of light-weight motor oil was added to retard evaporation. The depth of precipitation which had accumulated was measured using a meter stick when access to the study area was possible. One plastic throughfall gauge was set up each time to collect a precipitation sample for chemical analysis.

Stemflow measurements were made between May 24, 1969--November 13, 1969, and April 18, 1970--June 2, 1970, on 24 trees representing three species and various tree size classes and stand types. Collars constructed of Johns-Manville Adhesive No. 57 (C. Thomas, personal communication) were installed on each tree. Each was equipped with a plastic funnel and a Tygon delivery tube connected to either 5, 15, or 30-gallon plastic drums. Small trees were equipped with five-gallon drums while as many as four 30-gallon drums were required for larger Fraser fir trees. Depth of water was measured and volume calculated. Samples were collected for chemical analysis. All precipitation samples were stored in either polyethylene or glass containers. Distilled water samples were also periodically
stored for analysis to determine whether nutrients were being leached by storage containers. Spectro-grade chloroform was added as a preservative to all samples.

Nutrient analysis of plant tissues and precipitation involved wet digestion of samples in a HNO$_3$ - HC1O$_4$ - HCl system (Freeman, 1965) followed by nutrient determination using flame emission spectrophotometry, atomic absorption spectrophotometry, or colorimetry. In preparation for digestion, plant tissues, including samples of 01 and 02 horizons from the forest floor, were ground in a Wiley Mill to pass a 2 mm sieve. It was necessary to saw bole and branch samples into thin discs with a saber saw prior to milling. All samples were stored in sealed glass containers. Prior to digestion, lids were removed and samples oven-dried for 24 hours at 80° C in a forced draft oven. Samples were removed from the oven, sealed and rotated to remix fine fragments which might have separated during drying. Subsamples of approximately 0.5 g were weighed to the nearest tenth-milligram after samples had cooled to room temperature. Somewhat larger subsamples of bole tissues and smaller subsamples of herbaceous plants were digested. Up to 120 samples were digested simultaneously on an electric hot plate by using a digestion block constructed from 2" x 3" x 24" aluminum plate drilled for 25 mm diameter test tubes. Subsamples were placed in test
tubes along with two glass beads. Three ml concentrated HNO₃ were added and samples were allowed to predigest at room temperature overnight. Nitric acid digestion was continued at 100°C for one hour in a fume hood. Throughout the digestion, test tubes were covered with 35 mm glass funnels which served as reflux condensers. Two ml 60 per cent HCl0₄ were added through funnels and digested at about 235°C for two hours. Funnels were removed 15 minutes prior to the end of HCl0₄ digestion. Samples were cooled to near room temperature and 1 ml concentrated HCl added and digested at 100°C for 15 minutes. Cooled samples were transferred to 100 ml volumetric flasks, made to volume and stored in 125 ml polyethylene bottles. Digestates from all plant tissues, including samples from plants harvested during the summer of 1969, samples from the forest floor (01 and 02 horizons), and litterfall were analyzed for Ca, K, Mg, and P concentrations using a Technicon Autoanalyzer. With this system, Ca and K were determined by flame emission spectrophotometry and Mg and P by colorimetry. Concentrations of each of these four nutrients were determined in more than 600 plant tissue samples, more than 80 forest floor samples, and 275 litterfall samples. Laboratory facilities of the Departments of Forestry and Agronomy, The University of Tennessee and Department of Botany, Southern Illinois University were utilized in these analyses.
Precipitation samples, especially throughfall and stemflow samples, often contained appreciable quantities of organic matter leached from leaves, branches and boles and were digested by the same procedure employed for plant tissues. Samples of 100 ml were placed in digestion tubes and evaporated to near dryness prior to digestion. Digestates were made to either 50 ml or 100 ml volumes and stored in polyethylene bottles. Calcium, Mg, and K were determined with a Beckman atomic absorption spectrophotometer in the Forest Ecology Laboratory, Forestry Department, The University of Tennessee, Knoxville. Phosphorus was determined by the 1, 2, 4-Aminonaphtholsulfonic acid-reduced molybdophosphoric Blue color method, in perchloric acid system (Jackson, 1958) with color development read with a Klett-Summerson photo-electric colorimeter and No. 66 red filter (660 mu).

Soil morphology was described and samples collected for physical and chemical analysis from soil pits located within each of the twenty 0.04 ha intensive study plots. One or two pits were dug in each plot depending on the homogeneity of the microrelief. The microrelief was noted to be either uniform or characterized by pits and mounds and sampled at 20 points along two randomly selected transects. In plots with uniform microrelief, i.e., essentially free of pit-mounds associated with past windthrows, one soil pit was dug. Where pits-mounds were more common, soil pits were
located in areas of both uniform microrelief and pits-mounds. Twenty-six pits were distributed among twenty plots selected for intensive sampling. Three soil clods of 50-100 cm$^3$ volume were collected from each horizon of 15 selected pits for bulk density determinations (total ca 160) by the Saran-coated method (Soil Conservation Service, 1967). Bulk samples were collected from each horizon for analysis of chemical and physical properties. In addition, distribution of roots was noted and per cent volume occupied by stones 25.4 mm and larger in diameter was estimated.

In the laboratory, bulk samples (total ca 100) were air-dried and crushed in a mortar to pass a 2 mm sieve. The proportion of coarse fragments (2-25.4 mm) in the samples was determined by weighing each fraction. Sieved samples ($\leq$ 2 mm diameter) were used in all subsequent analyses. Color of dry samples was determined in the laboratory using Munsell color charts (Munsell Color Company, 1954). Soil reaction (pH) was measured with a Northrop-Leeds pH meter in 1:1 soil-water solution (Soil Conservation Service, 1967) and 1:1 soil-0.1N KCl solution. In some cases where organic matter content was high and additional water or KCl solution was required to wet the soil, samples were made to a paste and reaction determined.

Organic matter as per cent of oven dry weight of each bulk sample was determined by digestion with chromic acid
and H$_2$SO$_4$ (Jackson, 1958). Particle-size analysis of samples from nine soil pits was determined by the hydrometer method (Day, 1965). Samples high in organic matter (usually 5 percent or more) were treated with hydrogen peroxide (Soil Conservation Service, 1967) prior to analysis.

Exchangeable Ca, Mg, and K of bulk samples were determined by leaching samples with 1N ammonium acetate (Wolfe, 1962) and analyzed for nutrient concentration using a Perkin-Elmer Model 305 Atomic Absorption Spectrophotometer. Cation exchange capacity of these samples was determined by saturating leached soil with NH$_4$Cl and subsequent leaching with sodium acetate and subsequent analysis of leachates for exchangeable ammonia using Nessler's reagent (Wolfe, 1962). Color development in samples was read with a Bausch and Lomb Spectronic 20 spectrophotometer at 410 m$\mu$.

Soil phosphorus concentration in bulk samples was determined by dilute acid-fluoride extraction, a molybdophosphoric Blue method employing 1, 2, 4-Aminonaphthol-sulfonic acid reductant (Wolfe, 1962). Color development was read in a Klett-Summerson photoelectric colorimeter with a No. 66 red filter.
V. RESULTS AND DISCUSSION

Community Attributes

Aerial photographs showed that stands in which spruce and/or fir were important components were limited to about 2000 ha (5000 acres) within the study area. Although a large stand of several hundred hectares occupied west, south, and east slopes of Richland Balsam Mountain, many stands occupied less than 100 ha and were isolated within deciduous stands. Frequently larger stands were broken with stands of deciduous trees several meters wide extending up and down slopes. Reconnaissance showed that deciduous stands consisted primarily of yellow birch, Sorbus americana (mountain ash) and Prunus pensylvanica (fire cherry); these stands were similar to variants of the fire cherry community described by Ramseur (1960).

Red spruce was ubiquitous throughout coniferous stands but only rarely was the leading dominant; the stands selected for this study probably over-represented the aerial extent of stands dominated by red spruce relative to Fraser fir. Spruce-fir stands originally were more extensive in the Balsam Mountains (Holmes, 1911; Korstian, 1937). The relative importance of red spruce and Fraser fir in coniferous stands and the development of deciduous stands on former
spruce-fir sites supported Korstian's (1937) conclusions concerning succession as affected by type of logging operation and occurrence of fire following logging. Fraser fir is apparently a more prolific seed producer, more resistant to seedling desiccation (Hart, 1959a; Hart, 1959b), and together with fire cherry and yellow birch has faster growth rates than red spruce (Korstan, 1937). Where residual Fraser fir remained after logging and sites did not burn, Fraser fir stands developed. Ages of fir stands (Table I) indicated establishment of most trees prior to 1930, in agreement with the logging history of the area (Holmes, 1911; Korstan, 1937). Diameter size-class distribution of many stands was typical of even-aged structure (Baker, 1950), but increment cores indicated a more complex age structure. Often two age classes were present; the majority of the trees were ca 40-50 years of age at dbh but occasional Fraser fir trees aged up to 98 years (at dbh) were present in many stands. These were residual trees remaining after logging and probably provided seeds for re-establishment of stands. Where residual conifers were destroyed by skidding operations, fire, or were removed in pulping operations subsequent to logging, fire cherry and yellow birch stands developed. Somewhat younger ages of yellow birch populations were indicated (Table I: Stands 1, 8, 16, 31, 38, and 64) and together with the absence of
TABLE I

VEGETATIONAL ATTRIBUTES OF STANDS

<table>
<thead>
<tr>
<th>Stand</th>
<th>Composition, IV-200a</th>
<th>Age, Yearsb</th>
<th>Density Trees/Ha</th>
<th>Basal Area m²/Ha</th>
<th>Bole Volume m³/Ha</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abies fraseri</td>
<td>Picea rubens</td>
<td>Betula lutea</td>
<td>Mean</td>
<td>Maximum</td>
</tr>
<tr>
<td>1</td>
<td>10.8</td>
<td>46.9</td>
<td>137.2</td>
<td>28</td>
<td>47</td>
</tr>
<tr>
<td>8</td>
<td>2.1</td>
<td>42.8</td>
<td>126.4</td>
<td>42</td>
<td>65</td>
</tr>
<tr>
<td>16</td>
<td>3.9</td>
<td>1.7</td>
<td>143.2</td>
<td>38</td>
<td>84</td>
</tr>
<tr>
<td>31</td>
<td>1.4</td>
<td>10.2</td>
<td>167.0</td>
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<td>74</td>
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</tr>
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<td>50</td>
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<td>138.5</td>
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<td>50</td>
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<tr>
<td>11</td>
<td>131.4</td>
<td>62.1</td>
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<td>41</td>
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<tr>
<td>Stand</td>
<td>Abies fraseri</td>
<td>Picea rubens</td>
<td>Betula lutea</td>
<td>Age, Years&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Density Trees/Ha&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>-------</td>
<td>--------------</td>
<td>--------------</td>
<td>--------------</td>
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<td>32.6</td>
<td>13.4</td>
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<td>1235 I&lt;sub&gt;c&lt;/sub&gt;</td>
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<td>38.8</td>
<td>2.3</td>
<td>46 Mean, 55 Max</td>
<td>1161 I&lt;sub&gt;c&lt;/sub&gt;</td>
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<td>168.4</td>
<td>31.6</td>
<td>0</td>
<td>45 Mean, 58 Max</td>
<td>890 I&lt;sub&gt;c&lt;/sub&gt;</td>
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<td>19</td>
<td>131.0</td>
<td>31.9</td>
<td>18.3</td>
<td>40 Mean, 51 Max</td>
<td>1903 I&lt;sub&gt;c&lt;/sub&gt;</td>
</tr>
<tr>
<td>20</td>
<td>183.1</td>
<td>13.5</td>
<td>0</td>
<td>39 Mean, 52 Max</td>
<td>2372 I&lt;sub&gt;c&lt;/sub&gt;</td>
</tr>
<tr>
<td>21</td>
<td>163.6</td>
<td>21.8</td>
<td>7.8</td>
<td>38 Mean, 49 Max</td>
<td>2520 I&lt;sub&gt;c&lt;/sub&gt;</td>
</tr>
<tr>
<td>22</td>
<td>101.0</td>
<td>34.8</td>
<td>46.9</td>
<td>41 Mean, 56 Max</td>
<td>1062 2473</td>
</tr>
<tr>
<td>23</td>
<td>157.1</td>
<td>26.1</td>
<td>2.0</td>
<td>38 Mean, 54 Max</td>
<td>2026 -</td>
</tr>
<tr>
<td>24</td>
<td>132.8</td>
<td>41.8</td>
<td>20.7</td>
<td>39 Mean, 56 Max</td>
<td>1730 -</td>
</tr>
<tr>
<td>26</td>
<td>128.1</td>
<td>39.3</td>
<td>2.9</td>
<td>36 Mean, 50 Max</td>
<td>3879 3333</td>
</tr>
<tr>
<td>32</td>
<td>142.5</td>
<td>26.9</td>
<td>19.0</td>
<td>40 Mean, 57 Max</td>
<td>1384 753</td>
</tr>
<tr>
<td>47</td>
<td>154.0</td>
<td>46.0</td>
<td>0</td>
<td>44 Mean, 56 Max</td>
<td>1534 -</td>
</tr>
<tr>
<td>48</td>
<td>162.9</td>
<td>37.1</td>
<td>0</td>
<td>41 Mean, 53 Max</td>
<td>1557 -</td>
</tr>
<tr>
<td>49</td>
<td>97.1</td>
<td>57.1</td>
<td>8.5</td>
<td>36 Mean, 53 Max</td>
<td>1631 1828</td>
</tr>
<tr>
<td>51</td>
<td>127.1</td>
<td>58.7</td>
<td>3.7</td>
<td>39 Mean, 50 Max</td>
<td>2496 -</td>
</tr>
<tr>
<td>52</td>
<td>173.1</td>
<td>18.3</td>
<td>2.0</td>
<td>38 Mean, 47 Max</td>
<td>2965 -</td>
</tr>
<tr>
<td>54</td>
<td>169.7</td>
<td>17.3</td>
<td>6.5</td>
<td>39 Mean, 50 Max</td>
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<tr>
<td>57</td>
<td>175.0</td>
<td>22.6</td>
<td>0</td>
<td>38 Mean, 53 Max</td>
<td>2323 0</td>
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<tr>
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<td>107.0</td>
<td>90.0</td>
<td>3.0</td>
<td>46 Mean, 54 Max</td>
<td>890 -</td>
</tr>
</tbody>
</table>
TABLE I (continued)

<table>
<thead>
<tr>
<th>Stand</th>
<th>Composition, IV-200&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Age, Years&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Density Trees/Ha</th>
<th>Basal Area m²/Ha</th>
<th>Bole Volume Ic, m³/Ha</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abies fraseri</td>
<td>Picea rubens</td>
<td>Betula lutea</td>
<td>Mean</td>
<td>Maximum</td>
</tr>
<tr>
<td>60</td>
<td>152.0</td>
<td>39.4</td>
<td>0</td>
<td>40</td>
<td>48</td>
</tr>
<tr>
<td>61</td>
<td>177.2</td>
<td>17.2</td>
<td>1.9</td>
<td>42</td>
<td>53</td>
</tr>
<tr>
<td>62</td>
<td>156.8</td>
<td>28.2</td>
<td>4.1</td>
<td>34</td>
<td>50</td>
</tr>
</tbody>
</table>

<sup>a</sup>Relative basal area + relative density.

<sup>b</sup>Estimated from regression equations of age on diameter of stems > 2.54 cm dbh.

<sup>c</sup>Tree-tall shrub stratum (stems > 2.54 cm dbh).

<sup>d</sup>Sapling-low shrub stratum (stems > 0.5 m tall < 2.54 cm dbh).

<sup>e</sup>Not sampled.
five cherry supported Ramseur's (1960) conclusion that fire cherry became established first, and invasion by yellow birch followed on many sites.

The limited stands of red spruce were generally at lower elevations relative to fir stands (Appendix A) and may have reflected less severe environmental conditions and/or less intensive logging of original stands. Older trees were usually more important components of spruce stands with some attaining ages and diameters at 1.4 m (dbh) of 131 years, 45 cm; 151 years, 48 cm; 216 years, 34 cm; and 247 years, 47 cm. The apparent higher elevational limit of spruce-fir stands in the Balsam Mountains as compared with the Great Smoky Mountains (Whittaker, 1956) may reflect in part the logging history of the former. Fraser fir occurs at higher elevations than red spruce (Whittaker, 1956), and its establishment may have been limited at lower elevations where red spruce occurred. Red spruce would have been at a competitive disadvantage in association with more rapidly growing hardwoods; and after fire cherry and yellow birch communities were established, development of red spruce stands would be delayed for generations (Korstian, 1937).

The lower elevational limit of spruce-fir forests of 1372 m (4500 ft) in the Southern Appalachians is based largely on work done on the northwest slopes of the Great Smoky Mountains (Whittaker, 1956). In contrast, the Balsam
Mountains are oriented from northwest to southeast such that one slope has southwest exposure. Restriction of spruce-fir stands to higher elevations seems probable at least on this exposure. Between Lone Bald and Wesner Bald in the study area, deciduous forests in which *Quercus rubra* was an important component extended to the tops of most mountain peaks. Similar vegetation has been described elsewhere in the Southern Appalachians (Braun, 1950; Whittaker, 1956). On northeast exposures in this portion of the study area, stands of yellow birch and other northern hardwoods were predominant well above elevations of 1372 m. It seems probable that the lower altitudinal limit of the original spruce-fir forests in the Balsam Mountains and perhaps other cross ranges in the Southern Appalachians was higher than the limit on northwest slopes of the Great Smoky Mountains.

All major tree species and most shrubs generally reported in Southern Appalachian spruce-fir forests (Braun, 1950; Oosting and Billings, 1951; Whittaker, 1956; Ramseur, 1960) were present (Table II) although only a limited number of stands were sampled. Yellow birch, mountain ash, and *Acer spicatum* (mountain maple) were the more important deciduous species in the tree-tall shrub stratum. Densities (tree/ha) of this stratum were similar to those reported in the Smokies (Whittaker, 1966) but basal area, canopy height, and bole volume were lower reflecting their younger age.
### TABLE II

**COMPOSITION AND STRUCTURE OF TREE-TALL SHRUB STRATUM OF THE SPRUCE-FIR ECOSYSTEM**

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Density (Tree/Ha.)</th>
<th>Basal Area (M²/Ha.)</th>
<th>IV-200&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean (Tree/Ha.) STD</td>
<td>Mean (M²/Ha.) STD</td>
<td>Mean (M²/Ha.) STD</td>
</tr>
<tr>
<td><strong>Abies fraseri</strong></td>
<td>100.0</td>
<td>1151</td>
<td>735</td>
<td>36.20</td>
</tr>
<tr>
<td><strong>Acer pensylvanicum</strong></td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Acer spicatum</strong></td>
<td>36.7</td>
<td>23</td>
<td>44</td>
<td>0.07</td>
</tr>
<tr>
<td><strong>Aesculus octandra</strong></td>
<td>3.3</td>
<td>8</td>
<td>4</td>
<td>0.002</td>
</tr>
<tr>
<td><strong>Amelanchier arborea</strong></td>
<td>30.0</td>
<td>13</td>
<td>26</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>Betula lutea</strong></td>
<td>73.3</td>
<td>89</td>
<td>107</td>
<td>1.16</td>
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<tr>
<td><strong>Fagus grandifolia</strong></td>
<td>6.7</td>
<td>4</td>
<td>16</td>
<td>0.13</td>
</tr>
<tr>
<td><strong>Picea rubens</strong></td>
<td>100.0</td>
<td>558</td>
<td>484</td>
<td>13.60</td>
</tr>
<tr>
<td><strong>Prunus pensylvanica</strong></td>
<td>16.7</td>
<td>6</td>
<td>15</td>
<td>0.05</td>
</tr>
<tr>
<td><strong>Quercus rubra</strong></td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Rhododendron catawbiense</strong></td>
<td>13.3</td>
<td>36</td>
<td>124</td>
<td>0.06</td>
</tr>
</tbody>
</table>

<sup>a</sup> Frequency Per Cent: Percentage of total frequency

<sup>b</sup> Density (Tree/Ha.): Average number of trees per hectare

<sup>c</sup> IV-200: Index of Value at 200 years

STD: Standard Deviation
TABLE II (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Density (Tree/Ha.)</th>
<th>Basal Area (M&lt;sup&gt;2&lt;/sup&gt;/Ha.)</th>
<th>IV-200&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean (Tree/Ha.)</td>
<td>Mean (M&lt;sup&gt;2&lt;/sup&gt;/Ha.)</td>
<td>Mean (M&lt;sup&gt;2&lt;/sup&gt;/Ha.)</td>
</tr>
<tr>
<td>Rhododendron maximum</td>
<td>3.3</td>
<td>5</td>
<td>27</td>
<td>0.004</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>36.7</td>
<td>45</td>
<td>88</td>
<td>0.18</td>
</tr>
<tr>
<td>Vaccinium spp.</td>
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<td>112</td>
<td>0.02</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>3.3</td>
<td>4</td>
<td>23</td>
<td>0.003</td>
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<tr>
<td>All species</td>
<td>-</td>
<td>1965</td>
<td>785</td>
<td>51.6</td>
</tr>
</tbody>
</table>

<sup>a</sup>Per cent of plots in which species were present.

<sup>b</sup>Standard deviation.

<sup>c</sup>Sum of relative basal area and relative density.
Maximum density of stands in the study area was only one-half and one-third the densities, respectively, of similar aged Canadian *Picea mariana* (black spruce) (Weetman and Harland, 1964) and *Abies balsamea* (balsam fir) stands in which net primary production has been studied (Baskerville, 1965). Development of sapling-low shrub and tree-shrub regeneration strata was limited or absent (Figures 2 and 3) similar to denser Canadian stands (Weetman and Harland, 1964; Baskerville, 1965) and in sharp contrast to many of the more mature stands in the Great Smoky Mountains (Crandall, 1958; Whittaker, 1966). Fraser fir was the most important species in these strata (Tables III and IV) but occurred in fewer than 60 percent of the plots. Red spruce was as widely distributed in the sapling stratum but was absent from the regeneration stratum as is typical of limited red spruce regeneration in many other spruce-fir forests (Long, 1940). Fraser fir regeneration was abundant only near the summit of Richland Balsam (such as plot 49, Table I, page 99) where dense stands (Figure 4) 0.5 m or less in height occurred.

Development of herbaceous and bryophytic strata varied widely from stand to stand and with season. In less dense stands, *Oxalis acetosella* (Figure 5), *Aster acuminatus*, and *Dryopteris* spp. (Figure 6) formed nearly continuous stands. The latter two were especially prominent from mid- to late summer and were apparently best developed in association with
Figure 2. Fraser fir stand on slopes of lickstone ridge with limited red spruce (right foreground). (Plot 48, August 20, 1971).
Figure 3. Red spruce stand near buckeye gap with dense ground cover of *Dryopteris* spp. (Plot 2, August 20, 1971).
### TABLE III

**COMPOSITION AND STRUCTURE OF SAPLING-LOW SHRUB STRATUM OF THE SPRUCE-FIR ECOSYSTEM**

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent$^a$</th>
<th>Density (Stems/Ha.) Mean</th>
<th>Standard Deviation (Stems/Ha.)</th>
<th>Basal Area (M²/Ha.) Mean</th>
<th>Standard Deviation (M²/Ha.)</th>
<th>IV-200c Mean</th>
<th>Standard Deviation (IV-200c)</th>
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<tbody>
<tr>
<td>Abies fraseri</td>
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<td>384</td>
<td>573</td>
<td>0.03</td>
<td>0.06</td>
<td>39.1</td>
<td>54.3</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td>7.1</td>
<td>15</td>
<td>57</td>
<td>0.0004</td>
<td>0.001</td>
<td>2.78</td>
<td>10.42</td>
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<tr>
<td>Acer saccharum</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acer spicatum</td>
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<td>123</td>
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<td>0.008</td>
<td>0.03</td>
<td>4.02</td>
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<td>Amelanchier arborea</td>
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<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Betula lutea</td>
<td>14.3</td>
<td>115</td>
<td>401</td>
<td>0.01</td>
<td>0.03</td>
<td>4.47</td>
<td>12.96</td>
</tr>
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<td>31</td>
<td>115</td>
<td>0.01</td>
<td>0.04</td>
<td>3.34</td>
<td>12.50</td>
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<tr>
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<tr>
<td>Fagus grandifolia</td>
<td>14.3</td>
<td>15</td>
<td>57</td>
<td>0.001</td>
<td>0.003</td>
<td>3.13</td>
<td>8.00</td>
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<tr>
<td>Picea rubens</td>
<td>42.8</td>
<td>84</td>
<td>105</td>
<td>0.02</td>
<td>0.03</td>
<td>18.68</td>
<td>33.45</td>
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<tr>
<td>Rhododendron catawbiense</td>
<td>7.1</td>
<td>15</td>
<td>57</td>
<td>0.006</td>
<td>0.02</td>
<td>4.43</td>
<td>16.56</td>
</tr>
</tbody>
</table>

$^a$ Frequency is based on the relative abundance of trees in the study area.
TABLE III (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Density (Stems/Ha.) Mean</th>
<th>Basal Area (M²/Ha.) Mean</th>
<th>IV-200&lt;sup&gt;c&lt;/sup&gt; Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhododendron maximum</td>
<td>7.1</td>
<td>23</td>
<td>86</td>
<td>0.01</td>
</tr>
<tr>
<td>Ribes rotundifolium</td>
<td>7.1</td>
<td>8</td>
<td>29</td>
<td>0.0001</td>
</tr>
<tr>
<td>Rubus allegheniensis</td>
<td>7.1</td>
<td>38</td>
<td>144</td>
<td>0.0005</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>14.3</td>
<td>38</td>
<td>100</td>
<td>0.001</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>7.1</td>
<td>92</td>
<td>345</td>
<td>0.002</td>
</tr>
<tr>
<td>Vaccinium spp.</td>
<td>28.6</td>
<td>161</td>
<td>347</td>
<td>0.006</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>14.3</td>
<td>46</td>
<td>144</td>
<td>0.002</td>
</tr>
<tr>
<td>All species</td>
<td>-</td>
<td>1190</td>
<td>1641</td>
<td>0.11</td>
</tr>
</tbody>
</table>

<sup>a</sup>Per cent of plots in which species were present.

<sup>b</sup>Standard deviation.

<sup>c</sup>Sum of relative basal area and relative density.
### TABLE IV

COMPOSITION, FREQUENCY, AND CLIPPING WEIGHTS OF TREE-SHRUB REGENERATION OF SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Spruce-Fir Ecosystem (14 Stands)</th>
<th>Yellow Birch Ecosystem (6 Stands)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Frequency Per Cent</td>
<td>Clipping Weight Per Cent</td>
</tr>
<tr>
<td>Abies <em>fraseri</em></td>
<td>57.1</td>
<td>47.624</td>
</tr>
<tr>
<td><em>Acer spicatum</em></td>
<td>14.3</td>
<td>0.014</td>
</tr>
<tr>
<td><em>Betula lutea</em></td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Rhododendron</em> spp.</td>
<td>7.1</td>
<td>0.016</td>
</tr>
<tr>
<td><em>Ribes glandulosa</em></td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Rubus</em> spp.</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Sorbus americana</em></td>
<td>7.1</td>
<td>0.002</td>
</tr>
<tr>
<td><em>Vaccinium</em> spp.</td>
<td>7.1</td>
<td>0.021</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><em>47.678</em></td>
<td><em>100.000</em></td>
</tr>
</tbody>
</table>

*aPercentages rounded numerically.

*bBased on average values.*
Figure 4. Dense Fraser fir regeneration at 1952 meters elevation on a steep, northeast slope of Richland Balsam. (Plot 49, August 20, 1971).
Figure 5. Ground cover of *Oxalis acetosella* beneath Fraser Fir on Richland Balsam. (Near Plot 26, August 20, 1971).
Figure 6. Ground cover of Dryopteris spp. beneath red spruce on Lone Bald. (Near Plot 43, August 20, 1971).
openings in the overstory. Other species were sparsely distributed (Table V) and in some stands both herbs and bryophytes were absent (Figure 7); in others, bryophytes were predominant in the ground cover and herbs only poorly developed.

Yellow birch stands were in coves which with one exception had northwest through northeast exposures (Appendix A). Basal area (Table VI) and bole volume were lower than in spruce-fir stands and were also significantly lower (0.1 percent level) in immature than in mature yellow birch stands. Inferior woody strata were poorly developed (Figure 8) as in spruce fir stands although species differences were evident. Yellow birch and mountain maple were predominant tree species in the regeneration layer, and Ribes glandulosum, especially prominent in stands with block valley fill, was the predominant shrub (Table IV, page 111). The importance value of yellow birch in the sapling-low shrub stratum (Table VII) was significantly higher (10 percent level) than in spruce-fir stands. Several species of this stratum occurred only in yellow birch stands and many were more widely distributed than in spruce-fir stands. The herbaceous stratum was especially well-developed in late summer (Figure 9) and the number of herbaceous species in yellow birch stands was greater than in spruce-fir stands by a factor of nearly 1.7 times (Table V). Bryophytes were absent from some stands,
<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency (Per Cent)</th>
<th>Clipping Weight (kg/ha)</th>
<th>Frequency (Per Cent)</th>
<th>Clipping Weight (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Phanerogams, total</strong></td>
<td>0.0</td>
<td>51.694</td>
<td>0.0</td>
<td>182.300</td>
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<tr>
<td>Arisaema triphyllum</td>
<td>21.4</td>
<td>0.219</td>
<td>100.0</td>
<td>2.330</td>
</tr>
<tr>
<td>Aster acuminatus</td>
<td>78.6</td>
<td>20.476</td>
<td>100.0</td>
<td>47.645</td>
</tr>
<tr>
<td>A. divaricatus</td>
<td>14.3</td>
<td>2.326</td>
<td>50.0</td>
<td>3.005</td>
</tr>
<tr>
<td>Cardamine clematitis</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
<td>0.178</td>
</tr>
<tr>
<td>Carex spp.</td>
<td>7.2</td>
<td>0.002</td>
<td>100.0</td>
<td>21.447</td>
</tr>
<tr>
<td>Circaea alpina</td>
<td>21.4</td>
<td>0.056</td>
<td>16.7</td>
<td>2.983</td>
</tr>
<tr>
<td>Claytonia caroliniana</td>
<td>14.3</td>
<td>1.574</td>
<td>66.7</td>
<td>18.008</td>
</tr>
<tr>
<td>Clintonia borealis</td>
<td>7.2</td>
<td>0.009</td>
<td>16.7</td>
<td>3.912</td>
</tr>
<tr>
<td>Dioscorea villosa</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
<td>0.217</td>
</tr>
<tr>
<td>Erythronium americanum</td>
<td>14.3</td>
<td>1.421</td>
<td>33.3</td>
<td>0.310</td>
</tr>
<tr>
<td>Eupatorium rugosum</td>
<td>7.2</td>
<td>0.107</td>
<td>50.0</td>
<td>17.500</td>
</tr>
<tr>
<td>Impatiens pallida</td>
<td>14.3</td>
<td>0.026</td>
<td>50.0</td>
<td>3.733</td>
</tr>
<tr>
<td>Lilium superbum</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
<td>1.112</td>
</tr>
<tr>
<td>Luzula acuminata</td>
<td>7.2</td>
<td>0.014</td>
<td>33.3</td>
<td>0.433</td>
</tr>
<tr>
<td>Maianthemum canadense</td>
<td>21.4</td>
<td>1.176</td>
<td>50.0</td>
<td>4.117</td>
</tr>
<tr>
<td>Species</td>
<td>Spruce-Fir Ecosystem (n=14)</td>
<td>Yellow Birch Ecosystem (n=6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------------------------------------</td>
<td>----------------------------</td>
<td>------------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Frequency (Per Cent)</td>
<td>Clip %</td>
<td>Weight (kg/ha)</td>
<td>Frequency (Per Cent)</td>
</tr>
<tr>
<td>Oxalis acetosella</td>
<td>85.7</td>
<td>15.829</td>
<td>23.821</td>
<td>66.7</td>
</tr>
<tr>
<td>Phacelia sp.</td>
<td>14.3</td>
<td>0.009</td>
<td>0.014</td>
<td>33.3</td>
</tr>
<tr>
<td>Phlox sp.</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Podophyllum pellatum</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Polygonatum pubescens</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Potentilla simplex</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Sanguinaria canadensis</td>
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<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Smilax sp.</td>
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<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Solidago glomerata</td>
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<td>0.213</td>
<td>0.321</td>
<td>16.7</td>
</tr>
<tr>
<td>S. caesia</td>
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<td>0.0</td>
<td>0.0</td>
<td>33.3</td>
</tr>
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<td>Stachys clingmanii</td>
<td>7.2</td>
<td>0.005</td>
<td>0.007</td>
<td>16.7</td>
</tr>
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<td>Thaspium barbinode</td>
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<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
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<tr>
<td>Tiarella cordifolia</td>
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<td>0.0</td>
<td>0.0</td>
<td>66.7</td>
</tr>
<tr>
<td>Trillium erectum</td>
<td>7.2</td>
<td>0.065</td>
<td>0.097</td>
<td>0.0</td>
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<tr>
<td>Veratrum viride</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>16.7</td>
</tr>
<tr>
<td>Viola blanda</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>50.0</td>
</tr>
<tr>
<td>Undetermined Compositae</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>33.3</td>
</tr>
<tr>
<td>Undetermined Graminae</td>
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<td>0.0</td>
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</tr>
<tr>
<td>Undetermined seedlings</td>
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<td>0.016</td>
<td>0.024</td>
<td>66.7</td>
</tr>
<tr>
<td>Other undetermined herbs</td>
<td>0.0</td>
<td>0.235</td>
<td>0.0</td>
<td>16.7</td>
</tr>
</tbody>
</table>
TABLE V (continued)

<table>
<thead>
<tr>
<th></th>
<th>Spruce-Fir Ecosystem (n=14)</th>
<th></th>
<th>Yellow Birch Ecosystem (n=6)</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Clipping Weight (Per Cent of Total)</td>
<td>Clipping Weight (Per Cent of Total)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency (Per Cent)</td>
<td>(kg/ha)</td>
<td>(kg/ha)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptogams, total</td>
<td>0.0</td>
<td>98.794</td>
<td>0.0</td>
<td>77.645</td>
</tr>
<tr>
<td></td>
<td>98.794</td>
<td>65.649</td>
<td>65.649</td>
<td>29.870</td>
</tr>
<tr>
<td>Dryopteris spp.(^a)</td>
<td>71.5</td>
<td>97.415</td>
<td>83.4</td>
<td>74.045</td>
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<td></td>
<td>97.415</td>
<td>64.733</td>
<td>64.733</td>
<td>28.485</td>
</tr>
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<td>Lycopodium lucidulum</td>
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<td>1.279</td>
<td>0.0</td>
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</tr>
<tr>
<td></td>
<td>1.279</td>
<td>0.850</td>
<td>0.850</td>
<td>1.385</td>
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<tr>
<td>Polypodium polypodioides</td>
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<td>0.0</td>
<td>33.3</td>
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</tr>
<tr>
<td></td>
<td>0.0</td>
<td>0.0</td>
<td>3.600</td>
<td>1.385</td>
</tr>
<tr>
<td>Herbs, total</td>
<td>0.0</td>
<td>150.488</td>
<td>0.0</td>
<td>259.944</td>
</tr>
</tbody>
</table>

\(^a\)Includes Dryopteris intermedia and D. spinulosa.
Figure 7. Absence of herbaceous ground cover beneath a dense red spruce stand on Wolf Bald. (Plot 6, August 20, 1971).
### TABLE VI

**COMPOSITION AND STRUCTURE OF TREE-TALL SHRUB STRATUM OF THE YELLOW BIRCH ECOSYSTEM**

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Centa</th>
<th>Density (Tree/ Ha.) Mean</th>
<th>Density (Tree/ Ha.) STD</th>
<th>Basal Area (M²/ Ha.) Mean</th>
<th>Basal Area (M²/ Ha.) STD</th>
<th>IV-200c Mean</th>
<th>IV-200c STD</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Abies fraseri</em></td>
<td>50.0</td>
<td>20</td>
<td>23</td>
<td>0.31</td>
<td>0.85</td>
<td>2.09</td>
<td>3.37</td>
</tr>
<tr>
<td><em>Acer pensylvanicum</em></td>
<td>20.0</td>
<td>5</td>
<td>10</td>
<td>0.005</td>
<td>0.01</td>
<td>0.74</td>
<td>1.66</td>
</tr>
<tr>
<td><em>Acer spicatum</em></td>
<td>60.0</td>
<td>242</td>
<td>298</td>
<td>0.82</td>
<td>0.90</td>
<td>26.28</td>
<td>30.14</td>
</tr>
<tr>
<td><em>Aesculus octandra</em></td>
<td>40.0</td>
<td>39</td>
<td>67</td>
<td>0.04</td>
<td>0.05</td>
<td>7.58</td>
<td>20.35</td>
</tr>
<tr>
<td><em>Amelanchier arborea</em></td>
<td>70.0</td>
<td>42</td>
<td>59</td>
<td>0.11</td>
<td>0.18</td>
<td>1.93</td>
<td>1.99</td>
</tr>
<tr>
<td><em>Betula lutea</em></td>
<td>100.0</td>
<td>1502</td>
<td>1611</td>
<td>24.10</td>
<td>9.80</td>
<td>149.60</td>
<td>26.20</td>
</tr>
<tr>
<td><em>Fagus grandifolia</em></td>
<td>30.0</td>
<td>47</td>
<td>90</td>
<td>0.06</td>
<td>0.10</td>
<td>1.81</td>
<td>3.57</td>
</tr>
<tr>
<td><em>Picea rubens</em></td>
<td>50.0</td>
<td>175</td>
<td>336</td>
<td>1.64</td>
<td>2.61</td>
<td>12.98</td>
<td>18.99</td>
</tr>
<tr>
<td><em>Prunus pensylvanica</em></td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Quercus rubra</em></td>
<td>10.0</td>
<td>25</td>
<td>78</td>
<td>0.14</td>
<td>0.43</td>
<td>1.05</td>
<td>3.33</td>
</tr>
<tr>
<td><em>Rhododendron catawbiense</em></td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
TABLE VI (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Density (Tree/Ha.)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Basal Area (M²/Ha.)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>IV-200&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Mean</td>
</tr>
<tr>
<td>Rhododendron maximum</td>
<td>10.0</td>
<td>17</td>
<td>55</td>
<td>0.02</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>10.0</td>
<td>3</td>
<td>8</td>
<td>0.002</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>10.0</td>
<td>2</td>
<td>8</td>
<td>0.03</td>
</tr>
<tr>
<td>Vaccinium spp.</td>
<td>10.0</td>
<td>10</td>
<td>31</td>
<td>0.008</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>10.0</td>
<td>2</td>
<td>8</td>
<td>0.03</td>
</tr>
<tr>
<td>All species</td>
<td>-</td>
<td>2113</td>
<td>1776</td>
<td>27.30</td>
</tr>
</tbody>
</table>

<sup>a</sup>Per cent of plots in which species were present.

<sup>b</sup>Standard deviation.

<sup>c</sup>Sum of relative basal area and relative density.
Figure 8. Immature yellow birch stand in a cove near Buckeye Gap. (Plot 8, August 20, 1971).
### TABLE VII

**COMPOSITION AND STRUCTURE OF SAPLING-LOW SHRUB STRATUM OF THE YELLOW BIRCH Ecosystem**

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent</th>
<th>Density (Stems/Ha.)</th>
<th>Basal Area (M²/Ha.)</th>
<th>IV-200c Mean</th>
<th>STD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Abies fraseri</strong></td>
<td>16.7</td>
<td>36</td>
<td>88</td>
<td>0.003</td>
<td>0.007</td>
</tr>
<tr>
<td><strong>Acer pensylvanicum</strong></td>
<td>33.3</td>
<td>54</td>
<td>90</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td><strong>Acer saccharum</strong></td>
<td>16.7</td>
<td>18</td>
<td>44</td>
<td>0.001</td>
<td>0.002</td>
</tr>
<tr>
<td><strong>Acer spicatum</strong></td>
<td>33.3</td>
<td>448</td>
<td>788</td>
<td>0.06</td>
<td>0.12</td>
</tr>
<tr>
<td><strong>Amelanchier arborea</strong></td>
<td>16.7</td>
<td>18</td>
<td>44</td>
<td>0.004</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>Betula lutea</strong></td>
<td>66.7</td>
<td>215</td>
<td>245</td>
<td>0.05</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>Cornus alternifolia</strong></td>
<td>16.7</td>
<td>72</td>
<td>176</td>
<td>0.001</td>
<td>0.003</td>
</tr>
<tr>
<td><strong>Crataegus sp.</strong></td>
<td>16.7</td>
<td>18</td>
<td>44</td>
<td>0.001</td>
<td>0.003</td>
</tr>
<tr>
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</table>
**TABLE VII (continued)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency Per Cent&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Density (Stems/Ha.)</th>
<th>Basal Area (M²/Ha.)</th>
<th>IV-200c&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean&lt;br&gt;STD&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Mean&lt;br&gt;STD</td>
<td>Mean&lt;br&gt;STD</td>
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<td>Rhododendron maximum</td>
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<td>Ribes rotundifolium</td>
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<td>Rubus allegheniensis</td>
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<td>18</td>
<td>44</td>
<td>-&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>1308</td>
<td>873</td>
<td>0.02</td>
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<sup>a</sup>Per cent of plots in which species were present.

<sup>b</sup>Standard deviation.

<sup>c</sup>Sum of relative basal area and relative density.

<sup>d</sup> < 0.0001.
Figure 9. Late summer ground cover in an immature yellow birch cove near Buckeye Gap. (Plot 8, August 20, 1971).
but were especially prominent on rocky slopes.

Stands representing yellow birch populations of two ages were sampled. Immature stands were similar to spruce-fir stands in size-class distribution of stems, composition of tree and shrub strata although species roles shifted, and with one exception were within the spruce-fir elevational zone. Stand 38 was in a west-facing cove at 1585 m (5200 ft) elevation. The principal component of contiguous deciduous forests was *Quercus rubra* which, as suggested by oak logging residue and living 5-15 cm trees, was important in the original vegetation of the cove. *Acer spicatum* (mountain maple) together with mountain ash, Fraser fir, and red spruce, all important in yellow birch stands at higher elevations were absent from this stand. Among all yellow birch stands, mountain maple was more important and mountain ash less important (differences significant at 5 per cent level) than in spruce-fir stands, similar to distributions in the Great Smoky Mountains (Whittaker, 1956). Bryophytes were essentially absent, but several herbaceous species which occurred in this stand were absent elsewhere.

In immature yellow birch stands at higher elevations, sapling-low shrub and herbaceous strata were more highly developed than in spruce-fir stands but variability was large among stands and differences were not significant (10 per cent level). In contrast to spruce-fir stands, *Claytonia*
caroliniana was particularly prominent during spring and Eupatorium rugosum was prominent during late summer. Other species prominent during the summer included Carex spp. and Aster acuminatus; Oxalis acetosella was present in many stands but was less important than in spruce-fir stands.

Mature yellow birch stands occupied block fields in steep, north coves near Wesner and Steestachee Balds (Appendix A, stands 37, 39, 40, and 53). Block fields were similar to those in the Great Smoky Mountains (Hadley and Goldsmith, 1963) and occupied areas up to several hectares. Dimensions of boulders varied from several centimeters to one or more meters in width and length. Boulders were concentrated in the cove bottom with varying degrees of density and in extreme cases, interstitial spaces were devoid of soil material to a depth of several centimeters. Runoff following storms was subterranean and road cuts through coves showed that the block fill was several meters thick. The interfaces between block fields and soil of adjacent slopes and between vegetation of block fields and adjacent slopes were exceedingly abrupt. Vegetation on block fields consisted of yellow birch in the canopy with an understory predominantly of mountain maple. Ribes glandulosum and Acer pensylvanicum were also present. On adjacent slopes, northern hardwoods including yellow birch, Aesculus octandra, Fagus grandifolia, Tilia heterophylla, and Acer
Saccharum formed the canopy. The understory of small trees and shrubs was frequently dense although Ribes glandulosum was absent. On block fields, coverage of boulders by bryophytes was 100 per cent nearly without exception (Figure 10). Herbaceous species grew both with bryophytes on boulders and in leaf litter which collected to a few centimeters depth between boulders (Figure 11). Important species were Aster acuminatus, Clintonia borealis, Impatiens pallida, Eupatorium rugosum, Circaea alpina, Dryopteris spp., and Oxalis acetosella. The herbaceous stratum of adjacent slopes was much more diverse in species and presumably of greater biomass. Bryophytic ground cover was poorly developed on these slopes.

The distribution of stems in the tree-tall shrub stratum was discontinuous and in sharp contrast to both immature yellow birch and spruce-fir stands (Appendix A). Most of the stems of this stratum were in the smaller size-classes in which mountain maple was predominant and yellow birch frequently absent. Trees of intermediate size-classes were often absent or were limited to an occasional yellow birch. Yellow birch with few exceptions was the exclusive canopy species. Ages and diameters at 1.4 m of some of these canopy trees were 150 years, 33 cm; 160 years, 55 cm; 175 years, 58 cm; 185 years, 46 cm; 192 years, 2 cm; 200 years, 64 cm; and 265 years, 46 cm. Yellow birch attained diameters of 125 cm in the study area and larger diameters
Figure 10. *Hylocomium* sp. on boulders and *Aster acuminatus* in areas between boulders in a mature yellow birch stand near Steestachee Bald. (Plot 40, August 20, 1971).
Figure 11. Clintonia borealis, Aster acuminatus, and Impatiens sp. in an area between boulders in a mature yellow birch stand near Steestachee Bald. (Plot 40, August 20, 1971).
elsewhere in the Southern Appalachians (Stupka, 1964). These data indicate that maximum ages of yellow birch in the Southern Appalachians was closer to that of red spruce than that of Fraser fir and suggest that earlier age estimates (Oosting and Billings, 1951) were conservative. Density of the tree-tall shrub stratum in mature stands was low relative to that in immature yellow birch stands but both bole volume and basal area of the mature yellow birch stands were greater by factors of 1.2 and 1.6, respectively.

Yellow birch gaps occur on moist northerly slopes and dips in the Great Smoky Mountains where study has been limited to ground vegetation patterns (Crandall, 1958). The birch gaps in the Smokies apparently were not on block fields, and stands similar to those in the Balsam Mountains have not been described previously (Russell, 1953; Whittaker, 1956; Crandall, 1958; Ramseur, 1960).

**Biomass**

Specific gravity of bole and branch sections (Appendix A) was used in estimating weights of wood and bark of harvested trees. These weights together with bole diameters at breast height were used to calculate regression equations (Appendix A) to estimate weights of components of trees, shrubs, and saplings. Biomass of above-ground vegetation ranged from 111 to 245 t/ha in spruce-fir stands (Table VIII).
### TABLE VIII

**ABOVE-GROUND BIOMASS OF VEGETATION WITHIN STANDS**

<table>
<thead>
<tr>
<th>Stand</th>
<th>Total Biomass t/ha</th>
<th>Tree-Tall Stratum t/ha</th>
<th>Sapling-Low Shrub Stratum t/ha</th>
<th>Tree-Shrub Regeneration t/ha</th>
<th>Herbs t/ha</th>
<th>Bryophytes t/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Per Cent</td>
<td>Per Cent</td>
<td>Per Cent</td>
<td>Per Cent</td>
<td>Per Cent</td>
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<tr>
<td>1</td>
<td>128.767</td>
<td>127.6</td>
<td>99.09</td>
<td>1.05</td>
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<td>0.117</td>
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<td>86.6</td>
<td>97.57</td>
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<td>0.663</td>
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</table>

_a_ Data for Stand 31 is not available for sapling-low shrub stratum.

_b_ Data for Stand 40 is not available for tree-shrub regeneration.

In stand 43, the tree-shrub regeneration biomass is 0.0001 t/ha.
<table>
<thead>
<tr>
<th>Stand</th>
<th>Total Biomass t/ha</th>
<th>Tree-Tall Shrub Stratum t/ha</th>
<th>Sapling-Low Shrub Stratum t/ha</th>
<th>Tree-Shrub Regeneration t/ha</th>
<th>Herbs t/ha</th>
<th>Bryophytes t/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Per Cent</td>
<td>Per Cent</td>
<td>Per Cent</td>
<td>Per Cent</td>
<td>Per Cent</td>
</tr>
<tr>
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</tr>
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<td>-</td>
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</tbody>
</table>

*aNot estimated.  

b < 0.0001 per cent.
and was significantly greater than in immature yellow birch stands (Table IX) where biomass ranged from 77 to 129 t/ha. Biomass of mature yellow birch stands ranged from 97 to 158 t/ha but was not significantly greater than immature stands. Biomass of yellow birch stands was similar to high elevation beech and red oak forests in the Great Smoky Mountains (Shanks, et al., 1961; Whittaker, 1966). Biomass of coniferous stands was similar to fir stands in Eastern Canada (Baskerville, 1966) and the Great Smoky Mountains (Whittaker, 1966), but was much lower than biomass of both mature and immature spruce-fir stands in the Smokies (Shanks, et al., 1961; Whittaker, 1966). Greater biomass would be expected in mature stands (Ovington and Madgwick, 1959a) but the results of this and the Canadian and Smoky Mountain studies suggest that, compared with spruce stands, lower biomass characterizes balsam and Fraser fir stands of various ages. This reflects not only the lower density of fir wood (Forest Products Laboratory, 1955) but also the greater ages attained by spruce stands, and the greater time period over which dry matter accumulates.

Differences in biomass of Balsam Mountain coniferous and deciduous forests reflect differences between tree-tall shrub strata. In these stands, and many other cool temperate forests (Baskerville, 1966; Whittaker, 1966; Ovington, 1965), the contribution of inferior strata
## TABLE IX

**BIOMASS OF VEGETATION IN SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS**

<table>
<thead>
<tr>
<th>Strata</th>
<th>Spruce-Fir</th>
<th>Yellow Birch</th>
<th>Immature Growth</th>
<th>Mature</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance</td>
<td>Mean</td>
<td>STD</td>
</tr>
<tr>
<td>Tree-tall shrub, t/ha</td>
<td>178.3</td>
<td>36.7</td>
<td>4</td>
<td>101.58</td>
<td>25.05</td>
</tr>
<tr>
<td>Boles, t/ha</td>
<td>138.5</td>
<td>28.7</td>
<td>4</td>
<td>73.5</td>
<td>17.9</td>
</tr>
<tr>
<td>Per cent in boles</td>
<td>78.0</td>
<td>1.5</td>
<td>4</td>
<td>72.1</td>
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</tr>
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<td>Branches, t/ha</td>
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<td>4.5</td>
<td>NS</td>
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</tr>
<tr>
<td>Per cent in branches</td>
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<td>4</td>
<td>24.3</td>
<td>1.3</td>
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<tr>
<td>Foliage, t/ha</td>
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<td>Per cent in leaves</td>
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<td>4</td>
<td>3.6</td>
<td>1.2</td>
</tr>
<tr>
<td>Per cent of total</td>
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<td>1.2</td>
<td>NS</td>
<td>98.2</td>
<td>1.4</td>
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<td>NS</td>
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<td>Per cent in leaves</td>
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</tr>
<tr>
<td>Tree-shrub regeneration, t/ha</td>
<td>0.05</td>
<td>0.09</td>
<td>NS</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.04</td>
<td>0.08</td>
<td>NS</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>Strata</td>
<td>Spruce-Fir</td>
<td></td>
<td>Immature Growth</td>
<td></td>
<td>Yellow Birch</td>
</tr>
<tr>
<td>------------------------------</td>
<td>------------</td>
<td>----------</td>
<td>-----------------</td>
<td>----------</td>
<td>--------------</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>STDa</td>
<td>Significanceb</td>
<td>Mean</td>
<td>STD</td>
</tr>
<tr>
<td>Herbs t/ha</td>
<td>0.15</td>
<td>0.18</td>
<td>NS</td>
<td>0.29</td>
<td>0.27</td>
</tr>
<tr>
<td>Phanerogams, per cent</td>
<td>60.8</td>
<td>33.6</td>
<td>NS</td>
<td>76.0</td>
<td>25.3</td>
</tr>
<tr>
<td>Cryptogams, per cent</td>
<td>39.2</td>
<td>33.6</td>
<td>NS</td>
<td>24.0</td>
<td>25.3</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.09</td>
<td>0.10</td>
<td>NS</td>
<td>0.30</td>
<td>0.31</td>
</tr>
<tr>
<td>Bryophytes t/ha</td>
<td>1.15</td>
<td>1.21</td>
<td>NS</td>
<td>0.82</td>
<td>0.95</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.71</td>
<td>0.93</td>
<td>NS</td>
<td>1.00</td>
<td>1.18</td>
</tr>
<tr>
<td>Total, all strata, t/ha</td>
<td>179.9</td>
<td>36.1</td>
<td>4</td>
<td>103.22</td>
<td>24.17</td>
</tr>
<tr>
<td>Bole volume, m³/ha</td>
<td>383.3</td>
<td>77.6</td>
<td>4</td>
<td>129.3</td>
<td>28.5</td>
</tr>
</tbody>
</table>

aStandard deviation of mean.

bT-test, significance of difference between means of spruce-fir and second growth yellow birch stands. Levels of significance: NS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.

cT-test, significance of difference between means of second growth and mature yellow birch stands.
TABLE IX (continued)

Means based on 30 spruce-fir and six immature growth and four mature yellow birch stands, respectively. All other means based on 14 spruce-fir and four immature growth and two mature yellow birch stands, respectively.

Means based on eight spruce fir, three immature growth yellow birch, and two immature yellow birch stands.
vegetation to total biomass was trivial (Table IX, page 135). Among inferior strata, biomass of bryophytes was significantly greater than other strata excepting in immature yellow birch stands. There, differences between sapling-low shrub among strata were generally insignificant. Differences between sapling-low shrub and herb strata were insignificant in all forest types. Tree-shrub regeneration biomass was significantly lower than all other strata in spruce-fir and mature yellow birch stands. Relative biomass of strata followed similar patterns.

Relatively high foliage biomass and rapid growth rates typical of stands 40 to 60 years, the age range of immature stands of this study, would be associated with decreased subcanopy light levels and intense root competition which would limit development of these strata. With maturity and decreasing stand density, the relative contribution to stand biomass of inferior strata should increase although with the exception of bryophytes, this trend was not apparent in the limited number of mature and immature stands sampled.

Biomass of the tree-tall shrub stratum ranged from 106 to 245 t/ha in coniferous stands and was significantly greater than immature yellow birch stands where biomass was between 75 and 123 t/ha. Biomass ranged from 97 to 158 t/ha in mature yellow birch stands and was significantly greater than in immature stands as would be expected.
Biomass Relationships

The greater biomass of spruce-fir stands resulted from significantly greater biomass of both bole and foliage (Table IX, page 135). Foliage biomass ranged from 12.7 to 25.2 t/ha and averaged from 2 to 4 t/ha less than balsam fir stands in Canada (Baskerville, 1965). The absolute foliage biomass of yellow birch stands was much lower than spruce-fir stands, and lower biomass in mature as compared with immature stands suggested that foliage decreased with stand maturity as reported in many other temperate forests (Kira and Shidei, 1967).

Ratios of leaf area per unit leaf weight from which stand leaf areas were calculated are given in Appendix A. Ratios for spruce were higher than fir and decreased with increasing needle age. In each case, ratios were somewhat greater than reported for other species of spruce and fir (Weetman and Harland, 1964; Kitteredge, 1948). Ratios varied widely among angiosperms. Ratios of *Rhododendron* spp. were lowest and in the range reported by Whittaker (1962). The data suggested that higher ratios characterized understory species which may be an adaptation to decreased sub-canopy light intensities.

Both foliage biomass and leaf area in immature yellow birch stands were slightly greater than values considered typical for most deciduous broad leaved forests (Tadaki,
1966) and leaf area exceeded that of high elevation beech in the Great Smoky Mountains (Whittaker, 1966) by a factor of nearly 3. The higher values in the Balsam Mountains resulted from the presence of red spruce in many of the stands. In mature yellow birch, leaf area was significantly lower and within the range of most deciduous forests (Whittaker, 1966; Tadaki, 1966).

Leaf area indices ranged from 12.3 to 36.8 in coniferous stands and were significantly higher than in deciduous stands. Maximum leaf areas were only slightly below the maximum of 38 reported in the literature (Utkin, 1969). The average leaf area index of 21.3 was well above values in spruce and fir forests of the Great Smoky Mountains (Whittaker, 1966) but together with mean foliage biomass was at or near the range of typical values of many coniferous forests (Tadaki, 1966). Needle ages up to nine years in Fraser fir and twelve years on red spruce were found in this study which compare with maximum ages of eight to ten years reported for balsam fir (Clark, 1961; Baskerville, 1965). Relative longevity of needles of these species is an important factor in the large foliage biomass of these stands (cf. Kira and Shidei, 1966). Considering both age and total biomass of spruce-fir stands in the Great Smoky Mountains, the range of leaf areas reported by Whittaker (1966) seems low compared with Balsam Mountains and other spruce-fir stands.
A direct relation between bole biomass and dry weight of mineral soil material and weight of dry matter of the B2 horizon was indicated (Table X). The two soil parameters were correlated, however, and a response to increased rooting volume or available moisture rather than separate responses to each is indicated. Calcium and Mg of the B2 horizon were also directly correlated and either or both may have affected bole biomass. Foliage biomass was less closely related to soil properties than bole biomass which supports the conclusions that biomass of crown components tends to remain more or less constant unless soil nutrients become severely limiting, and that crown biomass is less sensitive to site variations than bole biomass (Wegge, 1966). Biomass was not related to elevation although Whittaker (1966) reported a correlation in high elevation stands in the Great Smoky Mountains. Whittaker (1966) compared spruce and spruce-fir stands at low elevations with Fraser fir stands at high elevations and the differences were apparently related to forest types more closely than direct effects of differential environmental conditions such as increased precipitation and lower temperatures.

Structural characteristics seemed to be more closely related to biomass of components than were soil and site parameters (Table X). Biomass of all components was significantly and directly correlated with stand basal area,
### TABLE X

ASSOCIATION OF TREE-TALL SHRUB BIOMASS WITH SITE AND STRUCTURAL PARAMETERS (SIMPLE r)

<table>
<thead>
<tr>
<th>Independent Variable&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Spruce-Fir Stands</th>
<th>Yellow-Birch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bole</td>
<td>Branch</td>
</tr>
<tr>
<td>Soil weight&lt;sup&gt;b&lt;/sup&gt;, B&lt;sub&gt;1&lt;/sub&gt;</td>
<td>.974</td>
<td>.978</td>
</tr>
<tr>
<td>Dry matter, B&lt;sub&gt;1&lt;/sub&gt;</td>
<td>.611</td>
<td>.582</td>
</tr>
<tr>
<td>Phosphorus, B&lt;sub&gt;1&lt;/sub&gt;</td>
<td>.600</td>
<td>.613</td>
</tr>
<tr>
<td>Soil weight&lt;sup&gt;b&lt;/sup&gt;, B&lt;sub&gt;2&lt;/sub&gt;</td>
<td>.693</td>
<td>.539</td>
</tr>
<tr>
<td>Dry matter, B&lt;sub&gt;2&lt;/sub&gt;</td>
<td>.611</td>
<td>.582</td>
</tr>
<tr>
<td>Calcium, B&lt;sub&gt;2&lt;/sub&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magnesium, B&lt;sub&gt;2&lt;/sub&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight of horizon&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope position&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-.384</td>
<td></td>
</tr>
<tr>
<td>Aspect X form&lt;sup&gt;d&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density, stems/ha</td>
<td>.943</td>
<td>.894</td>
</tr>
<tr>
<td>Basal area, m&lt;sup&gt;2&lt;/sup&gt;/ha</td>
<td>.500</td>
<td>-.441</td>
</tr>
<tr>
<td>Birch density</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birch, basal area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce, density</td>
<td>.571</td>
<td></td>
</tr>
<tr>
<td>Spruce, basal area</td>
<td>.633</td>
<td></td>
</tr>
</tbody>
</table>
TABLE X (continued)

<table>
<thead>
<tr>
<th>Independent Variable&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Spruce-Fir Stands</th>
<th>Yellow-Birch</th>
<th>Immature</th>
<th>Mature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bole</td>
<td>Branch</td>
<td>Foliage</td>
<td>Bole</td>
</tr>
<tr>
<td>Fir, basal area</td>
<td>.523</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole volume, m&lt;sup&gt;3&lt;/sup&gt;/ha</td>
<td>.949</td>
<td>.790</td>
<td>.523</td>
<td></td>
</tr>
<tr>
<td>Age, years</td>
<td>.384</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Significance levels of soil and biomass correlation coefficients: spruce-fir P.05 = .532, P.01 = .661; immature yellow birch P.05 = .950, P.01 = .990. Significance levels of topographic-vegetation and biomass correlation coefficients: spruce-fir P.05 = .361, P.01 = .463; immature yellow birch P.05 = .811, P.01 = .917; mature yellow birch P.05 = .950, P.01 = .990.

<sup>b</sup>Weight (kg/ha) of organic matter and mineral fraction < 2 mm of horizon; calculated as bulk density X volume of < 2 mm fraction.

<sup>c</sup>Elevation or ridge crest up slope from plot minus elevation of plot.

<sup>d</sup>Slope form coded where 1 = convex slope, 2 = flat slope, and 3 = cove.
but examination of responses of species showed basic differences existed. The relation between foliage biomass and basal area of spruce and fir was similar to that in balsam fir stands (Baskerville, 1965) but opposite the results of many studies where foliage was independent of and constant over a broad range of stand stocking rates (Satoo, 1970; Möller, 1947). Foliage biomass of yellow birch was independent of stocking rates (density and basal area) of yellow birch over the range sampled in this study and supports conclusions of Satoo (1970) and Möller (1947). The differences apparently are related to interaction of species tolerance and favorability of site conditions (Wegge, 1966). Neither stand basal area nor biomass was related to stand density (stems/hectare) both of which are opposite to trends in immature balsam fir stands (Baskerville, 1965). The significance of species composition as a factor affecting biomass is indicated by the inverse relation between biomass and yellow birch density in coniferous stands and the direct relationships of spruce basal area and density to foliage biomass in both coniferous and deciduous stands. Frequently, red spruce accounted for a significant proportion of foliage biomass in immature yellow birch stands and sharply increased leaf area index. The direct relation between stand basal area and foliage biomass in those stands reflected the presence of red spruce (Table X, page 142).
The greatest proportion of biomass was in boles and least in foliage which is typical of most forest stands (Ovington, 1965), although significant differences existed between forest types (Table IX, page 135). The proportion of biomass in foliage decreased from coniferous to deciduous and from immature to mature yellow birch stands. Branches formed a significantly greater proportion of the biomass in yellow birch stands and the proportion increased with stand maturity. The presence of red spruce increased the proportion of foliage in the biomass of both coniferous and deciduous stands. Increasing proportion of boles and decreasing proportion of crown components with increasing density as occurred in mature yellow birch stands has been reported in dense immature balsam fir stands (Baskerville, 1965). The reverse characterized coniferous stands in the Balsam Mountains which emphasizes the importance of species composition on biomass distribution. High foliage biomass compared to fir and yellow birch was indicated for red spruce which tended to increase the proportion of foliage biomass in stands. Conversely, relative bole biomass varied inversely with spruce density and basal area, a trend reflected in the inverse relation of total stand density and relative bole biomass. Greater biomass of yellow birch in stands increased the proportion of biomass in branches. The relation of fir basal area to distribution of biomass, however, agreed with
Baskerville's (1965) results. In the study area, as fir basal area increased, the proportion of biomass in boles increased and proportions in branches and foliage decreased. These results show that in mixed stands, differences in morphology of species may greatly alter typical biomass distributional patterns.

Biomass, density, and basal area of the sapling-low shrub stratum were directly and significantly correlated in yellow birch and spruce-fir stands (Table XI). In contrast to the understory in yellow birch stands, in spruce-fir stands, sapling-low shrub density, basal area, and biomass each increased with increasing elevation and slope steepness, toward northeast aspects, and from flat slopes to coves. Together with the high relation between the aspect X slope steepness interaction and biomass, these trends indicate a response along both elevational and moisture complex gradients similar to that described in the Great Smoky Mountains (Whittaker, 1956) where development of the shrub layer in high elevation coniferous stands increased from xeric to mesic sites. The absence of biomass-site relations in yellow birch stands may reflect the limited range of site conditions sampled.

Tree-shrub regeneration biomass of coniferous stands was much greater than in dense balsam fir (Baskerville, 1966) and slightly greater than in spruce-fir stands in the
# TABLE XI

**ASSOCIATION OF SAPLING-LOW SHRUB BIOMASS WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE r)**

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir</th>
<th>Yellow Birch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bole</td>
<td>Branch</td>
</tr>
<tr>
<td>Aspect (A')&lt;sup&gt;c&lt;/sup&gt;</td>
<td>.671</td>
<td>.636</td>
</tr>
<tr>
<td>Stand elevation</td>
<td>.677</td>
<td></td>
</tr>
<tr>
<td>Per cent slope</td>
<td>.787</td>
<td></td>
</tr>
<tr>
<td>Elevation of mountain</td>
<td>.569</td>
<td></td>
</tr>
<tr>
<td>Aspect X slope form&lt;sup&gt;d&lt;/sup&gt;</td>
<td>.766</td>
<td>.620</td>
</tr>
<tr>
<td>Aspect X per cent slope</td>
<td>.927</td>
<td>.646</td>
</tr>
<tr>
<td>Density I + II&lt;sup&gt;e&lt;/sup&gt;</td>
<td>.751</td>
<td>.572</td>
</tr>
<tr>
<td>Birch basal area I&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td>.663</td>
</tr>
<tr>
<td>Tree height I&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-.559</td>
<td>-.579</td>
</tr>
<tr>
<td>Density II&lt;sup&gt;e&lt;/sup&gt;</td>
<td>.673</td>
<td>.564</td>
</tr>
<tr>
<td>Basal area II&lt;sup&gt;e&lt;/sup&gt;</td>
<td>.853</td>
<td>.565</td>
</tr>
<tr>
<td>Fir density II&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf area II&lt;sup&gt;e&lt;/sup&gt;</td>
<td>.774</td>
<td>.738</td>
</tr>
</tbody>
</table>

<sup>a</sup>r = .532 at P.05; r = .661 at P.01.  
<sup>b</sup>r = .811 at P.05; r = .917 at P.01.  
<sup>c</sup>CA' = Cos (45° - A) + 1 where A = azimuth from north in degrees: i.e., if A = 45° (NE), A' = 2.00; if A = 225° (SW) A' = 0.00.  
<sup>d</sup>Coded such that 1 = convex slope, 2 = flat slope, and 3 = concave slope.  
<sup>e</sup>I denotes tree tall-shrub stratum and II denotes sapling-low shrub stratum.
Great Smoky Mountains (Whittaker, 1966). Biomass in coniferous stands increased from southwest to northeast aspects, and decreased with increased development of the tree-shrub overstory (Table XII). The relation to aspect reflects the importance of Fraser fir regeneration which tended to develop dense stands only on northeast slopes. In the Smokies dense fir stands may be restricted to similar aspects (Crandall, 1958) and growth rates of Fraser fir and red spruce are highest on northeast slopes (Minckler, 1940). Fir regeneration may also be more tolerant of deep shade than other species (Good, 1963). Biomass was also directly related to certain soil nutrient levels but to a lesser extent than in yellow birch stands. In coniferous stands, exchangeable Ca and K (kg/ha) were significantly correlated with weight of the A horizon. The higher relation of biomass to A horizon weight suggests the response may have been related to some other unmeasured property which was related to the quantity of soil in the A horizon. Biomass of the regeneration stratum increased with elevation and generally with increased dry matter and nutrients in soil horizons. Separation of the effects of varying dry matter and nutrient supplies in the A horizon on biomass is again difficult since all were cross correlated. Many woody species apparently obtain nutrients directly from organic matter via mycorrhizae (Went and Stark, 1968), and considering the coarse texture of soils in the
TABLE XII

ASSOCIATION OF TREE-SHRUB REGENERATION WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE r)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir Net Biomass Production</th>
<th>Yellow Birch Net Biomass Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspect</td>
<td>.530</td>
<td>.857</td>
</tr>
<tr>
<td>Elevation</td>
<td>.560</td>
<td>.843</td>
</tr>
<tr>
<td>Elevation X slope per cent</td>
<td>.956</td>
<td>.968</td>
</tr>
<tr>
<td>Elevation X slope form</td>
<td></td>
<td>.920</td>
</tr>
<tr>
<td>Aspect X A horizon weight</td>
<td>.856</td>
<td>.764</td>
</tr>
<tr>
<td>Elevation X A horizon weight</td>
<td>.697</td>
<td>.608</td>
</tr>
<tr>
<td>Aspect X A + B horizon weight</td>
<td>.819</td>
<td>.716</td>
</tr>
<tr>
<td>Aspect X elevation</td>
<td>.547</td>
<td></td>
</tr>
<tr>
<td>Forest floor, bole and branch litter</td>
<td>.932</td>
<td>.936</td>
</tr>
<tr>
<td>A horizon, weight</td>
<td>.680</td>
<td>.596</td>
</tr>
<tr>
<td>A horizon, dry-matter weight</td>
<td>.955</td>
<td>.965</td>
</tr>
<tr>
<td>A horizon, calcium</td>
<td>.951</td>
<td>.939</td>
</tr>
<tr>
<td>A horizon, potassium</td>
<td>.949</td>
<td>.937</td>
</tr>
<tr>
<td>A horizon, magnesium</td>
<td>.952</td>
<td>.939</td>
</tr>
<tr>
<td>B1 horizon, dry-matter weight</td>
<td>-.847</td>
<td>-.841</td>
</tr>
<tr>
<td>B1 horizon, calcium</td>
<td>.930</td>
<td>.913</td>
</tr>
<tr>
<td>B1 horizon, potassium</td>
<td>.877</td>
<td>.856</td>
</tr>
<tr>
<td>B1 horizon, magnesium</td>
<td>.937</td>
<td>.922</td>
</tr>
</tbody>
</table>
TABLE XII (continued)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir&lt;sup&gt;a&lt;/sup&gt; Net Biomass Production</th>
<th>Yellow Birch&lt;sup&gt;b&lt;/sup&gt; Net Biomass Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area I&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-.675</td>
<td>-.627</td>
</tr>
<tr>
<td>Bole volume I</td>
<td>-.533</td>
<td></td>
</tr>
<tr>
<td>Crown cover I</td>
<td>-.737</td>
<td>-.724</td>
</tr>
<tr>
<td>Crown surface area I</td>
<td>-.737</td>
<td>-.724</td>
</tr>
<tr>
<td>Leaf area I</td>
<td>-.504</td>
<td>-.500</td>
</tr>
<tr>
<td>Bole biomass I</td>
<td>-.568</td>
<td></td>
</tr>
<tr>
<td>Branch biomass I</td>
<td>-.683</td>
<td>-.632</td>
</tr>
<tr>
<td>Foliage biomass I</td>
<td>-.551</td>
<td>-.542</td>
</tr>
<tr>
<td>Biomass III&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1.000</td>
<td>.986</td>
</tr>
<tr>
<td>Log&lt;sub&gt;10&lt;/sub&gt; Throughfall II&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td>-.698&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>\( r = .532 \text{ at } P.05; \ r = .661 \text{ at } P.01. \)

<sup>b</sup>\( r = .811 \text{ at } P.05; \ r = .917 \text{ at } P.01. \)

<sup>c</sup>Weight (kg/ha) of organic matter and mineral fraction < 2 mm in horizon; calculated as bulk density \times volume of < 2 mm fraction.

<sup>d</sup>I denotes tree-tall shrub stratum; III denotes tree-shrub regeneration.

<sup>1</sup>II denotes throughfall during period June 3, 1969 - November 12, 1969.

<sup>f</sup>Significant at P.05, n = 4.
study area, this suggests that soil organic matter may be an important source of nutrient for trees. Determining whether any specific nutrient was limiting was not possible from these data due to cross correlations. The lack of relation of regeneration biomass and structure of the overstory in yellow birch stands suggests that light and moisture may have been less limiting than in coniferous stands (Anderson, et al., 1970), and in other deciduous stands where inhibition of yellow birch regeneration has been shown (Barrett, et al., 1962; Hatcher, 1966).

Regeneration of yellow birch, red spruce, and certain other coniferous species is inhibited by thick, well-developed forest floor litter (Long, 1940; Gilbert, 1960; Hatcher, 1966; Marquis, 1964) although no relation between regeneration and development of the forest floor was suggested in this study. Regeneration of yellow birch may be restricted to cracks in boulders or rotted logs and stumps (Gilbert, 1960) which may explain the relation between regeneration biomass and quantity of bole and branch litter on the forest floor in yellow birch stands. Many of these species depend on local disturbances (Marquis, 1965; Gilbert, 1960; Davis and Hart, 1961) such as windthrow which produces pit-mount microtopography common to many coniferous forests (Stephens, 1956; Lutz, 1940). Windthrows expose mineral soil and so disrupt soil horizons that both physical and chemical
properties are changed (Lutz, 1940; Lyford and MacLean, 1966). Litter thickness is less on mounds (Lyford and MacLean, 1966) where regeneration of several species is often most abundant (Gilbert, 1960; Dixon and Place, 1952). Pit-mound microtopography characterized many of the stands—coniferous and immature yellow birch—but apparently were less abundant than in many eastern forests (Stephens, 1956) and relatively recent disturbances were limited. The result would be relatively fewer favorable sites and limited regeneration.

Biomass of vegetation of the herb stratum of coniferous stands (Table VIII, page 132) was similar to that of balsam fir stands of lower density studied by Baskerville (1966) but lower than biomass of most mature spruce and fir stands in the Great Smoky Mountains (Whittaker, 1966). In yellow birch stands, herb biomass was greater than in northern hardwoods in New Hampshire (Siccama, et al., 1970) but similar to that in high elevation beech stands in the Great Smoky Mountains (Whittaker, 1966). Species diversity of this stratum in yellow birch stands was much greater than in coniferous stands (Table V, page 116) as reported elsewhere (Whittaker, 1966; Crandall, 1958) but, although the differences were not significant, the trend was toward lower biomass in coniferous stands which is the reverse of the usual relationship (Crandall, 1958; Whittaker, 1966).
These trends were observed in comparing mature stands which were less dense (Whittaker, 1966) than the immature stands in the Balsam Mountains; Crandall (1958) reported the virtual absence of all ground cover beneath young, dense fir stands in the Great Smoky Mountains. The current study along with those in the Great Smoky Mountains and New Hampshire point out the significance of ferns which frequently accounted for the major portion of herb stratum biomass.

Variations in herb stratum biomass in coniferous stands were related to stand structure and precipitation beneath stands (Table XIII). Little relation to stand structure was observed in yellow birch stands except that herb biomass seemed to be limited by increased development of saplings and shrubs. Inverse relationships between tree cover and herb stratum development have been shown in other stands (Crandall, 1958; Siccama, et al., 1970) and may result from competition for light (Siccama, et al., 1970; Anderson, et al., 1970; Good, 1963) and moisture, either through root competition or reduced throughfall related to canopy development. The presence of yellow birch in coniferous stands was directly related to higher herb biomass. Throughfall and light intensity were apparently higher in deciduous than coniferous stands both in early spring and throughout the growing season in response to decreased foliage weights and leaf areas. (These precipitation relationships will be
ASSOCIATION OF HERBACEOUS CLIPPING WEIGHTS WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE r)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir</th>
<th>Yellow Birch</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Crypto-Total</td>
<td>Phanero-gams</td>
<td>Total</td>
</tr>
<tr>
<td></td>
<td>gams</td>
<td>gams</td>
<td>gams</td>
</tr>
<tr>
<td>02 horizon, magnesium</td>
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<td>- .382</td>
<td>.593</td>
</tr>
<tr>
<td>02 horizon, phosphorus</td>
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<td>- .631</td>
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</tr>
<tr>
<td>Density Ic</td>
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<td>- .593</td>
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</tr>
<tr>
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<td>-.666</td>
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<tr>
<td>Fir basal area I</td>
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<td>-.536</td>
<td>-.560</td>
</tr>
<tr>
<td>Birch basal area I</td>
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<td>+.562</td>
</tr>
<tr>
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<tr>
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<td></td>
</tr>
<tr>
<td>Crown surface area I</td>
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</tr>
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</tr>
<tr>
<td>Basal area I + IId</td>
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<td>Net primary production, I + IIC, IId</td>
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<td>-.628</td>
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<tr>
<td>boles</td>
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<tr>
<td>A horizon, P</td>
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<td></td>
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<tr>
<td>Interception II, adjusted, per cent</td>
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<td>Throughfall IIe</td>
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TABLE XIII (continued)

<table>
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<th>Independent Variables</th>
<th>Spruce-Fir&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Yellow Birch&lt;sup&gt;b&lt;/sup&gt;</th>
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<td>Phanerogams</td>
</tr>
<tr>
<td>Stemflow II&lt;sup&gt;e&lt;/sup&gt;</td>
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<td></td>
</tr>
<tr>
<td>Stemflow II&lt;sup&gt;e&lt;/sup&gt;, per cent of gross</td>
<td>-.820</td>
<td>-.708</td>
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</tbody>
</table>

<sup>a</sup> $r = .532$ at $P.05$; $r = .661$ at $P.01$.

<sup>b</sup> $r = .811$ at $P.05$; $r = .917$ at $P.01$.

<sup>c</sup>I denoted tree-tall shrub strata.

<sup>d</sup>II denotes sapling-low shrub strata.

<sup>e</sup>Denotes precipitation during period June 3, 1969, to November 12, 1969.
discussed in a later section.) Magnesium and P levels of the 02 horizon varied directly with fir density, which probably explains the apparent inverse relation with herb biomass. Unlike other Southern Appalachian stands (Whittaker, 1956), variations related to aspect and slope form were not observed. The inverse relation of herb clipping weights to net primary production of the overstory (Table XIII, page 154) also may indicate that with reduced growth by the overstory, competition for light and moisture decreased and herb production increased (Siccama, et al., 1970).

Biomass of bryophytes in coniferous stands was within the range observed in other spruce-fir forests in the eastern United States and Canada (Damman, 1971; Weetman and Timmer, 1967; Baskerville, 1966; Forman, 1969; Whittaker, 1966); in yellow birch stands, especially if mature, biomass was higher than in other high elevation deciduous stands (Whittaker, 1966). Variations in biomass were closely related to topographic features in coniferous stands and structure of overstory vegetation in immature yellow birch stands (Table XIV). Bryophyte coverage and biomass generally increase with elevation (Whittaker, 1966; Crandall, 1958; Forman, 1969); and are highest on open, north slopes (Whittaker, 1956; Crandall, 1958); in subalpine forests, site moisture relations are especially important (Cain and Sharp, 1938).
## TABLE XIV

**ASSOCIATION OF BRYOPHYTIC BIOMASS WITH SITE AND STRUCTURAL PARAMETERS (SIMPLE r)**

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir&lt;sup&gt;a&lt;/sup&gt; (n=14)</th>
<th>Yellow Birch&lt;sup&gt;b&lt;/sup&gt; Immature (n=4)</th>
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<tr>
<td>Elevation</td>
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<td>Elevation X slope per cent</td>
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<td></td>
</tr>
<tr>
<td>Aspect X slope form</td>
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<td></td>
</tr>
<tr>
<td>Slope position</td>
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<td>.969</td>
</tr>
<tr>
<td>Bl horizon dry-matter</td>
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<tr>
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<td>-.876</td>
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<tr>
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<td>Birch density I</td>
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<td>-.984</td>
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<tr>
<td>Age</td>
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<td>-.937</td>
</tr>
<tr>
<td>Density I + II&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td>.562</td>
</tr>
<tr>
<td>Density II</td>
<td></td>
<td>.678</td>
</tr>
<tr>
<td>Basal area II</td>
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<td>.674</td>
</tr>
<tr>
<td>Biomass II</td>
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<td>.766</td>
</tr>
<tr>
<td>Leaf area I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf area II</td>
<td></td>
<td>.632</td>
</tr>
<tr>
<td>Crown surface area I</td>
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<td></td>
</tr>
<tr>
<td>Net primary production</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I + II, total</td>
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<td>-.555</td>
</tr>
<tr>
<td>Net primary production</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I + II, foliage</td>
<td></td>
<td>-.670</td>
</tr>
<tr>
<td>Net primary production</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I + II, boles</td>
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<td>-.991</td>
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<tr>
<td>Net primary production</td>
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<td></td>
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<tr>
<td>I + II, branches</td>
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<td>-.998</td>
</tr>
<tr>
<td>Biomass III&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>.602</td>
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<tr>
<td>Production III</td>
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<td>.555</td>
</tr>
<tr>
<td>Precipitation I, bulk&lt;sup&gt;e&lt;/sup&gt;</td>
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<td>.986</td>
</tr>
<tr>
<td>Precipitation I, K&lt;sup&gt;f&lt;/sup&gt;</td>
<td></td>
<td>.725</td>
</tr>
</tbody>
</table>
TABLE XIV (continued)

\[ a_r = .532 \text{ at } P.05; \quad r = .661 \text{ at } P.01. \]

\[ b_r = .811 \text{ at } P.05; \quad r = .917 \text{ at } P.01. \]

- cI denotes tree-tall shrub strata; II denotes sapling-low shrub stratum.
- dBiomass of tree-shrub regeneration stratum.
- eTotal bulk precipitation between November 13, 1969 and June 2, 1970.
- fK (kg/ha) in bulk precipitation between November 13, 1969 and June 2, 1970.
Biomass of mosses increases with increased light intensities associated with decreased density of the tree overstory (Tamm, 1953; 1964; Weetman and Timmer, 1967). Understands where light is not limiting, biomass may be directly related to throughfall and quantities of nutrients in precipitation (Tamm, 1953; Weetman and Timmer, 1967). Similar relations apparently affected bryophytic biomass in the present study. Structural relations of the sapling-low shrub stratum were directly related to aspect and may not have directly affected bryophytic biomass, as indicated in Table XIV, page 157.

The high biomass of bryophytes in mature yellow birch stands seemed anomalous relative to other deciduous stands, but indicates the importance of suitable habitats. The mature stands were in steep north-northeast coves where boulder coverage of the surface was near 100 per cent. Moss coverage was nearly continuous excepting between boulders where leaf litter had collected. Coverage of bryophytes has also been related to the frequency of surface boulders in other northern hardwood forests (Siccama, et al., 1970).

**Annual Litterfall**

High variability of bole and large branch litterfall is indicated by the data in Table XV. Local weather conditions strongly influence litterfall of twigs, larger twigs, and trees such that high variability is expected, particularly
<table>
<thead>
<tr>
<th>Litterfall Components</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature Growth (n=4)</th>
<th>Mature (n=2)</th>
<th>Significancea</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>Annual litterfall, kg/ha</td>
<td>28119.2</td>
<td>72446.4</td>
<td>NS</td>
<td>4474.5</td>
</tr>
<tr>
<td>Boles and branches, kg/ha</td>
<td>22616.1</td>
<td>72441.9</td>
<td>NS</td>
<td>440.0</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>80.44</td>
<td>32.16</td>
<td>4</td>
<td>9.6</td>
</tr>
<tr>
<td>Leaf litterfall, kg/ha</td>
<td>5503.0</td>
<td>1513.7</td>
<td>3</td>
<td>4034.5</td>
</tr>
<tr>
<td>Reproductive components, kg/ha</td>
<td>1071.0</td>
<td>486.9</td>
<td>4</td>
<td>213.0</td>
</tr>
<tr>
<td>Per cent leaf litter</td>
<td>14.2</td>
<td>6.0</td>
<td>2</td>
<td>9.3</td>
</tr>
<tr>
<td>Deciduous leaves, kg/ha</td>
<td>284.67</td>
<td>284.81</td>
<td>4</td>
<td>2883.0</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>5.2</td>
<td>3.9</td>
<td>4</td>
<td>56.7</td>
</tr>
<tr>
<td>Needles, kg/ha</td>
<td>3114.86</td>
<td>773.93</td>
<td>4</td>
<td>523.1</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>67.8</td>
<td>5.5</td>
<td>4</td>
<td>17.1</td>
</tr>
<tr>
<td>Twigs and bark, kg/ha</td>
<td>1032.55</td>
<td>568.48</td>
<td>3</td>
<td>415.3</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>11.9</td>
<td>4.6</td>
<td>1</td>
<td>16.9</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>19.56</td>
<td>32.16</td>
<td>4</td>
<td>90.4</td>
</tr>
</tbody>
</table>

aNS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.
over short periods of time (Bray and Gorham, 1964). The extremely high production of bole and large branch litter indicated in spruce-fir stands resulted from a large Fraser fir tree which fell across the sampling transect in stand 32 during an early spring windstorm. Bole and branch litterfall in coniferous stands averaged 3696 kg/ha/yr when this stand was excluded from the data. Higher production of non-leaf litter by coniferous stands (Bray and Gorham, 1964) was supported by the data although variability remained high after recalculation of means, and the difference was not significant between coniferous and immature yellow birch stands. Bole and branch litter made up from ca 10 per cent to 17 per cent of total litterfall in yellow birch stand and although differences were not significant, the trend toward increased production with stand maturity (Bray and Gorham, 1964) was suggested. Quantities increased directly with leaf litterfall \( r = .811 \) in all yellow birch plots, and in immature stands directly with weight of reproductive components \( r = .964 \). In coniferous stands, bole and branch litterfall was correlated only with basal area of red spruce in stands \( r = .882 \).

This study re-emphasizes the necessity of sampling bole and branch litterfall from large areas over long time periods if reliable estimates are to be obtained; in the current study, sample areas covering entire 0.04 ha (0.1 acre)
plots used for sampling overstory vegetation may have been required to increase reliability of estimates to an acceptable level.

Annual leaf litterfall in the present study included reproductive components, deciduous leaves, needles and small twigs and bark and ranged from 2710 to 8879 kg/ha in spruce-fir stands, 3824 to 5264 kg/ha in mature yellow birch stands, and from 3716 to 4464 kg/ha in immature yellow birch stands. Leaf litterfall in yellow birch stands of different ages was not significantly different, but was significantly higher in spruce-fir stands (Table XV, page 160), where production was approximately 25 per cent greater. Coniferous forests in various climatic conditions produce approximately one-sixth more litter than deciduous stands (Bray and Gorham, 1964). Average leaf litterfall in coniferous stands was in close agreement with leaf litterfall in a red spruce stand in the Great Smoky Mountains (Shanks, et al., 1961) but considerably above the range reported (cf. Literature Review) in similar stands in the northeast United States and Canada. Leaf litterfall in yellow birch was less than in a Smoky Mountain beech stand (Shanks, et al., 1961), but values were higher than those reported from many northeastern United States forests and near the maximum of the range of most cool temperate deciduous forests (Bray and Gorham, 1964). Leaf litterfall in the yellow birch stands was similar to values
reported from some low elevation Southern Appalachian hardwoods (Hursch, 1928) and many warm temperate deciduous forests (Bray and Gorham, 1964).

The proportions of components in leaf litter in coniferous stands was similar to those in litter of most coniferous stands (Rodin and Basilevic, 1967; Bray and Gorham, 1964). The relative production of reproductive components during the study period probably exceeded the long-term mean since the collection period apparently coincided with peak seed production of Fraser fir which follows a 2 to 4 year cycle (Forest Service, 1948). Proportions of reproductive components and small twigs and bark in yellow birch litter exceeded typical ranges (Rodin and Basilevic, 1967; Bray and Gorham, 1964). Little difference was observed between the proportions of reproductive components in litter of the types of yellow birch stands, although the sources differed. Yellow birch seed production usually does not begin until age 40 and reaches maximum rates after age 70 years (Gilbert, 1960). Examination of litter from the Balsam Mountain stands showed that while birch seeds and fruits comprised the greatest proportion of the reproductive fraction in mature stands, red spruce cones and seeds were prominent and yellow birch seeds nearly absent from litter of immature stands. In coniferous stands, seed production was most closely related to the presence and
importance of Fraser fir (Table XVI) indicating the effects of seed year. Seed production is sensitive to light (Morris, 1951) and varies with tree diameter (Franklin, 1968; Thorbjornsen, 1960) and crown class (Boe, 1968). The relation of seed production to basal area but not density suggests tree size and perhaps light were important variables in the present study as well. Sensitivity of seed production to low temperatures (Fraser, 1958) may be indicated in Balsam Mountain stands by lower quantities of reproductive components in litter on north aspects especially with steepest slopes and in valleys where lower temperatures would occur.

Neither site characteristics nor structural attributes such as basal area and density were related to the yield of deciduous leaf litterfall in yellow birch stands (Table XVI). These results reflect the apparent insensitivity of foliage biomass to site variation over the range of topographic related environmental gradients sampled in this study. Also, the lack of correlation between foliage litterfall and yellow birch density and basal area supports the earlier conclusion that yellow birch foliage biomass is independent of both stand density and basal area over the range of structural attributes sampled. In spruce-fir stands, yield of deciduous leaves increased as the basal area of yellow birch increased and as the importance of spruce and fir decreased. Although there was some indication that deciduous leaf litter
<table>
<thead>
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<th>Independent Variables</th>
<th>Spruce-Fir (n = 14)</th>
<th>Yellow Birch Stands</th>
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<td>Reproductive Component</td>
<td>Deciduous Twigs</td>
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<tr>
<td></td>
<td>Leaves</td>
<td>Needles</td>
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<tr>
<td>Per cent slope</td>
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<td>-.629</td>
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<tr>
<td>Aspect</td>
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<td>Aspect X per cent slope</td>
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<td>Aspect X elevation</td>
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<td>Aspect X slope form</td>
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<td>Aspect X biomass I</td>
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<td>Boles II</td>
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\( a \)\( b \)\( c \)\( d \)\( e \)
TABLE XVI (continued)

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<th>Independent Variables</th>
<th>Reproductive Component</th>
<th>Deciduous Leaves</th>
<th>Needles</th>
<th>Bark</th>
<th>Deciduous Leaves</th>
<th>Needles</th>
<th>Bark</th>
<th>Twigs and</th>
<th>Twigs and</th>
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<td>Branches II</td>
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<td>Biomass II - boles</td>
<td></td>
<td></td>
<td>-.622</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Biomass II - branches</td>
<td></td>
<td>-.549</td>
<td>-.541</td>
<td></td>
<td></td>
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<tr>
<td>01 + 02 horizon</td>
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<tr>
<td>01 horizon thickness</td>
<td></td>
<td></td>
<td>.726</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>01 horizon weight f</td>
<td></td>
<td></td>
<td>.584</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>01 horizon Ca f</td>
<td></td>
<td></td>
<td>.588</td>
<td></td>
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<tr>
<td>01 horizon K f</td>
<td></td>
<td></td>
<td>.675</td>
<td>-.845</td>
<td></td>
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<td>01 horizon Mg f</td>
<td></td>
<td></td>
<td>.608</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>01 horizon Pf</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>02 horizon - Pf</td>
<td></td>
<td></td>
<td>.935</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[ a_r = .532 \text{ at } P.05; \ r = .661 \text{ at } P.01. \]
\[ b_r = .811 \text{ at } P.05; \ r = .917 \text{ at } P.01. \]
\[ c_I \text{ denotes tree-tall shrub stratum; } II \text{ denotes sapling-low shrub stratum.} \]
\[ d\text{Immature stands only (n=4) } P.05 = .950; P.01 = .990. \]
\[ e\text{Importance value } = \text{ relative dominance + relative density.} \]
\[ f\text{Kg/ha.} \]
decreased on steep slopes with northeast aspect, the importance of yellow birch was not related to aspect, slope steepness, or elevation in the Balsam Mountains as would be expected at these elevations (Whittaker, 1956).

The production of needles in yellow birch stands was directly related to the density and basal area of red spruce which was scattered throughout many of the immature stands. In coniferous stands, needle litterfall increased as basal area and Importance Value 200 (IV 200) of Fraser fir increased and decreased on steeper northeastern slopes at higher elevations. In contrast, foliage biomass was generally insensitive to these topographic parameters which suggests that foliage production was more sensitive to elevational and temperature gradients than standing crop of foliage. Fraser fir needle turnover may be more rapid than spruce due to greater needle longevity of spruce which may partially account for the relation of needle fall and fir structural parameters.

Twig and bark litterfall increased in yellow birch stands as stand basal area, yellow birch basal area, and stand biomass increased reflecting increased biomass of branches with higher basal area and biomass and the greater branch biomass in mature stands. Development of rough, exfoliating bark which occurs with maturity and declining of growth rates of yellow birch trees (Clausen and Godman, 1969) would also be associated with increased bark litterfall (Bray
and Gorham, 1964). The direct relation with elevation x basal area interaction suggests greater competition with correspondingly higher mortality of small twigs in dense yellow birch stands at higher elevations where less favorable environmental conditions would be expected.

Twig and bark litterfall in coniferous stands was not significantly correlated with structural and site parameters with the exception of certain properties of the 01 horizon of the forest floor. Perennial components persist in forest floors of coniferous stands for many years (McFee and Stone, 1966) and the relation may indicate the effects of litterfall composition on forest floor structure. The variability in twig and bark litterfall was high further supporting the necessity of long-term studies, for reliable estimates of these litterfall components.

**Forest Floor**

Thickness of the forest floor of spruce-fir stands ranged from 3 to 20 cm and averaged (Table XVII) about 9 cm, the same as in 22 spruce-fir stands in the Great Smoky Mountains (Wolfe, 1967). Forest floor thickness ranged from 3 to 6 cm and was significantly lower in yellow birch stands but similar to the mean of 17 beech and yellow birch stands in the Great Smoky Mountains (Wolfe, 1967). Reduction of forest floors normally associated with logging (Wright, 1957;
### TABLE XVII

**THICKNESS, BULK DENSITY AND DRY WEIGHT OF FOREST FLOOR**

<table>
<thead>
<tr>
<th>Forest Floor Components</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance$^a,b$</td>
<td>Mean</td>
</tr>
<tr>
<td>Total, t/ha</td>
<td>119.92</td>
<td>65.06</td>
<td>1</td>
<td>72.45</td>
</tr>
<tr>
<td>Bole and large branches, t/ha</td>
<td>19.51</td>
<td>19.16</td>
<td>NS</td>
<td>33.58</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>15.16</td>
<td>12.01</td>
<td>NS</td>
<td>37.13</td>
</tr>
<tr>
<td>01 horizon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thickness, cm</td>
<td>4.50</td>
<td>2.20</td>
<td>3</td>
<td>2.43</td>
</tr>
<tr>
<td>Bulk density, g/cm$^3$</td>
<td>0.102</td>
<td>0.027</td>
<td>4</td>
<td>0.060</td>
</tr>
<tr>
<td>Dry weight, t/ha</td>
<td>43.52</td>
<td>16.50</td>
<td>4</td>
<td>14.12</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>39.72</td>
<td>12.80</td>
<td>3</td>
<td>22.02</td>
</tr>
<tr>
<td>02 horizon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thickness, cm</td>
<td>3.78</td>
<td>3.73</td>
<td>1</td>
<td>1.83</td>
</tr>
<tr>
<td>Bulk density, g/cm$^3$</td>
<td>0.168</td>
<td>0.033</td>
<td>NS</td>
<td>0.156</td>
</tr>
<tr>
<td>Dry weight, t/ha</td>
<td>56.89</td>
<td>43.80</td>
<td>2</td>
<td>25.75</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>45.12</td>
<td>12.30</td>
<td>NS</td>
<td>40.85</td>
</tr>
</tbody>
</table>

$^a$ T-test of difference between means of spruce-fir and immature yellow birch stands.

$^b$ NS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.

$^c$ T-test of difference between means of immature and mature yellow birch stands.
Hart, 1961) were not apparent and sufficient time may have elapsed to allow recovery. Higher values are generally reported from stands in the northeast, particularly in some spruce-hardwood stands (McFee and Stone, 1965) where forest floor thickness averaged about twice that of spruce-fir stands of this study. Bulk density of the 01 horizon of spruce-fir stands was similar to values reported from spruce-fir stands in the Great Smoky Mountains (Ritchie, 1962; McGinnis, 1958) but bulk densities in yellow birch stands exceeded values reported from beech stands. Bulk densities of the spruce-fir 01 horizons were significantly greater than in yellow birch stands; little difference occurred between bulk densities of 02 horizons in spruce-fir and yellow birch stands. Bulk density of 02 horizons were similar to those reported for F and H layers of other comparable forests (Ritchie, 1962; McGinnis, 1958; McFee and Stone, 1965).

Total forest floor weight ranged from 35 to 321 t/ha in spruce-fir stands and was significantly greater than in yellow birch stands (Table XVII, page 169) where weights ranged from 52 to 118 t/ha. Similar spruce fir forest floor weights were reported in the Great Smoky Mountains but forest floor weight in a south-facing beech stand was only about one-tenth as great (McGinnis, 1958). The greater similarity of yellow birch forest floors to spruce-fir than
deciduous forest floors indicates slow decay rates at high elevations in the Southern Appalachians (Shanks and Olson, 1961) especially of relatively nutrient-poor yellow birch litter. Many of these stands occupied former spruce-fir sites which apparently did not burn after logging and perhaps the high values indicate some carry over from previous forests. Variability of all horizons was large as expected due to the effects of wind on distribution of litter, persistence of stumps and logs, accumulation of litter around trees (McFee and Stone, 1965), and of pit-mound microrelief related to windthrow (Hart, et al., 1962; Lyford and MacLean, 1966). As in other stands (McFee and Stone, 1966), boles and branches formed an important portion of the forest floor, especially in immature yellow birch stands suggesting high mortality during natural thinning. Differences between 01 horizons, excluding bole and branch litter, of mature and immature yellow birch stands were not significant but absolute and relative weights of the 01 horizon of spruce-fir stands were significantly greater than immature yellow birch stands. Weights of 02 horizons of mature yellow birch and spruce-fir both exceeded that of immature yellow birch. In all forest types, weights increased from 01 to 02 horizons, and indicates both accumulation of organic matter (Trimble and Lu11, 1956) and increased incorporation of mineral material from the underlying A horizon. Transition from 02
to A horizons were gradual and exact delineation of the two was difficult. Organic matter content of the 02 horizon was 53.5 per cent ± 3.2 per cent (mean ± S. E.) which was similar to values from many stands (Kittredge, 1948). Differences between yellow birch and spruce-fir (55.3 per cent versus 53.0 per cent, respectively) were not significant, and adjusting mean weights of 02 horizons to exclude weight of inorganic materials indicated organic matter in spruce-fir, immature yellow birch, and mature yellow birch stands of 30.4 t/ha, 13.8 t/ha, and 23.2 t/ha, respectively. These adjustments did not produce appreciable changes relative to the forest floor weights in other stands in the Great Smoky Mountains and northeastern United States. Annual litterfall weight to forest floor weight ratios varied between 0.06 and 0.09; differences between deciduous and coniferous stands were not apparent and ratios were of the same order of magnitude as those of subalpine forests ( Olson, 1963). Leaf litterfall alone was from 4.5 to 7.5 per cent of forest floor in Balsam Mountain stands. Forest floor accumulations in these ecosystems were equivalent to from 10 to 16 years total litterfall or 14-22 years of leaf litterfall.

Variations in forest floor weight were correlated with neither slope steepness nor aspect, as in other studies (Knighton, 1970), but 01 horizons tended to increase toward higher elevations or in relation to elevation x basal area
interaction (Table XVIII). Lower 01 horizon weight char-
acterized yellow birch valleys of the current study sug-
gesting increased decay rates in relation to present
deciduous vegetation and perhaps increased importance of
deciduous species in valleys at higher elevations (Whittaker,
1956). Reduction of forest floor weights in coniferous stands
with increase of deciduous species, as suggested by Rodin and
Basilevic (1967), was indicated in this study by the inverse
relation of 01 horizon weight and yellow birch basal area and
IV-200. Forest floor weight also varied in relation to stand
density contrary to other studies such as those by Aldon
(1968) and Moer and Grier (1969). Forest floor weight also
increased with increased litterfall of perennial components.
The 01 horizon of coniferous stands varied in relation to
more structural characteristics than the 02 horizon as would
be expected if carry over from previous forest floor char-
acteristics existed. In yellow birch stands 02 horizon weight
was directly related to basal area and perennial component
biomass (Table XVIII) which apparently reflected the greater
stand age where greater forest floor weights generally
occur (Aldon, 1968; Williston, 1966; Gregory, 1950).

**Soil Organic Matter**

Organic matter as per cent of dry weight was high in
surface horizons of both spruce-fir and yellow birch stands
(Table XIX). Similar high values were reported (Wolfe, 1967)
# TABLE XVIII

ASSOCIATION OF FOREST FLOOR PROPERTIES WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE $r$)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>01</td>
</tr>
<tr>
<td>horizon thickness</td>
<td>.851</td>
</tr>
<tr>
<td>horizon thickness</td>
<td>.969</td>
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<tr>
<td>Elevation</td>
<td></td>
</tr>
<tr>
<td>Elevation X basal area IC</td>
<td>.558</td>
</tr>
<tr>
<td>Slope form</td>
<td></td>
</tr>
<tr>
<td>Density I - Fir</td>
<td>.559</td>
</tr>
<tr>
<td>Fir density II</td>
<td>-.532</td>
</tr>
<tr>
<td>Density I</td>
<td></td>
</tr>
<tr>
<td>Birch density IV 200</td>
<td>-.574</td>
</tr>
<tr>
<td>Birch basal area I</td>
<td>-.564</td>
</tr>
<tr>
<td>Basal area I</td>
<td></td>
</tr>
<tr>
<td>Density I X basal area I</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Density I + II</td>
<td>.559</td>
</tr>
<tr>
<td>Biomass I: Bole</td>
<td></td>
</tr>
<tr>
<td>Biomass I: Branch</td>
<td></td>
</tr>
<tr>
<td>Biomass I: Total</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Yellow Birch(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>01</td>
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<td>horizon thickness</td>
<td></td>
</tr>
<tr>
<td>horizon thickness</td>
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</tr>
<tr>
<td>Elevation</td>
<td></td>
</tr>
<tr>
<td>Elevation X basal area IC</td>
<td></td>
</tr>
<tr>
<td>Slope form</td>
<td></td>
</tr>
<tr>
<td>Density I - Fir</td>
<td></td>
</tr>
<tr>
<td>Fir density II</td>
<td></td>
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<tr>
<td>Density I</td>
<td></td>
</tr>
<tr>
<td>Birch density IV 200</td>
<td></td>
</tr>
<tr>
<td>Birch basal area I</td>
<td></td>
</tr>
<tr>
<td>Basal area I</td>
<td></td>
</tr>
<tr>
<td>Density I X basal area I</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Density I + II</td>
<td></td>
</tr>
<tr>
<td>Biomass I: Bole</td>
<td></td>
</tr>
<tr>
<td>Biomass I: Branch</td>
<td></td>
</tr>
<tr>
<td>Biomass I: Total</td>
<td></td>
</tr>
</tbody>
</table>

| Bole and branch litterfall | .589 |  
| Twig and branch litterfall | .584 |  
| Twig and branch litterfall, Mg | -.546 |
TABLE XVIII (continued)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Bole</th>
<th>Yellow Birch&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>01</td>
<td>02</td>
<td>and 01</td>
</tr>
<tr>
<td>Foliage as per cent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>leaf litterfall</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Needle litterfall, Ca</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>r = .532 at P.05; r = .661 at P.01.

<sup>b</sup>r = .950 at P.05; r = .661 at P.01.

<sup>c</sup>I denotes tree-tall shrub stratum; II denotes sapling-low shrub stratum; IV denotes herb stratum.
## TABLE XIX

ORGANIC MATTER (PER CENT OF OVEN-DRY WEIGHT) IN MINERAL SOIL HORIZONS

<table>
<thead>
<tr>
<th>Horizon</th>
<th>Spruce-Fir</th>
<th>Yellow Birch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>S.E.(^a)</td>
</tr>
<tr>
<td>A1</td>
<td>29.06</td>
<td>3.00</td>
</tr>
<tr>
<td>A2</td>
<td>36.22</td>
<td>10.18</td>
</tr>
<tr>
<td>A3</td>
<td>18.69</td>
<td>3.40</td>
</tr>
<tr>
<td>B1</td>
<td>16.38</td>
<td>6.05</td>
</tr>
<tr>
<td>B2ir</td>
<td>19.91</td>
<td>2.27</td>
</tr>
<tr>
<td>B2</td>
<td>13.19</td>
<td>1.09</td>
</tr>
<tr>
<td>B3</td>
<td>7.50</td>
<td>0.66</td>
</tr>
<tr>
<td>C</td>
<td>2.86</td>
<td>1.03</td>
</tr>
</tbody>
</table>

\(^a\)Standard error of mean.
in upper soil horizons of spruce-fir and beech stands in the Great Smoky Mountains; organic matter (per cent) decreased with increasing depth and proportion in spruce-fir stands exceeded those in deciduous stands in both the study area and the Great Smoky Mountains. Organic matter (per cent) in lower horizons in the study area were generally higher than in comparable horizons of the Great Smoky Mountains.

Tree roots were most abundant in 02 through B1 horizons, occasional in B2 horizons and usually absent from B3 horizons. A through B1 horizons were assumed to represent mineral soil available for rooting and calculations of total organic matter (t/ha) showed relatively large quantities compared with other studies (McFee and Stone, 1965) (Table XX). High variability of total organic matter within horizons reflected varying percentages of organic matter and depths of horizons. Both quantities and the distribution of organic matter were similar between spruce-fir and immature yellow birch stands. Soils of mature yellow birch stands contained greater quantities of organic matter but proportionally less in A and B1 horizons. In these rock soils, the A horizons were less well developed than in other soils sampled; B2 horizons had lower volumes of stones than the A and were often very thick, some extending to depths of 1.2 meters or more and contained large amounts of organic matter.
<table>
<thead>
<tr>
<th>Horizons</th>
<th>Spruce-Fir (n=14)</th>
<th>Yellow Birch</th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>Mean</td>
</tr>
<tr>
<td>Total, t/ha</td>
<td>369.26</td>
<td>14.00</td>
<td>NS</td>
<td>442.50</td>
</tr>
<tr>
<td>A, t/ha</td>
<td>176.77</td>
<td>99.60</td>
<td>NS</td>
<td>215.17</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>46.57</td>
<td>21.83</td>
<td>NS</td>
<td>47.73</td>
</tr>
<tr>
<td>B1, t/ha</td>
<td>24.21</td>
<td>42.06</td>
<td>NS</td>
<td>43.83</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>6.05</td>
<td>9.89</td>
<td>NS</td>
<td>13.76</td>
</tr>
<tr>
<td>B2, t/ha</td>
<td>168.28</td>
<td>110.01</td>
<td>NS</td>
<td>183.50</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>37.37</td>
<td>27.33</td>
<td>NS</td>
<td>38.51</td>
</tr>
</tbody>
</table>

<sup>a</sup>T-test of difference between means of spruce-fir and immature yellow birch stands.

<sup>b</sup>NS P < .10; 1 P > .10.

<sup>c</sup>T-test of difference between means of immature and mature yellow birch stands.
The quantity of organic matter (t/ha) in soil horizons was not generally related to topographic features except for a direct relation with slope steepness in immature yellow birch stands (Table XXI). Organic matter of B1 horizons was more closely related to forest floor properties, properties of other mineral horizons, and vegetational parameters than A or B2 horizons and in many cases the relationship was inverse. Both soil properties and vegetation are functions of similar environmental factors; each mutually affects the other (Jenny, 1941) such that it is difficult to determine cause-effect relationships, and their direction if indeed they exist.

**Net Ecosystem Primary Production**

Annual above-ground net ecosystem productivity ranged from 6.5 to 9.8 t/ha in spruce-fir, 6.0 to 8.4 t/ha in immature yellow birch, and 4.9 to 7.0 t/ha in mature yellow birch ecosystems. Although the means were not significantly different (Table XXII), increasing productivity was indicated along the sequence mature yellow birch < immature yellow birch < spruce-fir. These results were similar to production of comparable ecosystems in the Great Smoky Mountains except in a young spruce-fir forest there, where productivity exceeded maximum values in the Balsam Mountains by a factor of more than 1.4 (Whittaker, 1966). Greater production by conifers than deciduous species under similar
TABLE XXI

ASSOCIATION OF SOIL ORGANIC MATTER WEIGHT WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE r)

<table>
<thead>
<tr>
<th>Soil Horizon</th>
<th>Spruce-Fir$^a$</th>
<th>Yellow Birch$^b$ Immature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ac</td>
<td>B1</td>
</tr>
<tr>
<td>Per cent slope</td>
<td></td>
<td></td>
</tr>
<tr>
<td>01 phosphorus</td>
<td>-.616</td>
<td></td>
</tr>
<tr>
<td>02 phosphorus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A organic matter</td>
<td>.592</td>
<td></td>
</tr>
<tr>
<td>B2 horizon weight</td>
<td>-.616</td>
<td>-.557</td>
</tr>
<tr>
<td>B2 organic matter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree crown length</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree height</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole biomass Id</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole K I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole Mg I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole P I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf Ca I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf K I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf P I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Net primary production;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>reproductive components</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I + II</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole volume increment I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole biomass increment I</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a r = .532$ at $P.05$; $r = .661$ at $P.01$.

$^b r = .950$ at $P.05$; $r = .990$ at $P.01$.

$^c$ CA and B1 denote soil horizons.

$^d$ I denotes tree-tall shrub stratum; II denotes sapling-low shrub stratum.
<table>
<thead>
<tr>
<th>Strata</th>
<th>Spruce-Fir</th>
<th>Yellow Birch</th>
<th>Significance d</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Immature Growth</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree-shrub strata, t/ha e</td>
<td>7.58</td>
<td>0.45</td>
<td>6.62</td>
</tr>
<tr>
<td>Boles f</td>
<td>2.65</td>
<td>0.42</td>
<td>2.35</td>
</tr>
<tr>
<td>Per cent of stratum</td>
<td>35.6</td>
<td>8.5</td>
<td>34.4</td>
</tr>
<tr>
<td>Branches</td>
<td>0.44</td>
<td>0.08</td>
<td>0.81</td>
</tr>
<tr>
<td>Per cent of stratum</td>
<td>5.8</td>
<td>1.6</td>
<td>11.9</td>
</tr>
<tr>
<td>Leaves</td>
<td>3.42</td>
<td>0.78</td>
<td>3.24</td>
</tr>
<tr>
<td>Per cent of stratum</td>
<td>45.1</td>
<td>6.9</td>
<td>49.2</td>
</tr>
<tr>
<td>Reproductive components</td>
<td>1.07</td>
<td>0.49</td>
<td>0.21</td>
</tr>
<tr>
<td>Per cent of stratum</td>
<td>13.6</td>
<td>5.1</td>
<td>3.6</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>92.8</td>
<td>6.6</td>
<td>91.4</td>
</tr>
<tr>
<td>Bole volume increment, m³/ha</td>
<td>6.76</td>
<td>1.75</td>
<td>3.82</td>
</tr>
<tr>
<td>Tree-shrub regeneration, t/ha</td>
<td>0.047</td>
<td>0.087</td>
<td>0.008</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.14</td>
<td>0.25</td>
<td>0.12</td>
</tr>
<tr>
<td>Herbs, t/ha</td>
<td>0.15</td>
<td>0.17</td>
<td>0.29</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>2.05</td>
<td>2.26</td>
<td>4.28</td>
</tr>
<tr>
<td>Strata</td>
<td>Bryophytes, t/ha</td>
<td>Per cent of total</td>
<td>Total, all strata, t/ha</td>
</tr>
<tr>
<td>---------------------------</td>
<td>------------------</td>
<td>------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td></td>
<td>Mean  STD(^a)</td>
<td>Mean  STD</td>
<td>Mean  STD(^b),(^c)</td>
</tr>
<tr>
<td></td>
<td>0.38  0.40</td>
<td>5.02  5.70</td>
<td>8.16  1.10</td>
</tr>
</tbody>
</table>

\(^a\)Standard deviation of mean.

\(^b\)T-test, significance of difference between means of spruce-fir and immature growth yellow birch stands (16 df).

\(^c\)NS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.

\(^d\)T-test, significance of difference between means of immature growth and mature yellow birch stands (4 df).

\(^e\)Includes tree-tall shrub and sapling - low shrub strata.

\(^f\)Means based on 14 spruce-fir, four immature growth yellow birch, and two mature yellow birch stands, respectively.

\(^g\)34 df.

\(^h\)8 df.
macroenvironmental conditions and decreasing production with stand maturity, as reported by others (Rodin and Basilevic, 1967; Whittaker, 1966), was suggested although productivity was variable within ecosystems and ranges overlapped. Tree-shrub regeneration production was trivial in all ecosystems; herb production ranged as high as 6 per cent in spruce-fir and 11 per cent of total production in yellow birch ecosystems but was highly variable. These rates were similar to comparable forests in the Great Smoky Mountains and those in the northeast (Whittaker, 1966; Siccama, et al., 1970).

Differences between ecosystems were more obvious when biomass accumulation ratios (ecosystem biomass/ecosystem production) and distribution of net primary production among certain strata were compared. Biomass accumulation ratios were: spruce-fir, 22; immature yellow birch, 14; and mature yellow birch, 26 which indicated greatest production per unit biomass in immature yellow birch stands and least in oldest stands, the usual trend with increasing age (Whittaker, 1966). Greater efficiency of immature yellow birch compared with spruce-fir was also indicated. Bryophyte production ranged from 0 to 19 per cent and 0 to 10 per cent of total production in spruce-fir and immature yellow birch ecosystems, respectively, but differences were not significant. In mature yellow birch stands, however, bryophytes contributed a significant portion (18 to 23 per cent) of
total ecosystem production which was much greater than their proportion of total biomass.

The distribution of net primary production among components of tree-shrub strata (stems $\geq 0.5$ m tall) also showed departures from the distribution of biomass; differences among stand types were also indicated. Limited production by sapling-low shrub strata indicates that the distribution percentages in Table XXII, page 181, primarily reflect the distribution of production among components of tree-tall shrub strata. In all stands, the greatest proportion of net primary production was in foliage which was many times more important in production than in biomass relations. The foliage proportion was especially high in mature yellow birch stands where bole and branch production each was significantly lower than in immature stands but foliage production was similar. Boles and branches were less important in dry-matter production than in stand biomass. The proportion of dry-matter production in boles and branches was significantly lower in mature than immature yellow birch stands; branches in immature yellow birch stands accounted for a significantly greater portion of production than in spruce-fir stands.

Reproductive components formed a large proportion of production in spruce-fir stands compared with yellow birch stands and other coniferous stands elsewhere
(Baskerville, 1965). These high values were also reflected in somewhat lower proportions of production of foliage, branches, and boles as compared with other coniferous stands (Baskerville, 1965). In years of low flowering and seed production, both relative and absolute production of foliage and perennial components would increase since flowering correlates with decreased production of current foliage and twigs and radial wood increment (Fraser and McGuire, 1969). Cone and seed production were undoubtedly higher than average during the sampling period.

Production estimates of tree-tall shrub and sapling-low shrub strata were combined because foliage production of the latter could not be separated from foliage litter produced by larger trees and shrubs. Bole and branch production which were estimated separately showed that production by sapling-low shrub stratum of these (and presumably the foliage components) was trivial relative to tree-tall shrub production. Bole and branch production of this stratum ranged from 0 to 40 kg/ha in the three ecosystems. Differences were not apparent between systems. Low production by shrubs in forests at high elevations was also shown in the Great Smoky Mountains (Whittaker, 1966).

Distribution of net primary production among vegetational strata differed from the distribution of biomass. Contribution of inferior strata to net primary production
was relatively larger than their contribution to biomass, often by factors of 3-10. Percentage shifts were particularly large for tree-sapling and bryophytic strata in mature yellow birch stands. These shifts reflect the high ratio of current to older tissues of small woody plants from which net primary production was calculated. Ratios of current to older tissue ranged from 1.0 for one year seedlings downward to 0.2 for larger Fraser fir seedlings. These latter ratios were low compared with small shrubs (Whittaker, 1961, 1962).

**Environmental factors affecting production.** Net production of reproductive components and foliage of tree and shrub strata (stems > 0.5 m tall) decreased toward higher elevations on steep, northeast slopes and in coves (Table XXIII). Lower temperatures which reduce flowering (Fraser, 1958) and perhaps foliage production may be indicated. Net production of other components showed no relation to these and other topographic and soil factors. Net production of these strata was also generally unrelated to soil and site parameters in immature yellow birch stands. An exception was foliage production which was inversely related to the interaction elevation A horizon weight and to B horizon organic matter weight. Decreased production of yellow birch ecosystems would be expected on cooler sites (higher elevations and north aspects) although no relation was apparent
**TABLE XXIII**

ASSOCIATION OF NET PRODUCTION OF COMBINED TREE-SHRUB STRATA WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE r)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Reproductive Components</th>
<th>Foliage</th>
<th>Branches</th>
<th>Boles</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce-Fir Stands&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent slope</td>
<td>-.585</td>
<td>-.738</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation X slope per cent</td>
<td>-.567</td>
<td>-.736</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect X slope per cent</td>
<td>-.589</td>
<td>-.725</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect X slope form</td>
<td>-.569</td>
<td>-.674</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation X aspect</td>
<td>-.526</td>
<td>-.531</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A horizon P</td>
<td>-.558</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B2 horizon weight</td>
<td>.537</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B2 horizon Ca</td>
<td></td>
<td>.546</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>02 horizon Mg</td>
<td></td>
<td>.630</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>02 horizon P</td>
<td></td>
<td>.647</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fir density I&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td>.566</td>
<td>.608</td>
<td>.580</td>
<td>.777</td>
</tr>
<tr>
<td>Fir basal area I</td>
<td>.692</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density I + II&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-.565</td>
<td>-.656</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density II</td>
<td>-.594</td>
<td>-.669</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area II</td>
<td>-.540</td>
<td>-.767</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole volume I</td>
<td>.662</td>
<td></td>
<td></td>
<td></td>
<td>.632</td>
</tr>
<tr>
<td>Aged</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.649</td>
</tr>
</tbody>
</table>
TABLE XXIII (continued)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Reproductive Components</th>
<th>Foliage</th>
<th>Branches</th>
<th>Boles</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A horizon weight</td>
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<td></td>
</tr>
<tr>
<td>Aspect X slope per cent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass I, boles</td>
<td>.982</td>
<td>.995</td>
<td>.969</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass I, branches</td>
<td>.999</td>
<td>.989</td>
<td>.990</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass I, total</td>
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<td>.996</td>
<td>.961</td>
<td></td>
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</tr>
<tr>
<td>Age</td>
<td>-.952</td>
<td>-.952</td>
<td>-.971</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( \text{er} = .950 \text{ at P.01}; r = .990 \text{ at P.01}. \)

\( \text{ar} = .532 \text{ at P.05}; r = .661 \text{ at P.01}. \)

\( \text{b} \)Aspect = \( \cos (45-A) + 1 \) where \( A \) = azimuth from north in degrees.

\( \text{cI} \) denotes tree-tall shrub stratum; \( \text{II} \) denotes sapling-low shrub stratum.

\( \text{d} \)Mean age of stems in tree-tall shrub stratum.
between production and elevation, aspect, nor the interaction aspect x elevation. Many of the yellow birch stands particularly those toward higher elevations and north aspects were on former spruce-fir sites where greater development of A horizons and of organic matter in lower horizons are believed to have occurred. Perhaps sites previously occupied by coniferous stands were less favorable for yellow birch production as a result of topographic or soil variables not measured.

These relationships reflected the relation of tree-tall shrub production to environmental factors since sapling-low shrub production was very low in comparison and quite different in response to environmental factors. In spruce-fir and yellow birch stands both net production of boles and branches and development of sapling-low shrub strata were highly and directly correlated with aspect as it varied from southwest to northeast, increasing elevation, steeper slopes, cove positions, and various interactions of these factors (Table XXIV). Conversely bole and branch production by tree-tall shrub strata of coniferous and deciduous stands was either not correlated with environmental factors or correlations were inverse. Tree-tall shrub net production, particularly of perennial components, showed little variation in relation to environmental factors over the range of conditions sampled but both the biomass and net primary
TABLE XXIV

ASSOCIATION OF BOLE AND BRANCH DRY-MATTER PRODUCTION IN SAPLING-LOW SHRUB STRATA WITH SITE AND STAND STRUCTURAL PARAMETERS (SIMPLE r)

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Spruce-Fir&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Immature Yellow Birch&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bole Production</td>
<td>Branch Production</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bole Production</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Branch Production</td>
</tr>
<tr>
<td>Aspect</td>
<td>.670</td>
<td>.970</td>
</tr>
<tr>
<td>Elevation</td>
<td>.682</td>
<td>.974</td>
</tr>
<tr>
<td>Per cent slope</td>
<td>.783</td>
<td></td>
</tr>
<tr>
<td>Elevation X slope</td>
<td>.820</td>
<td>.970</td>
</tr>
<tr>
<td>per cent</td>
<td>.974</td>
<td></td>
</tr>
<tr>
<td>Aspect X slope</td>
<td>.934</td>
<td>.550</td>
</tr>
<tr>
<td>per cent</td>
<td>.767</td>
<td></td>
</tr>
<tr>
<td>Aspect X slope</td>
<td>.934</td>
<td>.550</td>
</tr>
<tr>
<td>form</td>
<td>.767</td>
<td></td>
</tr>
<tr>
<td>Aspect X elevation</td>
<td>.723</td>
<td>.981</td>
</tr>
<tr>
<td>01 horizon weight</td>
<td>- .981</td>
<td>- .985</td>
</tr>
<tr>
<td>02 horizon Mg</td>
<td>.977</td>
<td>.977</td>
</tr>
<tr>
<td>B2 horizon organic matter</td>
<td>.977</td>
<td></td>
</tr>
<tr>
<td>Density I + II&lt;sup&gt;c&lt;/sup&gt;</td>
<td>.766</td>
<td></td>
</tr>
<tr>
<td>Density II</td>
<td>.690</td>
<td>.968</td>
</tr>
<tr>
<td>Basal area II</td>
<td>.849</td>
<td>.966</td>
</tr>
<tr>
<td>Biomass II, boles</td>
<td>.996</td>
<td></td>
</tr>
<tr>
<td>Biomass II, branches</td>
<td></td>
<td>.835</td>
</tr>
<tr>
<td>Biomass II, foliage</td>
<td>.787</td>
<td></td>
</tr>
<tr>
<td>Biomass II, total</td>
<td>.961</td>
<td>.601</td>
</tr>
<tr>
<td>Leaf area index II</td>
<td>.756</td>
<td>.538</td>
</tr>
</tbody>
</table>

<sup>a</sup>r = .532 at P.05; r = .661 at P.01.

<sup>b</sup>r = .950 at P.05; r = .990 at P.01.

<sup>c</sup>I denotes tree-tall shrub stratum; II denotes sapling-low shrub stratum.
production of sapling-low shrub strata were closely related to environmental factors. Deciduous shrubs of the high elevation forests decreased in coverage from mesic to xeric sites (Whittaker, 1956); these trends were especially evident in yellow birch stands. In coniferous forests, Fraser fir was the most important species in the sapling low shrub stratum and the relation of both biomass and production rates of this stratum to topographic factors reflects the suitability of these habitats.

**Structural factors affecting production.** Total net production of tree and shrub strata (stems $\geq 0.5$ m tall) in spruce-fir stands was not significantly correlated with stand basal area, density, stand biomass, foliage biomass, or stand leaf area. The production of reproductive components was significantly and positively correlated with foliage production but generally not with production of other components.

Production of reproductive components increased with increasing basal area of Fraser fir in stands and together with foliage production decreased with increased density of stems $\geq 0.5$ m tall. The relation between reproductive component production and Fraser fir basal area reflects the heavy seed crop produced during 1969 and suggests greatest production in stands of lower density where trees had larger crowns. The relation of total net production
and fir basal area largely reflects the close correlation of total and reproductive component production. Foliage production in immature yellow birch stands was directly and significantly correlated (10 per cent level) with total density but not density of overstory trees and shrubs. Relatively large foliage production by understory species relative to larger trees and shrubs has also been reported in other forests (Scott, 1955; Shanks, et al., 1961).

Bole and branch production of sapling-low shrub strata in coniferous stands increased as sapling-low shrub biomass increased; bole production and biomass and branch production and biomass were highly correlated which accounted for the relation with total biomass. In yellow birch stands, sapling-low shrub bole and branch production tended to increase as bole biomass increased but the trend was less clear and significant just below the 5 per cent level. Bole production in coniferous stands increased as understory foliage biomass and leaf area increased. Neither foliage biomass nor leaf area was correlated with branch production in coniferous stands or with bole and branch production in yellow birch stands. In coniferous stands as indicated by differences in correlation coefficients, branch production was less sensitive to environmental and structural factors than was bole production. This is the relationship which would be expected between bole and branch
production of larger trees (Satoo, 1966; Wegge, 1966). However, little such sensitivity among yellow birch stands was indicated by correlations.

**Production of tree-tall shrub strata.** Bole volume increment and bole and branch dry-matter production of tree-tall shrub strata in coniferous stands increased with increased total stand density and particularly with density of Fraser fir in stands (Table XXV). Stand basal area, stand biomass, stand foliage biomass and leaf area were all cross-correlated but none were correlated with stand density or dry-matter production. Basal area of Fraser fir was related to bole volume increment. Both bole volume increment and bole dry-matter production decreased in stands where yellow birch was more important reflecting the greater annual productivity of conifers as compared with deciduous species growing in similar habitats (Safford, 1968).

In immature yellow birch stands the relation between stand structure and net production was quite different. Bole volume increment and bole and branch dry-matter production increased with increased stand density, stand basal area, total biomass, biomass of boles, and leaf area (Table XXV). In these stands, foliage biomass, stand biomass, and basal area were cross-correlated; although not significantly correlated at the 5 per cent level, there was a strong trend for density to increase as these parameters increased.
<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>$\text{p}_v^a$</th>
<th>$\text{P}_{bo}$</th>
<th>$\text{P}_{br}$</th>
<th>$\text{LE}_v^b$</th>
<th>$\text{LE}_bo$</th>
<th>$\text{LE}_br$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation X slope per cent</td>
<td>.376</td>
<td>.589</td>
<td>.608</td>
<td>.668</td>
<td>.391</td>
<td>.474</td>
</tr>
<tr>
<td>Density $\text{Id}$</td>
<td>.589</td>
<td>.608</td>
<td>.668</td>
<td>.391</td>
<td>.474</td>
<td></td>
</tr>
<tr>
<td>Basal area $\text{I}$</td>
<td>.389</td>
<td>.574</td>
<td>.555</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fir density</td>
<td>.664</td>
<td>.574</td>
<td>.555</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fir basal area $\text{I}$</td>
<td>.543</td>
<td>.444</td>
<td>.503</td>
<td>.542</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birch density $\text{I}$</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Birch basal area $\text{I}$</td>
<td>-.388</td>
<td>-.367</td>
<td></td>
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</tr>
<tr>
<td>Biomass $\text{I}$, boles</td>
<td>-.483</td>
<td>-.546</td>
<td>-.609</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass $\text{I}$, branches</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass $\text{I}$, foliage</td>
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<td>-.563</td>
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<tr>
<td>Biomass $\text{I}$, total</td>
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<td>LE$\text{v}$</td>
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<td>.636</td>
<td>.722</td>
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<tr>
<td>LE$\text{bo}$</td>
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<td>.593</td>
<td>.608</td>
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<tr>
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<tr>
<td>NAR$\text{v}^e$</td>
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<td>NAR$\text{bo}$</td>
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<td>.584</td>
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<td>.977</td>
<td>.992</td>
<td>.996</td>
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<td>Mean bole weight/tree</td>
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<td>Mean branch weight/tree</td>
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<td>Mean leaf weight/tree</td>
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TABLE XXV (continued)

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<th>$P_{br}$</th>
<th>$LE_v$</th>
<th>$LE_{bo}$</th>
<th>$LE_{br}$</th>
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<td><strong>Immature Yellow Birch</strong> ($n=6$)</td>
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<td>.963</td>
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<td>Biomass I, bole</td>
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<td>Biomass I, branch</td>
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<td>Biomass I, foliage</td>
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<td>$NAR_v$</td>
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<td>.926</td>
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<td>$NAR_{bo}$</td>
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<td>.986</td>
<td>.974</td>
<td>.964</td>
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<td>$NAR_{br}$</td>
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<td>.987</td>
<td>.986</td>
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<td>Spruce, bole, per cent biomass</td>
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<td>Spruce, branch, per cent biomass</td>
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<td>-.851</td>
<td>-.886</td>
<td>-.911</td>
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<td>Spruce, foliage, per cent biomass</td>
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<td>-.925</td>
<td>-.950</td>
<td>-.966</td>
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<tr>
<td>Mean branch weight per tree</td>
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<td>-.846</td>
<td>-.859</td>
<td>-.888</td>
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<tr>
<td>Crown length/tree height</td>
<td></td>
<td></td>
<td></td>
<td>.902</td>
<td>.872</td>
<td>.851</td>
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</table>

| **Mature Yellow Birch** ($n=4$) |
| Birch density I        | .955  |         |         |       |         |         |
| $NAR_v$               |         | .999   | .988   | .937 |         |         |
| $NAR_{bo}$            |         | .995   | .999   | .974 |         |         |
| $NAR_{br}$            |         | .954   | .984   | .999 |         |         |
| Crown length/tree height |         |         |         |       |         | -.978  |
\[ \text{Cr} = 0.361 \text{ at P.05; } r = 0.463 \text{ at P.01.} \]

**d**I denotes tree-tall shrub stratum.

\[ \text{fr} = 0.811 \text{ at P.05; } r = 0.917 \text{ at P.01.} \]

\[ \text{gr} = 0.950 \text{ at P.05; } r = 0.990 \text{ at P.01.} \]
In mature yellow birch stands, bole volume increment and bole and branch dry-matter increment increased as yellow birch density increased but showed no relation to stand basal area, density, biomass, or leaf area. In this respect, production patterns were similar to coniferous stands. The relation to yellow birch density but not to total stand density apparently reflects the low productivity of mountain maple which frequently accounted for a major proportion of the stems in mature stands.

The relation between net production and stand structure in coniferous stands was in sharp contrast to production patterns in balsam fir stands of similar age studied by Baskerville (1965). In those stands, density, basal area, and stand biomass were all interrelated and maximum production was in stands where these parameters attained greatest magnitudes. Production-stand structure relations in immature yellow birch stands were similar to those in his balsam fir stands, however. In the Balsam Mountains spruce-fir stands, there was no indication of an optimum basal area for maximum net production as proposed by Assmann (cited by Wegge, 1966) but rather production varied greatly and mean rates were more or less constant across the range of basal areas sampled similar to Möller's (1954) findings. The similarities in patterns between the stands, however, resulted from different mechanisms.
Möller (1954) concluded that foliage biomass was constant across a broad range of stand basal areas and was the principal factor regulating production. In the spruce-fir stands in the present study, foliage biomass was not constant but increased as basal area increased. In Möller's study, a constant net assimilation rate (NAR) is implied; in the current study NAR was not constant but decreased with increased foliage biomass.

Equations for estimating production \( P_i \) of various strata and of components within strata show that production was highly correlated with combinations of site and stand structural attributes in these stands (Table XXVI). Partial regression coefficients represent rates of change in \( P_i \) per unit dependent variable \( X_i \) and when compared, show the relative contribution of each to net production. For example: Equation (9), Table XXVI, shows that production of Phanerogams \( P_{ha} \) in spruce-fir stands increased at the rate of about 5.4 t/ha/yr per year of age of the tree-tall shrub stratum \( X_{77} \) but decreased at the rate of 5.2 t/ha/yr per unit density of the combined tree-shrub stratum \( X_{14} \).

Examination of NAR and the similar but somewhat different relation, leaf efficiency (Table XXVII) showed that production rates relative to unit area or unit weight of foliage were low compared with other cool temperate
### TABLE XXVI

**REGRESSION EQUATIONS FOR ESTIMATING ABOVE-GROUND ANNUAL NET PRIMARY PRODUCTION**

<table>
<thead>
<tr>
<th>Components</th>
<th>Regression Equations</th>
<th>S.E.E.</th>
<th>R²</th>
<th>n</th>
<th>Significance</th>
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<tbody>
<tr>
<td>Spruce-Fir Stands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree-shrub(^d) (t/ha)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>(1) Total:</td>
<td>[ P_{tst} = 11.409 - 1.280X_3 + 0.055X_8 - 0.404X_{22} - 0.0004X_{42} - 0.011X_{80} ]</td>
<td>0.32</td>
<td>0.982</td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td>(2) Reproductive components:</td>
<td>[ P_{tsr} = 0.143 - 0.010X_4 + 0.020X_8 - 0.00005X_{18} - 0.002X_{44} ]</td>
<td>0.16</td>
<td>0.963</td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td>(3) Foliage:</td>
<td>[ P_{tsf} = 2.166 - 5.823X_{16} + 0.00005X_{18} + 0.007X_{32} + 0.162X_{76} ]</td>
<td>0.26</td>
<td>0.962</td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td>Sapling-low shrub</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>(4) Boles:</td>
<td>[ P_{bo2} = 0.424 - 0.006X_9 + 0.053X_{30} ]</td>
<td>1.05</td>
<td>0.997</td>
<td>14</td>
<td>4</td>
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<tr>
<td>(5) Branches:</td>
<td>[ P_{br2} = 0.973 + 0.054X_{31} + 0.015X_{61} + 0.047X_{74} - 0.099X_{75} ]</td>
<td>1.47</td>
<td>0.946</td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td>Components</td>
<td>Regression Equations</td>
<td>S.E.E.</td>
<td>R</td>
<td>Significance</td>
<td></td>
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<td>-----------------------------</td>
<td>-------------------------------------------------------------------------------------</td>
<td>--------</td>
<td>----</td>
<td>--------------</td>
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<tr>
<td>Tree-shrub regeneration (kg/ha)</td>
<td><strong>(6) Total:</strong> ( P_r = 21.489 + 13.115X_1 + 0.309X_{20} - )( 0.308X_{46} + 0.250X_{62} )</td>
<td>6.20</td>
<td>.969</td>
<td>14</td>
<td>4</td>
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<tr>
<td>Herbs (kg/ha)</td>
<td><strong>(7) Total:</strong> ( P_{ht} = -3973.666 + 0.411X_2 + 101.499X_{10} + 0.003X_{42} + 37.866X_{77} )</td>
<td>79.7</td>
<td>.925</td>
<td>14</td>
<td>4</td>
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<tr>
<td>(8) Cryogams:</td>
<td>( P_{hf} = -61.174 + 42.471X_{10} + 6.009X_{12} + 2.742X_{74} - 5.680X_{75} )</td>
<td>65.2</td>
<td>.919</td>
<td>14</td>
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<tr>
<td>(9) Phanergams:</td>
<td>( P_{ha} = 110.790 - 5.213X_{14} - 0.00002X_{59} + 5.371X_{77} )</td>
<td>19.0</td>
<td>.956</td>
<td>14</td>
<td>4</td>
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<tr>
<td>Bryophytes (kg/ha)</td>
<td><strong>(10) Total:</strong> ( P_{bry} = 481.061 - 228.474X_3 - 0.082X_5 - 84.556X_{10} + 284.522X_{79} )</td>
<td>112.2</td>
<td>.973</td>
<td>14</td>
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TABLE XXVI (continued)

<table>
<thead>
<tr>
<th>Components</th>
<th>Regression Equations</th>
<th>S.E.E.</th>
<th>( p )</th>
<th>n</th>
<th>Significance</th>
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<td>Yellow Birch Stands</td>
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<tr>
<td>Tree-tall shrub</td>
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<tr>
<td>(immature, t/ha)</td>
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</tr>
<tr>
<td>(1) Total:</td>
<td>( P_{tst} = 0.078 + 0.00024X_{19} )</td>
<td>0.12</td>
<td>*</td>
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<tr>
<td>(2) Reproductive component:</td>
<td>( P_{tsr} = -0.336 + 0.053X_{64} )</td>
<td>0.08</td>
<td>*</td>
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<td>1</td>
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<tr>
<td>(3) Foliage:</td>
<td>( P_{tsf} = 6.833 - 0.120X_{45} )</td>
<td>2.53</td>
<td>*</td>
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<td>4</td>
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<tr>
<td>Sapling-low shrub</td>
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<td></td>
<td></td>
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<tr>
<td>(all stands, kg/ha)</td>
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<tr>
<td>(4) Boles:</td>
<td>( P_{bo2} = -30.775 + 0.019X_{15} + 0.820X_{45} )</td>
<td>2.53</td>
<td>*</td>
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<td>(5) Branches:</td>
<td>( P_{br2} = 3.693 + 0.008X_{15} - 0.00024X_{24} )</td>
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<td>*</td>
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<td>Tree-shrub regeneration:</td>
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<tr>
<td>(all stands, kg/ha)</td>
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<td>(6) Total:</td>
<td>( P_r = -100.5 + 0.017X_{81} + 0.00006X_{60} )</td>
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<td>*</td>
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<td>Components</td>
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<td>R</td>
<td>n</td>
<td>Significance</td>
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<tr>
<td>Herbs (all stands, kg/ha)</td>
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<tr>
<td>(7) Total:</td>
<td>$P_{ht} = 1152.160 - 0.172X_{15} - 204.687X_{57}$</td>
<td>47.00</td>
<td>.986</td>
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<td>(8) Cryptogams:</td>
<td>$P_{hf} = -625.491 + 0.005X_{18} + 52.448X_{64}$</td>
<td>22.60</td>
<td>.992</td>
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<tr>
<td>(9) Phanerogams:</td>
<td>$P_{ha} = -368.722 - 0.268X_{82} + 59.351X_{47}$</td>
<td>35.20</td>
<td>.970</td>
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<tr>
<td>Bryophytes (all stands, kg/ha)</td>
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<tr>
<td>(10) Total:</td>
<td>$P_{bry} = -156.877 - 5.654X_{49} + 29.449X_{77}$</td>
<td>135.50</td>
<td>.985</td>
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</table>

*aStandard error of estimate at mean values of $X_1$ and $Y_1$.

*bMultiple R.

*cSignificance of regressions based on F-test. 1 = significant at P.10; 2 = P.05; 3 = P.01; 4 = P.005.

*dTree-tall shrub and sapling-low shrub strata combined.

*e$X_1$ = aspect; $X_2$ = elevation, m; $X_3$ = slope form coded such that 1 = convex slope, 2 = flat slope, and 3 = cove; $X_4$ = slope steepness, per cent; $X_5$ = tree-tall shrub density, tree/ha; $X_8$ = Fraser fir density in tree-tall shrub stratum, tree/ha;
TABLE XXVI (continued)

\[ X_9 = \text{yellow birch density in tree-tall shrub stratum, tree/ha}; \]
\[ X_{10} = \text{yellow birch basal area in the tree-tall shrub stratum, m}^2/\text{ha}; \]
\[ X_{12} = \text{red spruce basal area in tree-tall shrub stratum, m}^2/\text{ha}; \]
\[ X_{14} = \text{density of combined tree-tall shrub and sapling-low shrub strata, tree/ha}; \]
\[ X_{15} = \text{density of sapling-low shrub stratum, tree/ha}; \]
\[ X_{16} = \text{basal area of sapling-low shrub stratum, m}^2/\text{ha}; \]
\[ X_{18} = \text{crown volume of tree-tall shrub stratum, m}^3/\text{ha}; \]
\[ X_{19} = \text{crown coverage of tree-tall shrub stratum, m}^2/\text{ha}; \]
\[ X_{20} = \text{crown surface area of tree-tall shrub stratum, m}^2/\text{ha}; \]
\[ X_{22} = \text{mean crown length of tree-tall shrub stratum, m}; \]
\[ X_{25} = \text{branch biomass of tree-tall shrub stratum, kg/ha}; \]
\[ X_{30} = \text{bole biomass of sapling low shrub stratum, kg/ha}; \]
\[ X_{31} = \text{branch biomass of sapling-low shrub stratum, kg/ha}; \]
\[ X_{32} = \text{foliage biomass of sapling-low shrub stratum, kg/ha}; \]
\[ X_{40} = \text{bole and branch litter on forest floor, kg/ha}; \]
\[ X_{44} = \text{A horizon calcium, kg/ha}; \]
\[ X_{45} = \text{A horizon potassium, kg/ha}; \]
\[ X_{46} = \text{A horizon magnesium, kg/ha}; \]
\[ X_{59} = \text{A horizon weight of soil particles < 2 mm, kg/ha}; \]
\[ X_{60} = \text{A horizon weight of organic matter, kg/ha}; \]
\[ X_{61} = \text{A horizon weight of calcium matter, kg/ha}; \]
\[ X_{62} = \text{A horizon weight of potassium, kg/ha}; \]
\[ X_{64} = \text{A horizon weight of phosphorus, kg/ha}; \]
\[ X_{74} = \text{B1 horizon weight of potassium, kg/ha}; \]
\[ X_{75} = \text{B1 horizon weight of magnesium, kg/ha}; \]
\[ X_{76} = \text{B1 horizon weight of phosphorus, kg/ha}; \]
\[ X_{77} = \text{mean age of tree-tall shrub stratum, years}; \]
\[ X_{79} = \text{aspect X slope form}; \]
\[ X_{80} = \text{aspect X slope steepness}; \]
\[ X_{81} = \text{maximum elevation of mountain on which stand was located, m}; \]
\[ X_{82} = \text{biomass of sapling-low shrub stratum, kg/ha}. \]

\[ X_{47} = \text{A1 horizon P, kg/ha}; \]
\[ X_{49} = \text{A2 horizon Ca, kg/ha}; \]
\[ X_{24} = \text{tree-shrub bole biomass, kg/ha}; \]
\[ X_{57} = \text{net foliage production of combined tree-shrub strata (stems > 0.5 m tall), kg/ha}. \]
TABLE XXVII

NET ASSIMILATION RATES AND LEAF EFFICIENCY RATES
OF TREE AND SHRUB STRATA

<table>
<thead>
<tr>
<th>Strata</th>
<th>A (\text{NAR}_{v}^a)</th>
<th>B (\text{NAR}_{bo})</th>
<th>C (\text{NAR}_{br})</th>
<th>Ratio: B/C</th>
<th>D (\text{LE}_{v}^e)</th>
<th>E (\text{LE}_{bo})</th>
<th>F (\text{LE}_{br})</th>
<th>Ratio: E/F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree-tall shrub stratum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Mean</td>
<td>0.0352</td>
<td>0.0124</td>
<td>0.0020</td>
<td>6.20***C</td>
<td>0.4827</td>
<td>0.1703</td>
<td>0.0276</td>
<td>6.17***</td>
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<tr>
<td>Std</td>
<td>(0.0135)</td>
<td>(0.0038)</td>
<td>(0.0007)</td>
<td></td>
<td>(0.1798)</td>
<td>(0.0508)</td>
<td>(0.0097)</td>
<td></td>
</tr>
<tr>
<td>Sapling-low shrub stratum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Mean</td>
<td>-</td>
<td>0.0121</td>
<td>0.0088</td>
<td>1.38 ns</td>
<td>-</td>
<td>0.2334</td>
<td>0.2436</td>
<td>0.95 ns</td>
</tr>
<tr>
<td>Std</td>
<td>(0.0118)</td>
<td>(0.0129)</td>
<td></td>
<td></td>
<td></td>
<td>(0.2673)</td>
<td>(0.5015)</td>
<td></td>
</tr>
<tr>
<td>3. Ratio: (1)/(2)</td>
<td>1.02 ns</td>
<td>0.23 ns</td>
<td>-</td>
<td>-</td>
<td>0.22 ns</td>
<td>0.11 ns</td>
<td>-</td>
<td></td>
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<tr>
<td>Immature Yellow Birch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Tree-tall shrub stratum</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>4. Mean</td>
<td>0.0532</td>
<td>0.0283</td>
<td>0.0099</td>
<td>2.85****</td>
<td>1.1402</td>
<td>0.6153</td>
<td>0.2159</td>
<td>2.84****</td>
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</tbody>
</table>

Spruce-Fir

Immature Yellow Birch
<table>
<thead>
<tr>
<th>Strata</th>
<th>A ( \text{NAR}_{v} ) dm(^3)/m(^2)</th>
<th>B ( \text{NAR}_{bo} ) kg/m</th>
<th>C ( \text{NAR}_{br} ) kg/m</th>
<th>Ratio: B/C</th>
<th>D ( \text{LE}_{v} ) dm(^3)/kg</th>
<th>E ( \text{LE}_{bo} ) kg/kg</th>
<th>F ( \text{LE}_{br} ) kg/kg</th>
<th>Ratio: E/F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Std</td>
<td>(0.0107)</td>
<td>(0.0056)</td>
<td>(0.0023)</td>
<td></td>
<td>(0.3890)</td>
<td>(0.1901)</td>
<td>(0.0755)</td>
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<tr>
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<td></td>
<td></td>
</tr>
<tr>
<td>5. Mean</td>
<td>-</td>
<td>0.0136</td>
<td>0.0060</td>
<td>2.27&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-</td>
<td>0.3724</td>
<td>0.1628</td>
<td>2.29&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>Std</td>
<td>-</td>
<td>(0.0118)</td>
<td>(0.0055)</td>
<td></td>
<td>-</td>
<td>(0.3816)</td>
<td>(0.1753)</td>
<td></td>
</tr>
<tr>
<td>6. Ratio:</td>
<td></td>
<td>2.08*</td>
<td>1.65&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>1.65&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>1.33&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td>(4)/(5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mature Yellow Birch&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Tree-tall shrub stratum</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Mean</td>
<td>0.0195</td>
<td>0.0115</td>
<td>0.0041</td>
<td>2.80&lt;sup&gt;***&lt;/sup&gt;</td>
<td>0.4811</td>
<td>0.2857</td>
<td>0.1017</td>
<td>2.81&lt;sup&gt;***&lt;/sup&gt;</td>
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<tr>
<td>Std</td>
<td>(0.0069)</td>
<td>(0.0032)</td>
<td>(0.0013)</td>
<td></td>
<td>(0.1680)</td>
<td>(0.0801)</td>
<td>(0.0308)</td>
<td></td>
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<tr>
<td>Sapling-low shrub stratum</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>8. Mean</td>
<td>-</td>
<td>(0.0008)</td>
<td>(0.0024)</td>
<td></td>
<td>(0.0389)</td>
<td>(0.0767)</td>
<td>3.40&lt;sup&gt;**&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Std</td>
<td>-</td>
<td>(0.0008)</td>
<td>(0.0024)</td>
<td></td>
<td>(0.0389)</td>
<td>(0.0767)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Ratio:</td>
<td></td>
<td>0.40&lt;sup&gt;****&lt;/sup&gt;</td>
<td>0.49*</td>
<td>-</td>
<td>-</td>
<td>0.34&lt;sup&gt;****&lt;/sup&gt;</td>
<td>0.41*</td>
<td>-</td>
</tr>
<tr>
<td>(7)/(8)</td>
<td></td>
<td></td>
<td></td>
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</table>
TABLE XXVI (continued)

<table>
<thead>
<tr>
<th>Strata</th>
<th>A NAR\textsubscript{v} \textsuperscript{a}</th>
<th>B NAR\textsubscript{bo}</th>
<th>C NAR\textsubscript{br}</th>
<th>Ratio: B/C</th>
<th>D LE\textsubscript{v}</th>
<th>E LE\textsubscript{bo}</th>
<th>F LE\textsubscript{br}</th>
<th>Ratio: E/F</th>
</tr>
</thead>
<tbody>
<tr>
<td>10. Ratio: (4)/(7)</td>
<td>2.73**</td>
<td>2.46****</td>
<td>2.41****</td>
<td>-</td>
<td>2.37*</td>
<td>2.15***</td>
<td>2.12**</td>
<td>-</td>
</tr>
<tr>
<td>11. Ratio: (4)/(1)</td>
<td>1.51**</td>
<td>2.28****</td>
<td>4.95****</td>
<td>-</td>
<td>2.36**</td>
<td>3.61****</td>
<td>7.82****</td>
<td>-</td>
</tr>
</tbody>
</table>

\textsuperscript{a}NAR = production \div leaf area; LE = production \div foliage biomass; v = bole volume increment, bo = bole dry-matter production; br = branch dry-matter production.

\textsuperscript{b}Tree-tall shrub stratum, n = 30; sapling-low shrub stratum, n = 8.

\textsuperscript{c}ns, < P.10; *, > P.10; **, > P.05; ***, > P.01; *****, > P.001. Based on t-tests of differences between appropriate means of NAR\textsubscript{bo} and NAR\textsubscript{br}.

\textsuperscript{d}Tree-tall shrub stratum, n = 4; sapling-low shrub stratum, n = 2.

\textsuperscript{e}Tree-tall shrub stratum, n = 6; sapling-low shrub stratum, n = 3.
spruce, fir, and deciduous forests. Volume increments per unit foliage weight of 1.3 to 1.4 dm³/kg characterize some spruce and fir forests (Möller, 1947; Tadaki, 1966), and these exceed rates in spruce-fir stands found in the current study by a factor of over 2.5 times. In other stands of spruce and fir where leaf efficiency of stemwood dry weight production was calculated (Burger, 1951, 1953; Satoo, 1966; Baskerville, 1965), rates were generally 0.20 to 0.50 kilograms of stemwood per kilogram of foliage; these rates were approximately 1.1 to 2.9 times production rates in Balsam Mountain spruce-fir stands. Total ecosystem leaf efficiency of the coniferous stands in the current study were also lower than other comparable forests. Total dry weight increment per unit foliage weight varied from 0.54 to 0.67 in Picea abies stands (Satoo, 1966), 0.54 to 0.64 in balsam fir stands (Baskerville, 1965) and 0.38 to 0.69 in Fraser fir and spruce-fir forests in the Great Smoky Mountains (Whittaker, 1966). The lowest of these rates was more than twice the mean rate in the Balsam Mountains. Lower rates of efficiency in stands of the current study reflect large foliage biomass rather than lower total production per unit stand area. Balsam fir stands studied by Baskerville (1965) where both foliage biomass and leaf efficiency were higher were exceptions to this trend. Only leaf efficiency of stemwood production in black spruce
stands studied by Weetman and Harland (1964) were similar to those of the present study.

Average bole volume increment was $1.14 \text{ dm}^3$ per kilogram of foliage in immature yellow birch and of $0.48 \text{ dm}^3$ per kilogram of foliage in mature stands (Table XXVII, page 204); these rates were low compared with rates of 1.8 to 4.4 in beech stands (Möller, 1947; Burger, 1950) and 3.8 to 6.6 in birch stands (Tadaki, 1966). Net assimilation rates of stemwood production in other birch stands (Satoo, 1970) are two to three times greater than in immature stands in the Balsam Mountains. Compared with immature stands, lower production rates are expected in mature stands as observed in the present study. Burger (1950) showed that increasing age was one of the principal factors in differences between leaf efficiencies among trees of the same species. Leaf efficiency (calculated from data in Tables IX, page 135, and XXII, page 181) of total production of trees and shrubs averaged 1.6 and 1.9 kilograms per kilogram of foliage in immature and mature yellow birch stands, respectively. These values were lower than rates reported in other birch and beech stands (Satoo, 1970; Whittaker, 1966; Ovington and Madgwick, 1959) which ranged from approximately 2.5 to 3.0 kilograms per kilogram of foliage.

Lower leaf efficiencies (or NAR) were also indicated in stands dominated by spruce relative to those composed
principally of Fraser fir. Lower production efficiencies of spruce, especially larger trees, is contrary to the relationship between white spruce and balsam fir (Baskerville, 1965; Clark, 1961). Maximum leaf efficiency of *Picea abies* also exceeded maximum leaf efficiency of *Abies alba* (Burger, 1951; 1953). At least part of the difference may be attributed to the age of stands since it has been shown that efficiency of production decreases with increasing age (Burger, 1951, 1952; Clark, 1961). The average age of stands dominated by red spruce was greater than Fraser fir stands and spruce stands frequently had trees whose maximum ages exceeded maxima of fir stands by 20 or more years (Table I, page 99). Age of coniferous stands was also inversely and significantly correlated with leaf efficiency and net assimilation rates which supports this conclusion.

Greater production of coniferous stands in the present and other studies relative to deciduous stands resulted from much larger leaf biomass and/or surface areas.

Distinct differences in production efficiency also existed between ecosystems and between components within systems. Mean assimilation rates and leaf efficiencies in Table XXVII, page 204, showed that deciduous stands were more efficient producers by factors of approximately 1.5 to 5.0 per unit leaf surface and by factors of approximately 2.4 to 7.8 per unit foliage biomass. These trends were
similar to those between many other spruce-fir and deciduous stands (Whittaker, 1966; Burger, 1950, 1951; Möller, 1947; Tadaki, 1966). Bole production per unit foliage was significantly higher and exceeded branch production per unit foliage by factors up to six times. Differences between rates were less in immature yellow birch stands due to their comparatively large branch biomass and production. Similar differences between leaf efficiency of bole and branch production also characterized balsam fir stands (Baskerville, 1965) where rates of bole production were greater than branch production by factors of 2.3 to 2.9. Net assimilation rates of sapling-low shrub and tree-tall shrub strata were similar in spruce-fir stands apparently reflecting the strong coniferous element in the understory. Efficiency of bole production was higher than branch production rates but the difference was not significant in spruce-fir stands. In deciduous stands NAR of sapling-low shrub strata were lower than overstory rates and bole production efficiency exceeded branch production.

Variations in production patterns among forest types result from differences in the relation of leaf efficiency to foliage biomass and variations in the ratio of photosynthetic to non-photosynthetic tissues which accompany changes in stand structure. In the current study, LE was not significantly correlated with leaf biomass in immature
and mature yellow birch stands (Table XXV, page 194), although the relationship is by no means constant in all types of forests (Tadaki, 1966; Baskerville, 1965). In yellow birch ecosystems in the Balsam Mountains, LE was constant at different levels of foliage biomass and dry-matter production increased directly as foliage biomass increased.

In coniferous stands foliage biomass increased as basal area and stand biomass increased, but LE (and NAR) decreased in a slightly curvilinear relationship with increased foliage biomass (Table XXVIII). This caused rapidly decreasing leaf efficiencies to counter increases of leaf biomass and consequently increased production did not accompany increased stand biomass, basal area, or foliage biomass.

Production did increase, however, with increased stand density. Stand basal area, stand biomass, and foliage biomass were constant over the range of stand densities sampled, but the ratio of non-photosynthetic to photosynthetic tissue decreased as stand density increased and as average tree size decreased. Although LE (or NAR) did not change with increasing stand density, leaf efficiency of bole and branch production increased as tree size decreased. Correlation coefficients relating mean tree size and leaf efficiency were significant at 10 per cent (bole efficiencies) and 5 per cent (branch efficiencies) levels. Greater
### TABLE XXVIII

**REGRESSION EQUATIONS FOR ESTIMATING NET ASSIMILATION RATES AND LEAF EFFICIENCY IN SPRUCE-FIR STANDS**

<table>
<thead>
<tr>
<th>Dependent Variable&lt;sup&gt;a&lt;/sup&gt;</th>
<th>A&lt;sub&gt;i&lt;/sub&gt;</th>
<th>b&lt;sub&gt;i&lt;/sub&gt;(X&lt;sub&gt;i&lt;/sub&gt;)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>S.E.E.&lt;sup&gt;c&lt;/sup&gt;</th>
<th>R&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Significance&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Increased with (X&lt;sub&gt;i&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt;)&lt;sup&gt;e&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>NAR&lt;sub&gt;v&lt;/sub&gt;</td>
<td>585.523</td>
<td>-11.907(LAI)</td>
<td>86.39</td>
<td>0.347</td>
<td>4</td>
<td>0.025</td>
</tr>
<tr>
<td>NAR&lt;sub&gt;bo&lt;/sub&gt;</td>
<td>216.416</td>
<td>-4.311(LAI)</td>
<td>31.06</td>
<td>0.350</td>
<td>4</td>
<td>0.068</td>
</tr>
<tr>
<td>NAR&lt;sub&gt;br&lt;/sub&gt;</td>
<td>37.750</td>
<td>-0.825(LAI)</td>
<td>5.770</td>
<td>0.364</td>
<td>4</td>
<td>0.088</td>
</tr>
<tr>
<td>LE&lt;sub&gt;v&lt;/sub&gt;</td>
<td>0.787</td>
<td>-0.0002(W&lt;sub&gt;F&lt;/sub&gt;)</td>
<td>0.199</td>
<td>0.299</td>
<td>4</td>
<td>0.018</td>
</tr>
<tr>
<td>LE&lt;sub&gt;bo&lt;/sub&gt;</td>
<td>0.296</td>
<td>-0.000001(W&lt;sub&gt;F&lt;/sub&gt;)</td>
<td>0.043</td>
<td>0.317</td>
<td>4</td>
<td>0.062</td>
</tr>
<tr>
<td>LE&lt;sub&gt;br&lt;/sub&gt;</td>
<td>0.052</td>
<td>-0.0000016(W&lt;sub&gt;F&lt;/sub&gt;)</td>
<td>0.008</td>
<td>0.344</td>
<td>4</td>
<td>0.080</td>
</tr>
</tbody>
</table>

<sup>a</sup>NAR<sub>v</sub> = volume increment (dm<sup>3</sup>/ha/yr) ÷ leaf area index.
NAR<sub>v</sub> = bole dry-weight increment (kg/ha/yr) ÷ LAI.
NAR<sub>v</sub> = branch dry-weight increment (kg/ha/yr) ÷ LAI.
LE<sub>v</sub> = volume increment (dm<sup>3</sup>/ha/yr) ÷ foliage biomass (kg/ha).
LE<sub>bo</sub> = bole dry-matter increment (kg/ha/yr) ÷ foliage biomass (kg/ha).
LE<sub>br</sub> = branch dry-matter increment (kg/ha/yr) ÷ foliage biomass (kg/ha).

<sup>b</sup>LA<sub>i</sub> = leaf area index.
W<sub>F</sub> = foliage biomass (kg/ha)

<sup>c</sup>Standard error of estimate.

<sup>d</sup>1 denotes that regression equations are significant at P = 0.005.

<sup>e</sup>Increase in R<sup>2</sup> by inclusion of (X<sub>i</sub><sup>2</sup>) in equations such that
\[ \hat{y} = a + b_i X_i + b_i X_i^2. \]
efficiency of smaller trees was also found in balsam fir stands (Baskerville, 1965) but efficiency increased with large tree size in both fir and beech stands studied by Burger (1950, 1951). In those stands tree size was apparently confounded with canopy position and the larger dominant and codominant were definitely more efficient than smaller overtopped trees. In the present study, stands were multi-storied but all trees were smaller in denser stands and many of the smaller trees occupied codominant canopy positions and could not be directly compared with small trees in Burger's (1950, 1951) studies.

In the present coniferous stands, as stand density increased and tree size decreased, efficiency increased which coupled with more or less constant foliage biomass resulted in greater net production in denser stands. Principal differences between these and stands studied by Baskerville (1965) and Möller (1954) were the relations between stand density, basal area, biomass, and leaf biomass, and the relation of leaf efficiency and leaf biomass.

An additional difference between yellow birch and coniferous stands was the relation of NAR and LE to net production. In yellow birch stands, net production was independent of NAR and LE but in coniferous stands, bole volume increment and bole and branch dry-matter production were directly and significantly correlated with production
efficiency rates (Table XXV, page 194). When LE (or NAR) is constant with increases of foliage biomass (or surface area), net production will be proportional to foliage biomass or surface area and independent of LE (NAR) such as observed in immature yellow birch stands of this study and in other studies (Satoo, 1966). When LE (NAR) decreases with increased foliage surface area, net production will not be in simple proportion to foliage quantity but will increase as leaf efficiency (or NAR) increases.

Many factors affect leaf efficiency including relative proportion of sun to shade leaves (Clark, 1961; Baskerville, 1965; Burger, 1951), stand structure (Baskerville, 1965) which may alter the ratio of sun to shade foliage or may change the ratio of photosynthetic to non-photosynthetic tissue, and site conditions (Burger, 1950). In the present study leaf efficiency or NAR of coniferous were not related to topographic or soil factors sampled. (Table XXV, page 194).

In immature yellow birch stands, NAR of total production of trees and shrubs increased with increasing slope steepness but was not related to other topographic or soil factors. In mature yellow birch stands, production efficiency was not related to topographic factors and insufficient stands were sampled to test for soil effects.

In the current study, principal factors affecting
production efficiency (NAR and LE) were species composition of stands and stand structure. In spruce-fir stands the ratio of non-photosynthetic to photosynthetic tissue did not increase with increasing stand basal area or biomass which suggests that the decreasing efficiency of larger crowns characteristic of stands of higher basal area was due to increased proportion of sun foliage relative to shade foliage.

Comparing the relationship of LE and NAR to bole and branch net production (Table XXIV, page 190) indicated that NAR was more closely related to production than LE. Results of this and other studies (Burger, 1953; Monk, et al., 1970; Whittaker, 1962) showed that leaf surface area:weight ratios varied widely among species and with leaf age and position in the crown within species. Since it is leaf surface more than leaf weight which determines the efficiency of light absorption, net assimilation rates which are based on leaf area would therefore reflect differences due to species composition of stands better than leaf weight and should be the more sensitive of the two.

Net production and biomass of tree-shrub regeneration strata were directly and significantly correlated (Table XII, page 149), so that net production varied in relation to site and topographic factors much the same as biomass. In spruce-fir stands net production increased
toward higher elevation northeast slopes where soil development of upper soil horizons was greatest. These trends generally reflect trends in Fraser fir seedling development. The correlation with nutrients of the A horizon may reflect the cross-correlation of nutrients and soil weight. Net production decreased where overstory stand development was greatest; either low light intensities or root competition or both could have been limiting factors.

In immature yellow birch stands, net production increased with increasing elevation especially on steeper slopes and in coves. As in spruce-fir stands, topographic and soil factors were confounded and specific effects were difficult to separate. The lack of relation between net production and overstory stand structure suggests less intensive light competition and perhaps root competition beneath deciduous stands where foliage and stand biomass were much lower. The relation to elevation and slope steepness was not due to increased coniferous components in stands. Rather the trend was due to relatively high production of *Ribes glandulosum* in a single stand on block valley fill at high elevation and with northeast aspect. This species also was common in lower elevation mature yellow birch stands which were in coves with block fill; consequently, the relationship apparently reflected the presence of suitable substratum rather than microclimatological changes associated with elevation.
Production estimates of herbs and bryophytes were based on total above-ground clipping weights or on constant ratios of net production to biomass, and it was not possible to determine whether biomass and net production varied differentially with respect to environmental and stand structural factors. Considering the high net primary production:biomass ratios which seem to characterize bryophytes (Tamm, 1953) and herbaceous species, production and biomass are more likely to show parallel trends in relation to environmental and site factors than production of plants whose biomass has accumulated over long periods during which production efficiency and competition may have undergone major alterations.

The large outlay of both labor and funds necessary to estimate net production of forests by the harvest method makes desirable reliable production indices which are relatively easy and inexpensive to obtain. Litterfall which makes up an appreciable proportion of annual net production in forests may meet these criteria (Rodin and Basilevic, 1967). In spruce-fir and immature yellow birch stands, leaf litterfall was 72.1 and 63.2 per cent of annual above-ground net primary production of combined tree-tall shrub and sapling-low shrub strata. In the same stands, foliage litterfall alone was 44.8 and 53.4 per cent of production, respectively. Differences between these percentages were
not significant and the proportions in relation to net production were somewhat higher than in other coniferous and deciduous forests (Rodin and Basilevic, 1967). In other forests the proportion of total litterfall to net production was comparable to these values; the unreliability of estimating bole and large branch litterfall with small samples and during single year intervals may have accounted for part of the differences.

In mature yellow birch stands, leaf litterfall (including small twigs and bark, foliage, reproductive components) and foliage litterfall were 101.5 and 71.6 per cent of net production (calculated from data in Tables XV, page 160 and XXII, page 181); these proportions were significantly higher (at 1 per cent and 5 per cent levels, respectively) than in immature yellow birch stands and indicate the fundamental difference between mature and immature ecosystems. As forest ecosystems mature, the ratio of gross production to respiration loss may approach 1.0 (Odum, 1969); consequently, annual increment of perennial components such as boles and branches decreases, forest biomass becomes asymptotic (Ovington and Madgwick, 1959; Ovington, 1959) and annual litterfall may nearly equal net production. The results from mature stands including the relatively low variability of biomass of trees in the present study suggest that annual litterfall
losses and annual dry-matter increments are nearly in balance and that stands are approaching maximum biomass in relation to existing species composition and site parameters.

In spruce-fir stands, net production of trees, saplings, and shrubs was directly and significantly correlated with litterfall of reproductive components, needles, and total leaf litterfall (Table XXIX); the inverse relation between litterfall of deciduous leaves and bole net production shows the effect of production of deciduous trees within coniferous stands. Litterfall of boles and large branches was not generally correlated with net production in either coniferous or immature yellow birch. Total, bole, and branch net production were related to total leaf litterfall. Litterfall of particular components was only related to production of seeds and fruits. Regression equations in Table XXX show that in coniferous and immature yellow birch stands total production can be estimated from total leaf litterfall (equations 1 and 5) and in coniferous stands from foliage litterfall (equation 2). Multiple regression equations based on various combinations of annual litterfall components increased the precision of estimates and accounted for 86.6 per cent of variability in spruce-fir stands (equation 3) and 99.4 per cent in immature yellow birch stands (equation 6). Bole and branch production may be estimated from total leaf litterfall in immature yellow
### TABLE XXIX

ASSOCIATION OF NET PRIMARY PRODUCTION OF COMBINED TREE AND SHRUB STRATA WITH ANNUAL LITTERFALL (SIMPLE r)

<table>
<thead>
<tr>
<th>Litterfall Component</th>
<th>Annual Net Production</th>
<th>Reproductive Components</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total Boles Branches Foliage</td>
<td></td>
</tr>
<tr>
<td><strong>Spruce-Fir (n=14)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bole and branch Reproductive components</td>
<td>.844</td>
<td>.762</td>
</tr>
<tr>
<td>Deciduous leaves</td>
<td></td>
<td>-.604</td>
</tr>
<tr>
<td>Needles</td>
<td>.854</td>
<td>.937</td>
</tr>
<tr>
<td>Small twigs and bark</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>.763</td>
<td>.942</td>
</tr>
</tbody>
</table>

**Immature Yellow Birch (n=4)**

| Bole and branch Reproductive components | .965 |
| Deciduous leaves | 1.000 |
| Needles | -.959 |
| Small twigs and bark | .918 |
| Total | .975 | .986 | .965 |

\(^a\) r = .532 at P.05; r = .661 at P.01.

\(^b\) r = .950 at P.05; r = .990 at P.01.
## TABLE XXX

**REGRESSION EQUATIONS FOR ESTIMATING TREE-SHRUB NET PRODUCTION FROM LITTERFALL PARAMETERS**

<table>
<thead>
<tr>
<th>Regression Equations</th>
<th>S.E.E.</th>
<th>R</th>
<th>Significance$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spruce-Fir Stands</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1) $P_T^b$ = 3864.963 + 0.674 $X_{64}$</td>
<td>587.5</td>
<td>.931</td>
<td>4</td>
</tr>
<tr>
<td>(2) $P_T$ = 3143.855 + 1.302 $X_{78}$</td>
<td>899.5</td>
<td>.763</td>
<td>4</td>
</tr>
<tr>
<td>(3) $P_T$ = 4283.289 - 0.004 $X_{50}$ + 1.602 $X_{60}$ + 1.428 $X_{62}$ - 0.819 $X_{78}$</td>
<td>587.5</td>
<td>.931</td>
<td>4</td>
</tr>
<tr>
<td>(4) $P_{bo}^c$ = 3008.024 - 1.273 $X_{61}$</td>
<td>497.6</td>
<td>.604</td>
<td>2</td>
</tr>
<tr>
<td><strong>Immature Yellow Birch Stands</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(5) $P_T$ = -12241.900 + 4.674 $X_{64}$</td>
<td>447.0</td>
<td>.975</td>
<td>4</td>
</tr>
<tr>
<td>(6) $P_T$ = -9418.611 - 6.798$X_{63}$ + 7.431$X_{64}$</td>
<td>227.7</td>
<td>.997</td>
<td>4</td>
</tr>
<tr>
<td>(7) $P_{bo}$ = -8535.133 + 2.699 $X_{64}$</td>
<td>206.0</td>
<td>.986</td>
<td>4</td>
</tr>
<tr>
<td>(8) $P_{br}$ = -2893.604 + 0.918 $X_{64}$</td>
<td>110.9</td>
<td>.965</td>
<td>4</td>
</tr>
</tbody>
</table>

$^a$Significance of regression equations based on F-tests; $2 \geq P.05$, $4 \geq P.01$.

$^b$Dependent variables (kg/ha/yr): $P_T$ = total above-ground net production of combined tree-tall shrub and sapling-low shrub strata (kg/ha/yr); $P_{bo}$ = net production of combined tree-shrub strata; $P_{br}$ = net branch production of combined tree-shrub strata.
TABLE XXX (continued)

\(^c\)Independent variables (kg/ha/yr): \(X_{50}\) = bole and large branch litterfall; \(X_{60}\) = reproductive component litterfall; \(X_{61}\) = deciduous leaf litterfall; \(X_{62}\) = needle litterfall; \(X_{63}\) = small twig and bark litterfall; \(X_{64}\) = total leaf litterfall; \(X_{78}\) = foliage litterfall (deciduous leaves and needles).
birch stands (equations 7 and 8); in spruce-fir stands only equations for estimating bole production were significant at or above P.10 (equation 4).

**Nutrient Concentrations of Plants**

Comparison of nutrient analyses of trees and shrubs (Tables XXXI through XXXVI) showed that concentrations were highest in foliage, intermediate in branches, and lowest in boles. In both boles and branches, Ca > K > Mg > P; in foliage, however, K was present in highest concentrations followed by Ca, Mg, and P in decreasing order. These trends among components and nutrients agree with results from other studies (Likens and Bormann, 1970; Young and Guinn, 1966). Appreciable differences in nutrient concentrations between components of different species were also apparent in the current study. Among deciduous species, boles (wood and bark combined) of fire cherry, *Rhododendron* spp., and *Amelanchier arborea* contained relatively low concentrations of all nutrients. High concentrations of potassium characterized boles of *Aesculus octandra* but these may reflect the small-sized trees harvested. Separate analysis of bole bark and wood of yellow birch, red spruce, and Fraser fir showed nutrient concentrations in bark exceeded concentrations in wood often by factors of 3 to 10. Nutrient concentrations in wood and bark of boles from fir and spruce were generally in the same range but yellow birch bole bark was
### TABLE XXXI

NUTRIENT CONCENTRATIONS IN BOLES OF TREES, SAPLINGS, AND SHRUBS HARVESTED DURING 1969

<table>
<thead>
<tr>
<th>Species</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies fraseri &lt; 2.54 cm</td>
<td>3767 ± 857</td>
<td>2980 ± 260</td>
<td>3724 ± 260</td>
<td>509 ± 164</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td>4641 ± 871(4)</td>
<td>1702 ± 585(4)</td>
<td>728 ± 40(4)</td>
<td>296 ± 89(4)</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>6915 ± 2326(1)</td>
<td>909 ± 370(1)</td>
<td>262 ± 10(27)</td>
<td></td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>3709 ± 211(27)</td>
<td>1662 ± 55(27)</td>
<td>625 ± 48(27)</td>
<td></td>
</tr>
<tr>
<td>Aesculus octandra</td>
<td>3398 ± 149(11)</td>
<td>3322 ± 297(11)</td>
<td>715 ± 54(11)</td>
<td></td>
</tr>
<tr>
<td>Amelanchier arborea</td>
<td>1883 ± 279(13)</td>
<td>1097 ± 137(13)</td>
<td>235 ± 58(13)</td>
<td></td>
</tr>
<tr>
<td>Betula lutea</td>
<td>2512 ± 170(4)</td>
<td>2295 ± 145(4)</td>
<td>1158 ± 50(4)</td>
<td></td>
</tr>
<tr>
<td>Cornus alternifolia</td>
<td>3729 ± 1142(2)</td>
<td>2656 ± 266(2)</td>
<td>876 ± 113(2)</td>
<td></td>
</tr>
<tr>
<td>Crataegus sp.</td>
<td>5036 ± 3270(1)</td>
<td>645 ± 537(1)</td>
<td>376 ± 98(17)</td>
<td></td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>3762 ± 452(17)</td>
<td>2959 ± 1022(17)</td>
<td>820 ± 320(17)</td>
<td></td>
</tr>
<tr>
<td>Picea rubens</td>
<td>3610 ± 324(4)</td>
<td>3025 ± 394(4)</td>
<td>1820 ± 282(4)</td>
<td></td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>1795 ± 182(12)</td>
<td>1361 ± 80(12)</td>
<td>539 ± 24(12)</td>
<td></td>
</tr>
</tbody>
</table>

(n) = number of samples

S.E. = standard error
TABLE XXXI (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Ca ppm ± S.E. (n)</th>
<th>K ppm ± S.E. (n)</th>
<th>Mg ppm ± S.E. (n)</th>
<th>P ppm ± S.E. (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus rubra</td>
<td>4590 ± 304 (12)</td>
<td>2343 ± 158 (12)</td>
<td>742 ± 106 (12)</td>
<td>222 ± 26 (12)</td>
</tr>
<tr>
<td>Rhododendron cataractense</td>
<td>522 ± 164 (1)</td>
<td>997 ± 123 (14)</td>
<td>317 ± 56 (14)</td>
<td>194 ± 14 (14)</td>
</tr>
<tr>
<td>Rhododendron maximum</td>
<td>976 ± 9 (3)</td>
<td>1811 ± 144 (3)</td>
<td>439 ± 99 (3)</td>
<td>212 ± 27 (3)</td>
</tr>
<tr>
<td>Ribes rotundifoliuma</td>
<td>3481 ± 322 (1)</td>
<td>2700 ± 733 (14)</td>
<td>887 ± 160 (14)</td>
<td>685 ± 122 (14)</td>
</tr>
<tr>
<td>Rubus allegheniensis</td>
<td>890 (1)</td>
<td>3133 (1)</td>
<td>2061 (1)</td>
<td>1072 (1)</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>2673 ± 329 (2)</td>
<td>5312 ± 515 (2)</td>
<td>1904 ± 437 (2)</td>
<td>988 ± 223 (2)</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>2832 ± 333 (24)</td>
<td>1885 ± 103 (24)</td>
<td>1432 ± 256 (24)</td>
<td>314 ± 35 (24)</td>
</tr>
<tr>
<td>Vaccinium constablaei</td>
<td>2254 ± 891 (2)</td>
<td>1620 ± 498 (7)</td>
<td>314 ± 113 (7)</td>
<td>316 ± 49 (7)</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>5466 ± 423 (2)</td>
<td>3683 ± 809 (2)</td>
<td>1146 ± 411 (2)</td>
<td>471 ± 88 (2)</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>3098 ± 250 (8)</td>
<td>1310 ± 132 (8)</td>
<td>682 ± 50 (8)</td>
<td>257 ± 18 (8)</td>
</tr>
</tbody>
</table>

aN=2.
### TABLE XXXII

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Abies fraseri</th>
<th>Picea rubens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>6352 657 5527 768 5188 940 5211 957 4340 1042</td>
<td>5225 851 5990 736 5890 802 5077 921</td>
</tr>
<tr>
<td>S.E.</td>
<td>558 73 339 77 462 119 663 135 468 418</td>
<td>103 35 925 58 383 112 533</td>
</tr>
<tr>
<td>n</td>
<td>9 9 9 9 8 7 4 4 3 3</td>
<td>4 9 5 7 8 2 8 2</td>
</tr>
</tbody>
</table>

| Potassium  |               |              |
| Mean       | 1702 432 1722 631 2093 886 2336 990 3460 774 | 1480 196 1996 245 2062 202 2904 339 |
| S.E.       | 188 46 98 66 178 57 415 99 762 143 | 100 11 222 61 321 63 301 |
| n          | 9 9 9 9 9 7 4 4 3 3 | 5 9 4 7 9 2 8 1 |

| Magnesium  |               |              |
| Mean       | 716 279 671 267 723 284 715 245 670 276 | 539 156 492 130 628 117 |
| S.E.       | 59 42 74 23 91 35 79 36 131 71 | 64 31 58 20 48 40 98 25 94 48 |
| n          | 9 9 9 9 9 7 4 4 3 3 | 9 9 9 8 8 7 4 4 3 3 |

| Phosphorus |               |              |
| Mean       | 539 156 492 130 628 117 599 106 776 152 | 539 156 492 130 628 117 |
| S.E.       | 64 31 58 20 48 40 98 25 94 48 | 64 31 58 20 48 40 98 25 94 48 |
| n          | 9 9 9 8 8 7 4 4 3 3 | 9 9 9 8 8 7 4 4 3 3 |

### NUTRIENT CONCENTRATIONS (ppm) IN STEM BARK AND STEM WOOD OF ABIES FRASERI, PICEA RUBENS, AND BETULA LUTEA

#### TABLE XXXII

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>1.25</th>
<th>5.0</th>
<th>10.0</th>
<th>15.0</th>
<th>20.0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bark Wood</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies fraseri</td>
<td>6352 657 5527 768 5188 940 5211 957 4340 1042</td>
<td>5225 851 5990 736 5890 802 5077 921</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.E.</td>
<td>558 73 339 77 462 119 663 135 468 418</td>
<td>103 35 925 58 383 112 533</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>9 9 9 9 8 7 4 4 3 3</td>
<td>4 9 5 7 8 2 8 2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Picea rubens</td>
<td>1702 432 1722 631 2093 886 2336 990 3460 774</td>
<td>1480 196 1996 245 2062 202 2904 339</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.E.</td>
<td>188 46 98 66 178 57 415 99 762 143</td>
<td>100 11 222 61 321 63 301</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>9 9 9 9 9 7 4 4 3 3</td>
<td>5 9 4 7 9 2 8 1</td>
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<td></td>
</tr>
</tbody>
</table>

#### NUTRIENT CONCENTRATIONS (ppm) IN STEM BARK AND STEM WOOD OF ABIES FRASERI, PICEA RUBENS, AND BETULA LUTEA
TABLE XXXII (continued)

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>1.25</th>
<th>5.0</th>
<th>10.0</th>
<th>15.0</th>
<th>20.0</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bark Wood</td>
<td>Bark Wood</td>
<td>Bark Wood</td>
<td>Bark Wood</td>
<td>Bark Wood</td>
</tr>
<tr>
<td>Magnesium</td>
<td>Mean</td>
<td>641</td>
<td>234</td>
<td>790</td>
<td>286</td>
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<tr>
<td></td>
<td>S.E.</td>
<td>81</td>
<td>36</td>
<td>59</td>
<td>93</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>5</td>
<td>8</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>Mean</td>
<td>425</td>
<td>100</td>
<td>534</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>S.E.</td>
<td>35</td>
<td>13</td>
<td>58</td>
<td>10</td>
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<td>n</td>
<td>11</td>
<td>12</td>
<td>10</td>
<td>10</td>
</tr>
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</table>

**Betula lutea**

<table>
<thead>
<tr>
<th>Calcium</th>
<th>Mean</th>
<th>7634</th>
<th>458</th>
<th>7655</th>
<th>488</th>
<th>12366</th>
<th>538</th>
<th>12957</th>
<th>3081</th>
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</thead>
<tbody>
<tr>
<td>S.E.</td>
<td>437</td>
<td>36</td>
<td>773</td>
<td>42</td>
<td>1841</td>
<td>24</td>
<td>762</td>
<td>288</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>5</td>
<td>7</td>
<td>6</td>
<td>7</td>
<td>4</td>
<td>7</td>
<td>3</td>
<td>3</td>
<td>-</td>
<td>-</td>
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</table>

<table>
<thead>
<tr>
<th>Potassium</th>
<th>Mean</th>
<th>1077</th>
<th>380</th>
<th>901</th>
<th>367</th>
<th>1311</th>
<th>440</th>
<th>1268</th>
<th>473</th>
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<th>-</th>
</tr>
</thead>
<tbody>
<tr>
<td>S.E.</td>
<td>65</td>
<td>33</td>
<td>89</td>
<td>41</td>
<td>96</td>
<td>55</td>
<td>101</td>
<td>169</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>5</td>
<td>7</td>
<td>6</td>
<td>7</td>
<td>4</td>
<td>7</td>
<td>3</td>
<td>2</td>
<td>-</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Magnesium</th>
<th>Mean</th>
<th>380</th>
<th>136</th>
<th>386</th>
<th>163</th>
<th>588</th>
<th>237</th>
<th>777</th>
<th>315</th>
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<tbody>
<tr>
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<td>45</td>
<td>21</td>
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<td>24</td>
<td>108</td>
<td>36</td>
<td>240</td>
<td>58</td>
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<td>n</td>
<td>6</td>
<td>8</td>
<td>7</td>
<td>8</td>
<td>4</td>
<td>7</td>
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</table>

<table>
<thead>
<tr>
<th>Phosphorus</th>
<th>Mean</th>
<th>345</th>
<th>100</th>
<th>382</th>
<th>111</th>
<th>440</th>
<th>113</th>
<th>413</th>
<th>150</th>
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<tbody>
<tr>
<td>S.E.</td>
<td>30</td>
<td>10</td>
<td>32</td>
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<td>63</td>
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<td>95</td>
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</tr>
<tr>
<td>n</td>
<td>5</td>
<td>7</td>
<td>6</td>
<td>7</td>
<td>4</td>
<td>7</td>
<td>3</td>
<td>3</td>
<td>-</td>
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<td></td>
</tr>
</tbody>
</table>

*H. R. DeSelm, unpublished data. Based on analyses of trees harvested from Blue Ridge Parkway right-of-way in the study area during 1959.*
### TABLE XXXIII

NUTRIENT CONCENTRATIONS IN TWIGS (WOOD PLUS BARK) AND LEAVES OF TREES, SAPLINGS, AND SHRUBS HARVESTED DURING 1969

<table>
<thead>
<tr>
<th>Species</th>
<th>Ca ppm ± S.E. (n)</th>
<th>K ppm ± S.E. (n)</th>
<th>Mg ppm ± S.E. (n)</th>
<th>P ppm ± S.E. (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies fraseri &lt; 2.54 cm dbh</td>
<td>4114 ± 591 (3)</td>
<td>3964 ± 308 (3)</td>
<td>1937 ± 231 (3)</td>
<td>728 ± 104 (3)</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td>9387 ± 899 (4)</td>
<td>1673 ± 2015 (4)</td>
<td>2587 ± 751 (4)</td>
<td>670 ± 179 (4)</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>12195 (1)</td>
<td>3599 (1)</td>
<td>1539 (1)</td>
<td>530 (1)</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>8423 ± 2690 (13)</td>
<td>3420 ± 441 (13)</td>
<td>1759 ± 166 (13)</td>
<td>613 ± 67 (13)</td>
</tr>
<tr>
<td>Aesculus octandra</td>
<td>6153 ± 335 (6)</td>
<td>5928 ± 267 (6)</td>
<td>1282 ± 118 (6)</td>
<td>1020 ± 47 (6)</td>
</tr>
<tr>
<td>Amelanchier arborea</td>
<td>5234 ± 799 (11)</td>
<td>2654 ± 207 (11)</td>
<td>1683 ± 338 (11)</td>
<td>458 ± 96 (11)</td>
</tr>
<tr>
<td>Betula lutea &lt; 2.54 cm dbh</td>
<td>7421 ± 1980 (2)</td>
<td>3213 ± 1331 (2)</td>
<td>2415 ± 660 (2)</td>
<td>828 ± 288 (2)</td>
</tr>
<tr>
<td>Cornus alternifolia</td>
<td>6178 ± 1540 (2)</td>
<td>4662 ± 858 (2)</td>
<td>1876 ± 276 (2)</td>
<td>1062 ± 142 (2)</td>
</tr>
<tr>
<td>Crataegus sp.</td>
<td>9900 (1)</td>
<td>3250 (1)</td>
<td>1850 (1)</td>
<td>840 (1)</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>6776 ± 380 (15)</td>
<td>2804 ± 368 (15)</td>
<td>1604 ± 128 (15)</td>
<td>794 ± 106 (15)</td>
</tr>
<tr>
<td>Picea rubens</td>
<td>3754 ± 164 (5)</td>
<td>4043 ± 354 (5)</td>
<td>2878 ± 396 (5)</td>
<td>754 ± 131 (5)</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>3707 ± 154 (8)</td>
<td>1684 ± 55 (8)</td>
<td>1139 ± 138 (8)</td>
<td>406 ± 39 (8)</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>6876 ± 644 (6)</td>
<td>3607 ± 191 (6)</td>
<td>1608 ± 115 (6)</td>
<td>708 ± 114 (6)</td>
</tr>
<tr>
<td>Rhododendron catawbiense, current</td>
<td>11872 ± 4138 (7)</td>
<td>9142 ± 642 (7)</td>
<td>3758 ± 425 (7)</td>
<td>1494 ± 122 (7)</td>
</tr>
<tr>
<td>Rhododendron catawbiense, old</td>
<td>2048 ± 367 (8)</td>
<td>1754 ± 137 (8)</td>
<td>1167 ± 143 (8)</td>
<td>339 ± 35 (8)</td>
</tr>
<tr>
<td>Rhododendron maximum</td>
<td>6246 ± 1131 (8)</td>
<td>4293 ± 1050 (8)</td>
<td>2001 ± 496 (8)</td>
<td>683 ± 196 (8)</td>
</tr>
<tr>
<td>Ribes rotundifolium</td>
<td>6600 ± 1248 (2)</td>
<td>6852 ± 748 (2)</td>
<td>1275 ± 20 (2)</td>
<td>1309 ± 38 (2)</td>
</tr>
<tr>
<td>Species</td>
<td>Ca ppm ± S.E.</td>
<td>K ppm ± S.E.</td>
<td>Mg ppm ± S.E.</td>
<td>P ppm ± S.E.</td>
</tr>
<tr>
<td>-------------------</td>
<td>--------------</td>
<td>--------------</td>
<td>---------------</td>
<td>--------------</td>
</tr>
<tr>
<td>Rubus allegheniensis</td>
<td>2985 (1)</td>
<td>3240 (1)</td>
<td>2101 (1)</td>
<td>1119 (1)</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>9336 ± 2542</td>
<td>8693 ± 2960</td>
<td>2233 ± 422</td>
<td>1260 ± 334</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>6518 ± 372</td>
<td>4143 ± 218</td>
<td>2822 ± 254</td>
<td>758 ± 67</td>
</tr>
<tr>
<td>Vaccinium constablaei</td>
<td>3053 ± 361</td>
<td>3616 ± 476</td>
<td>2171 ± 300</td>
<td>671 ± 89</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>8310 ± 21</td>
<td>5062 ± 985</td>
<td>3096 ± 949</td>
<td>647 ± 146</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>6112 ± 908</td>
<td>3566 ± 197</td>
<td>1975 ± 385</td>
<td>711 ± 65</td>
</tr>
</tbody>
</table>
TABLE XXXIV

NUTRIENT CONCENTRATIONS OF LEAVES OF TREES, SAPLINGS, AND SHRUBS
HARVESTED DURING 1969

<table>
<thead>
<tr>
<th>Species</th>
<th>Ca ppm ± S.E. (n)</th>
<th>K ppm ± S.E. (n)</th>
<th>Mg ppm ± S.E. (n)</th>
<th>P ppm ± S.E. (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies fraseri &lt; 2.54 cm dbh</td>
<td>3705 ± 544 (3)</td>
<td>5488 ± 273 (3)</td>
<td>2961 ± 230 (3)</td>
<td>1268 ± 188 (3)</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td>13201 ± 1486 (4)</td>
<td>11915 ± 950 (4)</td>
<td>4774 ± 212 (4)</td>
<td>1404 ± 149 (4)</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>8853 ± 645 (1)</td>
<td>7476 ± 2656 (1)</td>
<td>2961 ± 1141 (1)</td>
<td>2366 ± 172 (1)</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>10000 ± 10664 (15)</td>
<td>12664 ± 727 (15)</td>
<td>4197 ± 235 (15)</td>
<td>2366 ± 172 (15)</td>
</tr>
<tr>
<td>Aesculus octandra</td>
<td>9861 ± 15310 (7)</td>
<td>2985 ± 258 (7)</td>
<td>2734 ± 120 (7)</td>
<td></td>
</tr>
<tr>
<td>Amelanchier arborea</td>
<td>12373 ± 10574 (8)</td>
<td>5515 ± 294 (8)</td>
<td>1602 ± 236 (8)</td>
<td></td>
</tr>
<tr>
<td>Betula lutea &lt; 2.54 cm dbh</td>
<td>9459 ± 941 (3)</td>
<td>10664 ± 1178 (3)</td>
<td>6310 ± 355 (3)</td>
<td>2502 ± 295 (3)</td>
</tr>
<tr>
<td>Cornus alternifolia</td>
<td>12388 ± 23497 (2)</td>
<td>4644 ± 2352 (2)</td>
<td>1982 ± 455 (2)</td>
<td></td>
</tr>
<tr>
<td>Crataegus sp.</td>
<td>22161 ± 15829 (1)</td>
<td>6074 ± 1622 (1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>8031 ± 11003 (11)</td>
<td>3721 ± 492 (11)</td>
<td>1666 ± 48 (11)</td>
<td></td>
</tr>
<tr>
<td>Picea rubens</td>
<td>4373 ± 4780 (4)</td>
<td>3853 ± 484 (4)</td>
<td>1036 ± 84 (4)</td>
<td></td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>9911 ± 10955 (6)</td>
<td>4024 ± 237 (6)</td>
<td>2603 ± 664 (6)</td>
<td></td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>7437 ± 10031 (6)</td>
<td>3526 ± 239 (6)</td>
<td>1779 ± 120 (6)</td>
<td></td>
</tr>
<tr>
<td>Rhododendron catawbiense, current</td>
<td>16109 ± 9901 (11)</td>
<td>3688 ± 255 (11)</td>
<td>1610 ± 165 (11)</td>
<td></td>
</tr>
<tr>
<td>Rhododendron catawbiense, old</td>
<td>11329 ± 4802 (12)</td>
<td>3490 ± 187 (12)</td>
<td>854 ± 24 (12)</td>
<td></td>
</tr>
<tr>
<td>Rhododendron maximum</td>
<td>14237 ± 8810 (9)</td>
<td>3941 ± 188 (9)</td>
<td>998 ± 39 (9)</td>
<td></td>
</tr>
<tr>
<td>Ribes rotundifolium</td>
<td>10198 ± 19814 (1)</td>
<td>5342 ± 2195 (1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rubus allegheniensis</td>
<td>7488 ± 15107 (2)</td>
<td>7738 ± 426 (2)</td>
<td>1832 ± 19 (2)</td>
<td></td>
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</table>

(g ppm ± S.E. ppm ± S.E.)
<table>
<thead>
<tr>
<th>Species</th>
<th>Ca ppm ± S.E. (n)</th>
<th>K ppm ± S.E. (n)</th>
<th>Mg ppm ± S.E. (n)</th>
<th>P ppm ± S.E. (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sambucus pubens</td>
<td>11666 ± 2796 (3)</td>
<td>8851 (1)</td>
<td>8518 ± 1682 (3)</td>
<td>3412 ± 857 (3)</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>12643 ± 485 (13)</td>
<td>12022 ± 932 (13)</td>
<td>6168 ± 296 (13)</td>
<td>1782 ± 176 (13)</td>
</tr>
<tr>
<td>Vaccinium constablae</td>
<td>8539 ± 2113 (7)</td>
<td>11428 ± 3522 (7)</td>
<td>4141 ± 1098 (7)</td>
<td>1173 ± 220 (7)</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>11830 ± 1984 (2)</td>
<td>14958 ± 97 (2)</td>
<td>7358 ± 1191 (2)</td>
<td>1538 ± 264 (2)</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>16697 ± 1490 (6)</td>
<td>20178 ± 411 (6)</td>
<td>4389 ± 414 (6)</td>
<td>2582 ± 96 (6)</td>
</tr>
</tbody>
</table>

TABLE XXXIV (continued)
TABLE XXXV

NUTRIENT CONCENTRATIONS (PPM) IN BRANCHES AND FOLIAGE
OF *ABIES FRASERI* AND *PICEA RUBENS*

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Abies fraseri</th>
<th></th>
<th>Picea rubens</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Branch First Order</td>
<td>Branch Second Order</td>
<td>Foliage From Branch Order</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bark Wood</td>
<td>Wood</td>
<td>Bark Wood</td>
<td>Wood</td>
</tr>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>6083</td>
<td>785</td>
<td>5971</td>
<td>999</td>
</tr>
<tr>
<td>S.E.</td>
<td>609</td>
<td>39</td>
<td>558</td>
<td>109</td>
</tr>
<tr>
<td>n</td>
<td>15</td>
<td>14</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>3444</td>
<td>488</td>
<td>3002</td>
<td>454</td>
</tr>
<tr>
<td>S.E.</td>
<td>330</td>
<td>30</td>
<td>270</td>
<td>60</td>
</tr>
<tr>
<td>n</td>
<td>13</td>
<td>15</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Magnesium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1047</td>
<td>285</td>
<td>867</td>
<td>313</td>
</tr>
<tr>
<td>S.E.</td>
<td>65</td>
<td>15</td>
<td>85</td>
<td>51</td>
</tr>
<tr>
<td>n</td>
<td>14</td>
<td>15</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1208</td>
<td>206</td>
<td>1171</td>
<td>228</td>
</tr>
<tr>
<td>S.E.</td>
<td>150</td>
<td>15</td>
<td>180</td>
<td>29</td>
</tr>
<tr>
<td>n</td>
<td>14</td>
<td>15</td>
<td>10</td>
<td>8</td>
</tr>
</tbody>
</table>

*Calcium concentrations (ppm) in branches and foliage of *Abies fraseri* and *Picea rubens*. The table shows the mean and standard error (S.E.) for calcium, potassium, magnesium, and phosphorus in first and second order branches and from branch order 1 and 2, 3, 4. The table also includes the sample size (n) for each measurement.
TABLE XXXV (continued)

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Branch First Order</th>
<th>Branch Second Order</th>
<th>Foliage From Branch Order 1 and 2 3 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Magnesium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1022</td>
<td>276</td>
<td>887 86</td>
</tr>
<tr>
<td>S.E.</td>
<td>61 44</td>
<td>102 359</td>
<td>62 54 88</td>
</tr>
<tr>
<td>n</td>
<td>21 16</td>
<td>9 5</td>
<td>12 7 3</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>253 98</td>
<td>229 74</td>
<td>135 94 74</td>
</tr>
<tr>
<td>S.E.</td>
<td>26 9</td>
<td>52 18</td>
<td>21 21 -</td>
</tr>
<tr>
<td>n</td>
<td>19 12</td>
<td>12 5</td>
<td>13 6 1</td>
</tr>
</tbody>
</table>

aH. R. DeSelm, unpublished data.
<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Branch Diameter Class, Cm&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Foliage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.5-&lt;br&gt;12.7&lt;br&gt;25.4&lt;br&gt;&gt;25.4</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>16&lt;br&gt;17&lt;br&gt;24&lt;br&gt;1</td>
<td>10</td>
</tr>
<tr>
<td>Calcium</td>
<td>Mean 6528&lt;br&gt;S.E. 360</td>
<td>15191</td>
</tr>
<tr>
<td></td>
<td>4888&lt;br&gt;255&lt;br&gt;184&lt;br&gt;-</td>
<td>866</td>
</tr>
<tr>
<td>Potassium</td>
<td>Mean 1778&lt;br&gt;S.E. 121</td>
<td>6519</td>
</tr>
<tr>
<td></td>
<td>1100&lt;br&gt;67&lt;br&gt;24&lt;br&gt;-</td>
<td>562</td>
</tr>
<tr>
<td>Magnesium</td>
<td>Mean 1096&lt;br&gt;S.E. 49</td>
<td>3620</td>
</tr>
<tr>
<td></td>
<td>798&lt;br&gt;53&lt;br&gt;48&lt;br&gt;-</td>
<td>189</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>Mean 604&lt;br&gt;S.E. 42</td>
<td>1274</td>
</tr>
<tr>
<td></td>
<td>366&lt;br&gt;31&lt;br&gt;19&lt;br&gt;-</td>
<td>86</td>
</tr>
</tbody>
</table>

<sup>a</sup>H. R. DeSelm, unpublished data.

<sup>b</sup>Analyses of wood and bark combined.
especially high in calcium. Potassium, magnesium, and phosphorus concentrations in birch wood and bark, however, were often lower than in conifers. The importance of branch size as a factor affecting nutrient concentration is illustrated by yellow birch branches; concentrations of all nutrients decreased as branch size increased. Nutrient concentrations in red spruce and Fraser fir boles were similar to values reported in red spruce and balsam fir, respectively, in other studies (Likens and Bormann, 1970; Young and Guinn, 1966). Analysis of entire boles of small individuals showed high nutrient concentrations relative to large plants of the same species which reflects the high proportion of bark characteristic of these stems.

Higher concentrations of nutrients in branches compared to boles is expected since a greater proportion of branch weight is bark (Young, 1971). Comparison of wood and bark analyses from boles and branches indicated a higher concentration of Ca, K, and Mg in branch bark compared with bole bark of red spruce; a comparable relationship between K, Mg, and P concentrations in bole and branch bark of Fraser fir also occurred. Nutrient concentrations of Ca, K, and P in branches of yellow birch and fire cherry were similar to concentrations indicated in other studies (Likens and Bormann, 1970). Concentrations of Mg in branches of these species and of all four elements in
branches of beech and mountain maple were higher in trees from the study area than from the Northeast United States (Likens and Bormann, 1970). Concentrations of nutrients in spruce and fir branch wood and bark tended to be similar or somewhat higher than in analyses from northeastern red spruce and balsam fir. Exceptions were lower concentrations of Ca in branch wood and bark and lower concentrations of P in branch bark of red spruce in the study area.

Compared with analyses of whole branches and boles, nutrient concentrations in leaves were high. However, the important role of bark in nutrient dynamics is emphasized in that concentrations of each element in bark of Fraser fir and red spruce branches exceeded concentrations in foliage of these species. Phosphorus concentrations in foliage of beech, red spruce, Fraser fir, mountain maple, and fire cherry were within the ranges reported for the same or closely related species (balsam fir) in the Northeastern United States (Likens and Bormann, 1970; Scott, 1955; Young and Guinn, 1966). Concentrations of other nutrients varied considerably within species from different areas and levels both above and below those in the current study were indicated (Bard, 1945; Hoyle, 1955; Scott, 1955; Young and Guinn, 1966; Likens and Bormann, 1970). Differences probably reflect soil conditions, analytical techniques used, and sampling procedures. In the study area,
concentrations of Ca and K in red spruce and Fraser fir foliage were low when compared with concentrations in deciduous species.

Analysis of tree-shrub current apical stems and foliage tissue showed that distinctive differences characterized current and older tissues (Table XXXVII). Higher concentrations in current tissues often by factors of 2 or more in part reflect the inclusion of leaves with the samples; however, concentrations of nutrients were higher in current twigs of *Rhododendron catawbiense* (Table XXXIII, 228) and other species as well (Likens and Bormann, 1970) which indicates differences were due to age as well as types of tissues present.

High nutrient concentrations in above-ground shoots of herbs relative to both woody species and bryophytes is indicated (Table XXXVIII). Concentrations of K were especially high and together with concentrations of Ca, Mg, and P generally were in agreement with other reported analyses of similar species (Shanks, *et al.*, 1961; Scott, 1955; Likens and Bormann, 1970). Comparison of bryophytic concentrations showed that Ca and K were lower but Mg and P concentrations were similar to those of vascular herbs. Comparison of plants collected from different stand types showed that Ca and Mg concentrations were highest in bryophytes from deciduous stands. Nutrient concentrations
TABLE XXXVII

CONCENTRATIONS OF NUTRIENTS (PPM) IN CURRENT AND OLDER TISSUES
OF TREE-SHRUB REGENERATION

<table>
<thead>
<tr>
<th>Species</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>S.E. (n)</td>
<td>Mean</td>
<td>S.E. (n)</td>
</tr>
<tr>
<td>Abies fraseri</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Older tissue</td>
<td>3685 ± 458 (2)</td>
<td>4406 ± 19 (2)</td>
<td>3270 ± 44 (2)</td>
<td>1017 ± 58 (2)</td>
</tr>
<tr>
<td>Current tissue</td>
<td>1539 ± 150 (4)</td>
<td>6664 ± 240 (4)</td>
<td>2554 ± 275 (4)</td>
<td>1448 ± 41 (4)</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Older tissue</td>
<td>13274 (1)</td>
<td>20354 (1)</td>
<td>708 (1)</td>
<td>2301 (1)</td>
</tr>
<tr>
<td>Current tissue</td>
<td>18100 (1)</td>
<td>9050 (1)</td>
<td>4977 (1)</td>
<td>2564 (1)</td>
</tr>
<tr>
<td>Betula lutea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Older tissue</td>
<td>4256 ± 512 (4)</td>
<td>2661 ± 595 (4)</td>
<td>2208 ± 521 (4)</td>
<td>857 ± 15 (4)</td>
</tr>
<tr>
<td>Current tissue</td>
<td>8544 ± 734 (2)</td>
<td>9602 ± 1945 (2)</td>
<td>6632 ± (1)</td>
<td>1726 ± 47 (2)</td>
</tr>
<tr>
<td>Ribes glandulosum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Older tissue</td>
<td>3621 ± 83 (2)</td>
<td>4379 ± 526 (2)</td>
<td>2871 ± 22 (2)</td>
<td>1474 ± 130 (2)</td>
</tr>
<tr>
<td>Current tissue</td>
<td>11379 ± 3477 (2)</td>
<td>9757 ± 1181 (2)</td>
<td>6343 ± 791 (2)</td>
<td>1519 ± 149 (2)</td>
</tr>
<tr>
<td>Rubus allegheniensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Older tissue</td>
<td>2063 (1)</td>
<td>2003 (1)</td>
<td>2374 (1)</td>
<td>312</td>
</tr>
<tr>
<td>Current tissue</td>
<td>6040 ± 572 (2)</td>
<td>16320 ± 701 (2)</td>
<td>6760 ± 932 (2)</td>
<td>1182 ± 68 (2)</td>
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TABLE XXXVII (continued)

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<thead>
<tr>
<th>Species</th>
<th>Ca</th>
<th>Mean</th>
<th>S.E.</th>
<th>(n)</th>
<th>K</th>
<th>Mean</th>
<th>S.E.</th>
<th>(n)</th>
<th>Mg</th>
<th>Mean</th>
<th>S.E.</th>
<th>(n)</th>
<th>P</th>
<th>Mean</th>
<th>S.E.</th>
<th>(n)</th>
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<tr>
<td>Older tissue(^b)</td>
<td>5509</td>
<td>(1)</td>
<td>4744</td>
<td>(1)</td>
<td>2263</td>
<td>(1)</td>
<td>796</td>
<td>(1)</td>
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<tr>
<td>Current tissue(^a)</td>
<td>8696</td>
<td>(1)</td>
<td>7628</td>
<td>(1)</td>
<td>2263</td>
<td>(1)</td>
<td>1377</td>
<td>(1)</td>
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<tr>
<td>Older tissue(^b)</td>
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<td>2542</td>
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<td>2911</td>
<td>(1)</td>
<td>460</td>
<td>(1)</td>
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<td>(1)</td>
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\(^a\)Including foliage and twigs.

\(^b\)Twigs only.
TABLE XXXVIII

NUTRIENT CONCENTRATIONS (PPM) OF HERBS AND BRYOPHYES\(^a\)

<table>
<thead>
<tr>
<th>Species</th>
<th>Stand(^b)</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>P</th>
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<td>Aster acuminatus</td>
<td>8</td>
<td>11520</td>
<td>23652</td>
<td>7108</td>
<td>1544</td>
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<td>40</td>
<td>3041</td>
<td>20046</td>
<td>6106</td>
<td>2811</td>
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<tr>
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<td>32, 57</td>
<td>8807</td>
<td>24808</td>
<td>6822</td>
<td>1782</td>
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<tr>
<td>Aster acuminatus</td>
<td>All others</td>
<td>9952</td>
<td>28329</td>
<td>6826</td>
<td>2434</td>
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<td>Aster divaricatus</td>
<td></td>
<td>11437</td>
<td>25166</td>
<td>5945</td>
<td>3056</td>
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<td>Cardamine clematitidis</td>
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<td>3159</td>
<td>34023</td>
<td>6718</td>
<td>2687</td>
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<td>Circaea alpina</td>
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<td>17139</td>
<td>36016</td>
<td>7750</td>
<td>3179</td>
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<td>Clintonia borealis</td>
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<td>2282</td>
<td>22326</td>
<td>3076</td>
<td>3002</td>
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<td>Eupatorium rugosum</td>
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<td>11944</td>
<td>18424</td>
<td>3990</td>
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<td>37369</td>
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<td>2143</td>
<td>1798</td>
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<td>24353</td>
<td>2495</td>
<td>3017</td>
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<td>Phacelia sp.</td>
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<td>21253</td>
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<td>4119</td>
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<td>20190</td>
<td>4218</td>
<td>3300</td>
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<td><strong>Pteridophytes</strong></td>
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<td></td>
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</tr>
<tr>
<td>Dryopteris spp(^c)</td>
<td></td>
<td>4187</td>
<td>24424</td>
<td>6271</td>
<td>2352</td>
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</table>
TABLE XXXVIII (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Standb</th>
<th>CA</th>
<th>K</th>
<th>Mg</th>
<th>P</th>
</tr>
</thead>
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<tr>
<td><strong>Bryophytesd</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Spruce-fir stands</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Mean</td>
<td>3561</td>
<td>4479</td>
<td>3038</td>
<td>1651</td>
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<tr>
<td>S.E.</td>
<td>289</td>
<td>283</td>
<td>170</td>
<td>95</td>
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</tr>
<tr>
<td>n</td>
<td>(11)</td>
<td>(11)</td>
<td>(11)</td>
<td>(11)</td>
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</tr>
<tr>
<td>Yellow birch stands</td>
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<td>Mean</td>
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<td>4832</td>
<td>4308</td>
<td>1452</td>
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<td>S.E.</td>
<td>463</td>
<td>362</td>
<td>297</td>
<td>90</td>
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</tr>
<tr>
<td>n</td>
<td>(4)</td>
<td>(4)</td>
<td>(4)</td>
<td>(4)</td>
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</tr>
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aNutrient concentrations or sources used for species not listed were:

<table>
<thead>
<tr>
<th>Species</th>
<th>Source of Nutrient Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arisaema triphyllum</td>
<td>Undetermined herbs, mean</td>
</tr>
<tr>
<td>Claytonia caroliniana</td>
<td>Shanks, et al., 1961</td>
</tr>
<tr>
<td>Clintonia borealis</td>
<td>Shanks, et al., 1961</td>
</tr>
<tr>
<td>Carex spp.</td>
<td>Gramineae</td>
</tr>
<tr>
<td>Erythronium americanum</td>
<td>Trillium erectum</td>
</tr>
<tr>
<td>Lycopodium lucidulum</td>
<td>Dryopteris spp., mean</td>
</tr>
<tr>
<td>Maianthemum canadense</td>
<td>Trillium erectum</td>
</tr>
<tr>
<td>Oxalis acerosella</td>
<td>Shanks, et al., 1961</td>
</tr>
<tr>
<td>Phacelia sp.</td>
<td>Shanks, et al., 1961</td>
</tr>
<tr>
<td>Phlox sp.</td>
<td>Forb mean</td>
</tr>
<tr>
<td>Podophyllum peltatum</td>
<td>Forb mean</td>
</tr>
<tr>
<td>Polypodium polypodioides</td>
<td>Forb mean</td>
</tr>
<tr>
<td>Sanguinaria canadensis</td>
<td>Solidago glomerata</td>
</tr>
<tr>
<td>Stachys clingmanii</td>
<td>Compositae</td>
</tr>
<tr>
<td>Tiarella cordifolia</td>
<td>Liliaceae</td>
</tr>
<tr>
<td>Veratrum viride</td>
<td>Liliaceae</td>
</tr>
</tbody>
</table>

bWhere stand numbers are now shown, samples from all stands were combined for analysis.

cIncludes D. intermedia and D. spinulosa.

dIncludes Brotherrilla recurvans, Dicranum fuscescens, Hylocomium brevirostre, H. splendens, Nowellia curvifolia, Plagiothecium elegans, Platygyrium repens, Polytrichum commune.
in bryophytes were similar to those found by Tamm (1953) in older segments of *Hylocomium splendens*, which was predominant in many stands of the present study. The similarities to older segments analyzed by Tamm (1953) reflect the presence of large proportions of non-green segments forming the lower parts of harvested mats.

**Nutrient Pools in Vegetation**

Quantities of nutrients in each system followed the distributional patterns in tissues where Ca > K > Mg > P and were within the ranges reported from most spruce-fir and beech or birch forests (Cf. Section II, page 4). (Table XXXIX). Compared with stands in the Great Smoky Mountains (Shanks, *et al.*, 1961) both spruce-fir and yellow birch stands contained smaller total quantities of each nutrient which in part reflects the lower total stand biomass of the immature stands of the study area. Within the study area, spruce-fir stands contained the greatest quantity of each nutrient and mature yellow birch the least, although the differences generally were not statistically significant. The single exception was that K levels in spruce-fir stands were significantly greater than in immature yellow birch stands.

The distribution of nutrients among strata varied from system to system and according to nutrient. Trees contained 98 per cent, 96 per cent, and 91 per cent of the
### TABLE XXXIX

**DISTRIBUTION OF NUTRIENTS IN VEGETATION OF SPRUCE- FIR AND YELLOW BIRCH ECOSYSTEMS**

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature Growth (n=4)</th>
<th>Mature Growth (n=2)</th>
<th>Significance&lt;sup&gt;a, b&lt;/sup&gt;</th>
<th>Significance&lt;sup&gt;c, b&lt;/sup&gt;</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance&lt;sup&gt;a, b&lt;/sup&gt;</td>
<td>Mean</td>
<td>STD</td>
</tr>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tree-tall shrub, kg/ha</td>
<td>355.5</td>
<td>70.6</td>
<td>NS</td>
<td>367.3</td>
<td>164.0</td>
</tr>
<tr>
<td>Per cent in boles&lt;sup&gt;d&lt;/sup&gt;</td>
<td>59.4</td>
<td>8.3</td>
<td>4</td>
<td>36.8</td>
<td>5.7</td>
</tr>
<tr>
<td>Per cent in branches&lt;sup&gt;d&lt;/sup&gt;</td>
<td>23.8</td>
<td>6.6</td>
<td>4</td>
<td>49.2</td>
<td>4.6</td>
</tr>
<tr>
<td>Per cent in leaves&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16.8</td>
<td>2.5</td>
<td>2</td>
<td>14.0</td>
<td>1.6</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>98.4</td>
<td>1.6</td>
<td>NS</td>
<td>96.9</td>
<td>2.7</td>
</tr>
<tr>
<td>Sapling-low shrub, kg/ha</td>
<td>0.6</td>
<td>0.6</td>
<td>NS</td>
<td>1.6</td>
<td>1.4</td>
</tr>
<tr>
<td>Per cent in boles</td>
<td>38.4</td>
<td>12.4</td>
<td>NS</td>
<td>39.6</td>
<td>7.0</td>
</tr>
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<td>Per cent in branches</td>
<td>24.6</td>
<td>13.7</td>
<td>3</td>
<td>40.8</td>
<td>8.3</td>
</tr>
<tr>
<td>Per cent in leaves</td>
<td>37.0</td>
<td>10.1</td>
<td>4</td>
<td>19.6</td>
<td>4.0</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.16</td>
<td>0.18</td>
<td>NS</td>
<td>0.4</td>
<td>0.4</td>
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<tr>
<td>Tree-shrub regeneration, kg/ha</td>
<td>0.15</td>
<td>0.28</td>
<td>NS</td>
<td>0.13</td>
<td>0.25</td>
</tr>
<tr>
<td>Per cent of total</td>
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<td>0.11</td>
<td>NS</td>
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<td>0.11</td>
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<tr>
<td>Herbs, kg/ha</td>
<td>0.7</td>
<td>0.7</td>
<td>NS</td>
<td>2.0</td>
<td>1.8</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.26</td>
<td>0.23</td>
<td>NS</td>
<td>0.6</td>
<td>0.7</td>
</tr>
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<td>Nutrients</td>
<td>Spruce-Fir (n=14)</td>
<td>Immature Growth (n=4)</td>
<td>Mature (n=2)</td>
<td>Significance&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
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<td>-------------------</td>
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<td>-----------------------------</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Mean</td>
<td>STD</td>
<td>Mean</td>
</tr>
<tr>
<td>Bryophytes, kg/ha</td>
<td>3.7</td>
<td>3.4</td>
<td>4.6</td>
<td>5.6</td>
<td>25.3</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>1.2</td>
<td>1.3</td>
<td>1.9</td>
<td>2.4</td>
<td>8.0</td>
</tr>
<tr>
<td>Total, all strata, kg/ha</td>
<td>360.6</td>
<td>81.1</td>
<td>375.7</td>
<td>158.9</td>
<td>316.9</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tree-tall shrub, kg/ha</td>
<td>180.0</td>
<td>49.1</td>
<td>105.2</td>
<td>42.0</td>
<td>83.7</td>
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<tr>
<td>Per cent in boles&lt;sup&gt;d&lt;/sup&gt;</td>
<td>54.6</td>
<td>6.5</td>
<td>40.4</td>
<td>6.1</td>
<td>61.5</td>
</tr>
<tr>
<td>Per cent in branches&lt;sup&gt;d&lt;/sup&gt;</td>
<td>20.1</td>
<td>3.3</td>
<td>34.7</td>
<td>3.5</td>
<td>23.7</td>
</tr>
<tr>
<td>Per cent in leaves&lt;sup&gt;d&lt;/sup&gt;</td>
<td>25.3</td>
<td>3.8</td>
<td>24.8</td>
<td>3.6</td>
<td>14.8</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>94.7</td>
<td>4.8</td>
<td>86.1</td>
<td>10.7</td>
<td>78.7</td>
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<tr>
<td>Sapling-low shrub, kg/ha</td>
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<td>0.74</td>
<td>1.3</td>
<td>1.1</td>
<td>1.1</td>
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<tr>
<td>Per cent in boles</td>
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<td>6.6</td>
<td>36.5</td>
<td>8.0</td>
<td>48.5</td>
</tr>
<tr>
<td>Per cent in branches</td>
<td>27.5</td>
<td>3.8</td>
<td>32.4</td>
<td>9.0</td>
<td>19.4</td>
</tr>
<tr>
<td>Per cent in leaves</td>
<td>41.4</td>
<td>5.3</td>
<td>31.4</td>
<td>7.4</td>
<td>32.0</td>
</tr>
<tr>
<td>Per cent of total</td>
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<td>0.40</td>
<td>1.1</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Tree-shrub regeneration</td>
<td>0.24</td>
<td>0.43</td>
<td>0.22</td>
<td>0.42</td>
<td>0.04</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.14</td>
<td>0.30</td>
<td>0.28</td>
<td>0.53</td>
<td>0.03</td>
</tr>
<tr>
<td>Herbs, kg/ha</td>
<td>3.78</td>
<td>4.32</td>
<td>8.3</td>
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<tr>
<td>Per cent of total</td>
<td>1.86</td>
<td>2.39</td>
<td>7.5</td>
<td>8.2</td>
<td>4.5</td>
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TABLE XXXIX (continued)

<table>
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<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature Growth (n=4)</th>
<th>Yellow Birch Mature (n=2)</th>
<th>Significancea,b</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Mean  STD</td>
<td>Significance</td>
<td>Mean  STD</td>
<td>Mean  STD</td>
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<td>Bryophytes, kg/ha</td>
<td>5.16    5.10</td>
<td>NS</td>
<td>4.4      5.2</td>
<td>16.8    9.1</td>
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<td>Per cent of total</td>
<td>2.95    3.31</td>
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<td>5.0      6.2</td>
<td>15.7    8.41</td>
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<td>Total, all strata, kg/ha</td>
<td>189.3   48.4</td>
<td>3</td>
<td>119.5    35.3</td>
<td>106.4   0.8</td>
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<td>Magnesium</td>
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<td></td>
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<td></td>
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<tr>
<td>Tree-tall shrub, kg/ha</td>
<td>75.0     12.2</td>
<td>NS</td>
<td>57.1     25.3</td>
<td>37.4    2.2</td>
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<tr>
<td>Per cent in boles</td>
<td>62.8     3.5</td>
<td>4</td>
<td>33.0     4.8</td>
<td>44.5    0.8</td>
</tr>
<tr>
<td>Per cent in branches</td>
<td>20.3     2.3</td>
<td>4</td>
<td>44.6     3.5</td>
<td>37.4    0.4</td>
</tr>
<tr>
<td>Per cent in leaves</td>
<td>16.8     2.0</td>
<td>4</td>
<td>22.4     1.6</td>
<td>18.0    0.4</td>
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<td>Per cent of total</td>
<td>93.81    7.1</td>
<td>NS</td>
<td>88.4     9.9</td>
<td>66.4    7.8</td>
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<tr>
<td>Sapling-low shrub, kg/ha</td>
<td>0.34     0.1</td>
<td>NS</td>
<td>0.9      1.0</td>
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<tr>
<td>Per cent in boles</td>
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<td>NS</td>
<td>39.6     20.0</td>
<td>47.3    2.1</td>
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<tr>
<td>Per cent in branches</td>
<td>29.9     12.8</td>
<td>NS</td>
<td>36.5     19.4</td>
<td>26.0    2.2</td>
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<tr>
<td>Per cent in leaves</td>
<td>39.8     9.8</td>
<td>4</td>
<td>23.9     4.6</td>
<td>26.9    0.1</td>
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<td>Per cent of total</td>
<td>0.42     0.50</td>
<td>1</td>
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<td>0.9     0.8</td>
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<td>0.15     0.27</td>
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<td>NS</td>
<td>0.3      0.5</td>
<td>0.04    0.06</td>
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<td>Herbs, kg/ha</td>
<td>0.86     0.97</td>
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<td>Per cent of total</td>
<td>1.61     2.33</td>
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<td>1.9     0.4</td>
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<td>Nutrients</td>
<td>Spruce-Fir (n=14)</td>
<td>Yellow Birch</td>
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<td>Mean</td>
<td>STD</td>
<td>Significancea,b</td>
<td>Mean</td>
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<tr>
<td></td>
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<td></td>
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<td>Bryophytes, kg/ha</td>
<td>3.60</td>
<td>3.84</td>
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<td>5.65</td>
<td>NS</td>
<td>7.2</td>
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<td>Total, all strata, kg/ha</td>
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<td>13.8</td>
<td>NS</td>
<td>62.8</td>
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<td>Phosphorus</td>
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<tr>
<td>Tree-tall shrub, kg/ha</td>
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<td>6.6</td>
<td>NS</td>
<td>29.6</td>
</tr>
<tr>
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<td>9.0</td>
<td>4</td>
<td>39.7</td>
</tr>
<tr>
<td>Per cent in branches d</td>
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<td>1.7</td>
<td>4</td>
<td>42.7</td>
</tr>
<tr>
<td>Per cent in leaves d</td>
<td>16.5</td>
<td>8.5</td>
<td>NS</td>
<td>17.6</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>93.98</td>
<td>7.1</td>
<td>NS</td>
<td>90.4</td>
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<tr>
<td>Sapling-low shrub, kg/ha</td>
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<td>0.14</td>
<td>NS</td>
<td>0.6</td>
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<td>Per cent in boles</td>
<td>28.3</td>
<td>10.2</td>
<td>NS</td>
<td>45.8</td>
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<tr>
<td>Per cent in branches</td>
<td>27.0</td>
<td>9.7</td>
<td>NS</td>
<td>28.5</td>
</tr>
<tr>
<td>Per cent in leaves</td>
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<td>10.0</td>
<td>2</td>
<td>25.6</td>
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<td>0.30</td>
<td>NS</td>
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<td>Tree-shrub regeneration, kg/ha</td>
<td>0.05</td>
<td>0.10</td>
<td>NS</td>
<td>0.04</td>
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<tr>
<td>Per cent of total</td>
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<td>0.33</td>
<td>NS</td>
<td>0.16</td>
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<tr>
<td>Herbs, kg/ha</td>
<td>0.35</td>
<td>0.41</td>
<td>NS</td>
<td>0.7</td>
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<td>Per cent of total</td>
<td>0.88</td>
<td>1.11</td>
<td>NS</td>
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TABLE XXXIX (continued)

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<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature Growth (n=4)</th>
<th>Mature Yellow Birch (n=2)</th>
<th>Significance</th>
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<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>Mean</td>
</tr>
<tr>
<td>Bryophytes, kg/ha</td>
<td>1.94</td>
<td>2.06</td>
<td>NS</td>
<td>1.3</td>
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<tr>
<td>Per cent of total</td>
<td>4.89</td>
<td>6.14</td>
<td>NS</td>
<td>5.5</td>
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<tr>
<td>Total, all strata, kg/ha</td>
<td>39.66</td>
<td>8.1</td>
<td>NS</td>
<td>32.2</td>
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</table>

<sup>a</sup>T-test of significance of difference between means of spruce-fir and immature yellow birch stands.

<sup>b</sup>NS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.

<sup>c</sup>T-test of significance of difference between means of immature and mature yellow birch stands.

<sup>d</sup>Means based on 30 spruce-fir, six immature yellow birch, and four mature yellow birch stands, respectively. All other means based on 14 spruce-fir, four immature yellow birch and two mature yellow birch stands.
Ca in spruce-fir, immature yellow birch, and mature yellow birch stands, respectively. Smaller proportions of other nutrients were in trees which contained from 95 per cent of the K in spruce-fir stands to only 66 per cent of the Mg in mature yellow birch stands. The relatively high proportions of Ca in trees and tall shrubs reflect both the accumulation of Ca and the high percentage of total biomass in perennial components. In all stands sapling-low shrub and tree-shrub regeneration contained slight quantities of total nutrients. Reflecting the higher nutrient concentrations in herbs and relatively large biomass of bryophytes, these strata were more significant in the nutrient pools than in standing crop biomass (Cf. Tables XXXIX, page 243, and IX, page 135). With the exception of K which was higher, absolute quantities of nutrients in herbs of the spruce-fir ecosystems were similar to quantities of nutrients in a Great Smoky Mountain spruce-fir stand (Shanks, et al., 1961). Lesser quantities of nutrients were present in both ages of yellow birch stands than in beech stands in the Great Smoky Mountains which probably resulted from age and structural differences between young stands as well as site differences. Differences between mature yellow birch and beech stands indicated that the relative quantities among nutrients were the same, however (i.e., K > Ca > Mg > P). As in the Great Smoky Mountains, more nutrients occurred in the
herb stratum of deciduous than coniferous stands, although the differences were not statistically significant. Bryophytes were especially important in the nutrient pools of mature yellow birch stands where they contained between 8 and 31 per cent of the nutrients in the above-ground vegetation.

Within the tree-tall shrub stratum, boles generally contained the largest proportion of each nutrient and foliage the least, but the pattern differed from the distribution of biomass in that boles contained a smaller proportion of tree nutrients than biomass and both foliage and branches contained a larger percentage of tree nutrients than of tree biomass. A larger percentage of tree K in foliage than branches and similar proportions of tree P in branches and foliage of spruce-fir stands marked other significant departures between the distribution of nutrients and dry matter.

Although the relative distribution of nutrients among boles, branches and leaves of yellow birch agreed well with the distribution in hardwoods reported by Rennie (1955); the proportions of nutrients in conifers (non-pine) were higher in both foliage and branches and lower in boles than in the present study.

The absolute quantities of nutrients in tree components also varied with stand type. Boles in both
spruce-fir and mature yellow birch stands contained larger quantities each of Ca, K, Mg, and P than immature yellow birch stands. Relatively large branch biomass which in conjunction with high nutrient concentrations resulted in significantly larger quantities of Ca, K, and Mg in branches of immature yellow birch stands than either spruce-fir or mature yellow birch stands. The absolute quantity of P in branches of immature yellow birch stands was also significantly greater than in spruce-fir stands.

In comparison with the distribution of nutrients in tree boles, boles of plants of the sapling-low shrub stratum contained lower proportions of the nutrients which largely reflected the lower proportion of biomass in main stems in this stratum. Much larger proportions of nutrients of this stratum were in foliage.

### Annual Nutrient Retention

The small quantities of nutrients retained annually in woody components of spruce-fir stands (Table XL) were similar to quantities retained by many coniferous stands (Rodin and Basilevic, 1967). Although nutrient retention is often higher in deciduous stands, smaller quantities were retained annually in immature yellow birch than in spruce-fir stands of the study area. This apparent reverse relationship resulted from lower dry-matter production of yellow birch stands and relatively low nutrient concentrations
### TABLE XL

ANNUAL ACCUMULATION OF CALCIUM, POTASSIUM, MAGNESIUM AND PHOSPHORUS IN ABOVE-GROUND VEGETATION

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th></th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
<th>Significance&lt;sup&gt;b, c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance&lt;sup&gt;a, b&lt;/sup&gt;</td>
<td>Mean</td>
<td>STD</td>
</tr>
<tr>
<td>Calcium, kg/ha</td>
<td>8.9</td>
<td>2.6</td>
<td>NS</td>
<td>6.7</td>
<td>4.3</td>
</tr>
<tr>
<td>Tree-tall shrub, kg/ha</td>
<td>6.6</td>
<td>2.0</td>
<td>NS</td>
<td>7.8</td>
<td>4.4</td>
</tr>
<tr>
<td>Per cent in boles</td>
<td>57.9</td>
<td>14.9</td>
<td>NS</td>
<td>53.7</td>
<td>5.9</td>
</tr>
<tr>
<td>Per cent in branches</td>
<td>42.9</td>
<td>14.9</td>
<td>NS</td>
<td>46.3</td>
<td>5.9</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>87.0</td>
<td>12.9</td>
<td>NS</td>
<td>77.4</td>
<td>26.1</td>
</tr>
<tr>
<td>Sapling-low shrub, kg/ha</td>
<td>0.01</td>
<td>0.01</td>
<td>NS</td>
<td>0.07</td>
<td>0.07</td>
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<tr>
<td>Per cent in boles</td>
<td>61.7</td>
<td>26.4</td>
<td>NS</td>
<td>54.8</td>
<td>17.0</td>
</tr>
<tr>
<td>Per cent in branches</td>
<td>38.3</td>
<td>26.4</td>
<td>NS</td>
<td>45.2</td>
<td>17.0</td>
</tr>
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<td>Per cent of total</td>
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<td>0.1</td>
<td>NS</td>
<td>0.77</td>
<td>0.94</td>
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<td>Tree-shrub regeneration, kg/ha</td>
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<td>0.04</td>
<td>NS</td>
<td>0.84</td>
<td>0.15</td>
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<td>Per cent of total</td>
<td>0.21</td>
<td>0.35</td>
<td>NS</td>
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<td>Bryophytes, kg/ha</td>
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<td>1.22</td>
<td>NS</td>
<td>1.53</td>
<td>1.84</td>
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<tr>
<td>Per cent of total</td>
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<td>13.0</td>
<td>NS</td>
<td>20.77</td>
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<td>Potassium, kg/ha</td>
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<td>2.1</td>
<td>2</td>
<td>3.7</td>
<td>1.0</td>
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<tr>
<td>Tree-tall shrub, kg/ha</td>
<td>3.3</td>
<td>0.7</td>
<td>2</td>
<td>2.10</td>
<td>0.95</td>
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### TABLE XL (continued)

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
<th>Yellow Birch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significancea,b</td>
<td>Mean</td>
</tr>
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<td>Per cent in boles</td>
<td>63.9</td>
<td>11.2</td>
<td>NS</td>
<td>64.6</td>
</tr>
<tr>
<td>Per cent in branches</td>
<td>36.1</td>
<td>11.2</td>
<td>NS</td>
<td>35.9</td>
</tr>
<tr>
<td>Per cent of total</td>
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<td>NS</td>
<td>64.0</td>
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<td>0.03</td>
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<td>4.6</td>
<td>NS</td>
<td>58.2</td>
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<tr>
<td>Per cent in branches</td>
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<td>4.6</td>
<td>NS</td>
<td>41.8</td>
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<td>Per cent of total</td>
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<td>0.4</td>
<td>NS</td>
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<td>Tree-shrub regeneration, kg/ha</td>
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<td>NS</td>
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<td>2.03</td>
<td>NS</td>
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<td>1.8</td>
<td>NS</td>
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<td>NS</td>
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<td>1.5</td>
<td>NS</td>
<td>2.2</td>
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<tr>
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<td>0.3</td>
<td>NS</td>
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<td>5.8</td>
<td>4</td>
<td>50.2</td>
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<td>Per cent in branches</td>
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<td>5.8</td>
<td>4</td>
<td>49.8</td>
</tr>
<tr>
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<td>62.8</td>
<td>27.3</td>
<td>4</td>
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<td>0.01</td>
<td>NS</td>
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</tr>
<tr>
<td>Per cent in boles</td>
<td>48.0</td>
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<td>NS</td>
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**TABLE XL (continued)**

<table>
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<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
<th>Yellow Birch</th>
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<td>STD</td>
<td>Significancea,b</td>
<td>Mean</td>
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<td>17.3</td>
<td>NS</td>
<td>38.2</td>
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<td>Per cent of total</td>
<td>0.2</td>
<td>0.3</td>
<td>NS</td>
<td>2.10</td>
</tr>
<tr>
<td>Tree-shrub regeneration, kg/ha</td>
<td>0.04</td>
<td>0.06</td>
<td>NS</td>
<td>0.49</td>
</tr>
<tr>
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<td>1.05</td>
<td>1.78</td>
<td>NS</td>
<td>1.61</td>
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<td>NS</td>
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<tr>
<td>Per cent of total</td>
<td>35.9</td>
<td>26.1</td>
<td>NS</td>
<td>37.2</td>
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<td>Phosphorus, kg/ha</td>
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<td>NS</td>
<td>1.1</td>
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<td>0.48</td>
<td>0.13</td>
<td>NS</td>
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<tr>
<td>Per cent in boles</td>
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<td>2.3</td>
<td>4</td>
<td>56.9</td>
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<td>Per cent in branches</td>
<td>22.4</td>
<td>2.3</td>
<td>4</td>
<td>43.1</td>
</tr>
<tr>
<td>Per cent of total</td>
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<td>27.3</td>
<td>NS</td>
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<tr>
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<td>0.009</td>
<td>NS</td>
<td>0.034</td>
</tr>
<tr>
<td>Per cent in boles</td>
<td>64.4</td>
<td>14.5</td>
<td>NS</td>
<td>62.1</td>
</tr>
<tr>
<td>Per cent in branches</td>
<td>35.6</td>
<td>14.5</td>
<td>NS</td>
<td>37.9</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>0.3</td>
<td>0.4</td>
<td>NS</td>
<td>2.7</td>
</tr>
<tr>
<td>Tree-shrub regeneration, kg/ha</td>
<td>0.02</td>
<td>0.03</td>
<td>NS</td>
<td>0.001</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>1.17</td>
<td>2.03</td>
<td>NS</td>
<td>0.84</td>
</tr>
<tr>
<td>Nutrients</td>
<td>Spruce-Fir (n=14)</td>
<td>Immature (n=4)</td>
<td>Mature (n=2)</td>
<td>Yellow Birch</td>
</tr>
<tr>
<td>-----------------------</td>
<td>-------------------</td>
<td>----------------</td>
<td>--------------</td>
<td>--------------</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance</td>
<td>Mean</td>
</tr>
<tr>
<td>Bryophytes, kg/ha</td>
<td>0.7</td>
<td>0.7</td>
<td>NS</td>
<td>0.42</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>43.0</td>
<td>25.9</td>
<td>NS</td>
<td>34.1</td>
</tr>
</tbody>
</table>

*a*-test of difference between means of spruce-fir and immature yellow birch stands.  
  
b*NS* P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.  
  
c*T*-test of difference between means of immature and mature yellow birch stands.
of yellow birch wood. Retention of nutrients by trees and
tall shrubs of mature yellow birch stands was very low as
a result of the low rates of both bole and branch produc-
tion. Decreasing rates of retentions with increasing age
are typical (Rodin and Basilevic, 1967).

These quantities equalled 2.5 per cent, 2.9 per cent,
3.0 per cent, and 3.0 per cent of the total Ca, K, Mg, and
P pools, respectively, in above-ground vegetation in spruce-
fir stands. Retention of Ca was lower (1.8 per cent) in
immature yellow birch stands and K higher (3.6 per cent);
retention rates of Mg and P were similar to coniferous
stands. Retention patterns in mature yellow birch stands
varied markedly from other stands; Ca was 1.6 per cent; K,
4.9 per cent; Mg, 10.9 per cent; and P, 7.0 per cent, of
respective above-ground nutrient pools. In these mature
stands, trees, as indicated by low net production of per-
ennial components, played a minor role in nutrient reten-
tion. Of total retention shown in Table XL, page 251, ca
40 per cent of the Ca and less than 10 per cent of each of
the other nutrients was by trees; 56 per cent of the Ca
and from 89 to 96 per cent of the other nutrients were re-
tained by bryophytes. Mosses also had highly significant
roles in the nutrient dynamics of Canadian black spruce
stands (Weetman and Timmer, 1967) and various spruce stands
in Europe (Tamm, 1953) although proportions of total
nutrients in vegetation may have been somewhat less than in the mature yellow birch stands of the current study.

**Nutrient Dynamics of Litterfall**

Nutrient contents of litterfall components in order of decreasing concentrations generally were Ca > K > Mg > P (Table XLI). Apparent exceptions were reproductive components in spruce-fir stands where K > Ca and deciduous leaves and needles in yellow birch stands where Mg > K. Although none of these differences were statistically significant at P.10, the similarities in concentrations were a departure from general trends, particularly since the concentrations of K often exceeds Mg by a factor of two or more in living tissues. The susceptibility of K to leaching increases from living to senescent to dead tissues (Nihlgard, 1970) which may partially account for the apparent low K relative to Mg since litter remained in baskets as long as two weeks during spring, summer, and fall, and two or more months during winter before collected. Intense leaching of K from litter, especially if acid such as in coniferous stands under the high rainfall regime of high elevations in the Southern Appalachians would be expected. Absolute concentrations of nutrients varied considerably, however, among different components within ecosystems and within some components between systems. Deciduous leaves generally contained the highest concentrations of Ca, K, and Mg.
TABLE XLI

CONCENTRATIONS OF NUTRIENTS IN ANNUAL LITTERFALL IN SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS

<table>
<thead>
<tr>
<th>Litterfall Components</th>
<th>Ca Mean (n)</th>
<th>Ca S.E.</th>
<th>K Mean (n)</th>
<th>K S.E.</th>
<th>Mg Mean (n)</th>
<th>Mg S.E.</th>
<th>P Mean (n)</th>
<th>P S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce-Fir Stands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive compone-</td>
<td>3408 ± 381</td>
<td>(54)</td>
<td>3827 ± 263</td>
<td>(55)</td>
<td>1716 ± 96</td>
<td>(55)</td>
<td>1308 ± 75</td>
<td>(52)</td>
</tr>
<tr>
<td>ents</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous leaves</td>
<td>7752 ± 513</td>
<td>(34)</td>
<td>5095 ± 804</td>
<td>(34)</td>
<td>3920 ± 244</td>
<td>(32)</td>
<td>1093 ± 92</td>
<td>(34)</td>
</tr>
<tr>
<td>Needles</td>
<td>5170 ± 240</td>
<td>(54)</td>
<td>2895 ± 244</td>
<td>(54)</td>
<td>2522 ± 111</td>
<td>(54)</td>
<td>887 ± 33</td>
<td>(54)</td>
</tr>
<tr>
<td>Twigs</td>
<td>4185 ± 339</td>
<td>(52)</td>
<td>2968 ± 259</td>
<td>(52)</td>
<td>2310 ± 145</td>
<td>(51)</td>
<td>678 ± 34</td>
<td>(51)</td>
</tr>
<tr>
<td>Boles and branches</td>
<td>4951 ± 655</td>
<td>(11)</td>
<td>801 ± 64</td>
<td>(12)</td>
<td>4051 ± 395</td>
<td>(12)</td>
<td>250 ± 43</td>
<td>(12)</td>
</tr>
<tr>
<td>Yellow Birch Stands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive compone-</td>
<td>6335 ± 671</td>
<td>(17)</td>
<td>3501 ± 506</td>
<td>(17)</td>
<td>3309 ± 675</td>
<td>(17)</td>
<td>1256 ± 148</td>
<td>(18)</td>
</tr>
<tr>
<td>ents</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous leaves</td>
<td>9206 ± 956</td>
<td>(22)</td>
<td>3582 ± 337</td>
<td>(22)</td>
<td>4205 ± 328</td>
<td>(22)</td>
<td>1003 ± 63</td>
<td>(22)</td>
</tr>
<tr>
<td>Needles</td>
<td>5695 ± 229</td>
<td>(8)</td>
<td>3068 ± 127</td>
<td>(8)</td>
<td>3166 ± 259</td>
<td>(8)</td>
<td>962 ± 61</td>
<td>(8)</td>
</tr>
<tr>
<td>Twigs</td>
<td>7845 ± 411</td>
<td>(19)</td>
<td>3897 ± 643</td>
<td>(19)</td>
<td>2305 ± 258</td>
<td>(19)</td>
<td>642 ± 55</td>
<td>(19)</td>
</tr>
<tr>
<td>Boles and branches</td>
<td>8834 ± 662</td>
<td>(5)</td>
<td>930 ± 20</td>
<td>(5)</td>
<td>5464 ± 296</td>
<td>(5)</td>
<td>274 ± 14</td>
<td>(5)</td>
</tr>
</tbody>
</table>

*aStandard error of mean.
Reproductive components contained highest P concentrations. Among other components, P concentrations decreased in the order deciduous leaves > needles > twigs. Within components, variation of P between systems was generally low. The contents of other nutrients in reproductive components relative to other litterfall components were usually intermediate.

Needles contained low levels of K and Ca in yellow birch plots but intermediate levels of P and Mg (Table XLI, page 257). Although not statistically significant, needles from yellow birch plots contained higher nutrient concentrations than needles from spruce-fir plots. Different concentrations might be expected since red spruce was the major source of needles in yellow birch stands and Fraser fir the major producer in coniferous stands; comparison of analyses of nutrient content of red spruce and balsam fir needle litter from other areas (Lutz and Chandler, 1946; Damman, 1971) generally show higher concentrations in spruce needles but data for accurate comparison of red spruce and Fraser fir litter are not available. Some studies have shown that variations in concentrations of foliage nutrients in red spruce (Safford and Young, 1968) and other species (Bard, 1945; Scott, 1955) were related to soil nutrient differences and Rodin and Basilevic (1967) suggested that increased availability of nutrients due to the presence of deciduous species in stands would result in
higher concentrations of nutrients in coniferous litter. Perhaps similar factors are also related to the differences in nutrient contents of deciduous leaves between yellow birch and coniferous stands.

Small twigs and bark contained intermediate levels of Ca and K and low levels of Mg and P (Table XLI, page 257). Exceptions were high concentrations of Ca and K in litter from yellow birch plots, where calcium of twigs and bark was second to deciduous foliage litter and potassium contents exceeded those of all other components. Bole and large branch litterfall Ca and Mg contents were similar to several other litterfall components but both potassium and phosphorus contents were extremely low. Potassium and phosphorus are readily soluble in litter (Curlin, 1970) and the persistence of larger branches on trees for longer periods and the delayed fall of boles following death would permit intensive leaching of nutrients from these components in the Southern Appalachians.

The Ca content of foliage litterfall in spruce-fir stands was similar to concentrations in litterfall from a spruce-fir stand in the Smokies (Shanks, et al., 1961) but concentration of calcium in yellow birch stands and of other nutrients in both coniferous and deciduous stands were higher than in comparable high elevation forests of the Smokies. Differences between concentrations of potassium
and magnesium in foliage litterfall were most apparent, often exceeding respective concentrations from Great Smoky Mountain forests by factors of two or more. Concentrations of Ca and P of beech foliage litter from the Northeast were similar, but K and Mg contents lower than contents of yellow birch foliage litter from the study area (Lutz and Chandler, 1946). Compared with other non-beech species, nutrient contents of yellow birch foliage, particularly Ca and K, were low (Lutz and Chandler, 1946; Scott, 1955). Fewer data concerning the nutrient contents of non-foliage litter are available but results from beech and spruce-fir stands in the Smokies (Shanks, et al., 1961) indicate, with only limited exceptions, that nutrient concentrations were low compared to respective components in yellow birch and spruce-fir stands of the study area. Lower concentrations in litter from the Smokies could have resulted from species difference between stands and more intensive leaching during longer intervals between litter collections (two-three months in the Smokies).

The sum of nutrients in total litterfall was ca 177 kg/ha/yr in spruce-fir stands, 112 kg/ha/yr in mature yellow birch, and 87 kg/ha/yr in immature yellow birch stands (Table XLII). In spruce-fir stands, Ca was present in greatest quantities followed in decreasing order by K, Mg, and P. In both types of yellow birch stands, the
### TABLE XLII

**NUTRIENTS IN ANNUAL LITTERFALL IN SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS**

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature Growth (n=4)</th>
<th>Mature (n=2)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance a</td>
<td>Mean</td>
</tr>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual litterfall, kg/ha</td>
<td>88.56</td>
<td>174.31</td>
<td>NS</td>
<td>44.65</td>
</tr>
<tr>
<td>Boles and branches, kg/ha</td>
<td>61.38</td>
<td>173.28</td>
<td>NS</td>
<td>2.20</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>79.3</td>
<td>33.4</td>
<td>4</td>
<td>9.6</td>
</tr>
<tr>
<td>Leaf litterfall, kg/ha</td>
<td>27.18</td>
<td>8.35</td>
<td>4</td>
<td>42.46</td>
</tr>
<tr>
<td>Reproductive components, kg/ha</td>
<td>2.63</td>
<td>1.38</td>
<td>3</td>
<td>0.83</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>9.50</td>
<td>4.30</td>
<td>4</td>
<td>2.6</td>
</tr>
<tr>
<td>Deciduous leaves, kg/ha</td>
<td>2.97</td>
<td>2.53</td>
<td>3</td>
<td>35.72</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>10.91</td>
<td>8.05</td>
<td>4</td>
<td>79.8</td>
</tr>
<tr>
<td>Needles, kg/ha</td>
<td>17.50</td>
<td>6.10</td>
<td>4</td>
<td>3.18</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>64.23</td>
<td>9.48</td>
<td>4</td>
<td>10.6</td>
</tr>
<tr>
<td>Twigs and bark, kg/ha</td>
<td>4.08</td>
<td>2.07</td>
<td>NS</td>
<td>2.73</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>15.36</td>
<td>6.09</td>
<td>3</td>
<td>6.9</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>20.7</td>
<td>33.4</td>
<td>4</td>
<td>90.4</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual litterfall, kg/ha</td>
<td>51.43</td>
<td>92.19</td>
<td>NS</td>
<td>16.6</td>
</tr>
<tr>
<td>Boles and branches, kg/ha</td>
<td>36.00</td>
<td>92.20</td>
<td>NS</td>
<td>0.32</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>83.5</td>
<td>34.5</td>
<td>4</td>
<td>2.2</td>
</tr>
<tr>
<td>Nutrients</td>
<td>Spruce-Fir (n=14)</td>
<td></td>
<td>Immature Growth (n=4)</td>
<td></td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>-------------------</td>
<td>--------------</td>
<td>----------------------</td>
<td>--------------</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance a</td>
<td>Mean</td>
</tr>
<tr>
<td>Leaf litterfall, kg/ha</td>
<td>15.43</td>
<td>4.84</td>
<td>NS</td>
<td>16.31</td>
</tr>
<tr>
<td>Reproductive components, kg/ha</td>
<td>3.63</td>
<td>2.17</td>
<td>4</td>
<td>0.62</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>22.46</td>
<td>10.61</td>
<td>4</td>
<td>4.1</td>
</tr>
<tr>
<td>Deciduous leaves, kg/ha</td>
<td>0.97</td>
<td>0.55</td>
<td>4</td>
<td>12.84</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>6.65</td>
<td>3.72</td>
<td>4</td>
<td>77.4</td>
</tr>
<tr>
<td>Needles, kg/ha</td>
<td>8.53</td>
<td>2.88</td>
<td>4</td>
<td>1.78</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>56.21</td>
<td>11.76</td>
<td>4</td>
<td>12.0</td>
</tr>
<tr>
<td>Twigs and bark, kg/ha</td>
<td>2.29</td>
<td>1.34</td>
<td>2</td>
<td>1.08</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>14.67</td>
<td>7.55</td>
<td>3</td>
<td>6.6</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>16.6</td>
<td>34.3</td>
<td>4</td>
<td>97.8</td>
</tr>
</tbody>
</table>

Magnesium

<p>|                                   | Mean   | STD    | Significance |
| Annual litterfall, kg/ha          | 29.03  | 41.30  | NS           |
| Boles and branches, kg/ha         | 17.16  | 40.87  | NS           |
| Per cent of annual total          | 77.1   | 32.7   | 4            |
| Leaf litterfall, kg/ha            | 11.86  | 3.47   | 3            |
| Reproductive components, kg/ha    | 1.69   | 0.82   | 4            |
| Per cent of leaf litter           | 13.85  | 4.97   | 4            |
| Deciduous leaves, kg/ha           | 1.44   | 1.34   | 4            |
| Per cent of leaf litter           | 11.61  | 8.87   | 4            |
| Needles, kg/ha                    | 7.09   | 2.16   | 4            |
| Per cent of leaf litter           | 60.77  | 10.92  | 4            |</p>
<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Yellow Birch</th>
<th>Immature Growth (n=4)</th>
<th>Mature (n=2)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significance</td>
<td>Mean</td>
<td>STD</td>
</tr>
<tr>
<td>Twigs and bark, kg/ha</td>
<td>1.65</td>
<td>0.83</td>
<td>4</td>
<td>0.65</td>
<td>0.46</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>13.77</td>
<td>6.30</td>
<td>4</td>
<td>3.4</td>
<td>2.4</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>25.7</td>
<td>32.5</td>
<td>4</td>
<td>93.8</td>
<td>4.6</td>
</tr>
<tr>
<td><strong>Phosphorus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual litterfall, kg/ha</td>
<td>8.30</td>
<td>12.78</td>
<td>NS</td>
<td>4.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Boles and branches, kg/ha</td>
<td>3.71</td>
<td>12.78</td>
<td>NS</td>
<td>0.06</td>
<td>0.04</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>89.0</td>
<td>27.4</td>
<td>NS</td>
<td>1.6</td>
<td>1.1</td>
</tr>
<tr>
<td>Leaf litterfall, kg/ha</td>
<td>4.59</td>
<td>1.87</td>
<td>NS</td>
<td>3.89</td>
<td>0.97</td>
</tr>
<tr>
<td>Reproductive components,</td>
<td>1.17</td>
<td>0.66</td>
<td>4</td>
<td>0.18</td>
<td>0.12</td>
</tr>
<tr>
<td>kg/ha</td>
<td>24.20</td>
<td>8.47</td>
<td>4</td>
<td>4.2</td>
<td>2.3</td>
</tr>
<tr>
<td>Deciduous leaves, kg/ha</td>
<td>0.33</td>
<td>0.23</td>
<td>4</td>
<td>2.96</td>
<td>0.54</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>7.30</td>
<td>4.69</td>
<td>4</td>
<td>78.0</td>
<td>15.7</td>
</tr>
<tr>
<td>Needles, kg/ha</td>
<td>2.55</td>
<td>1.05</td>
<td>4</td>
<td>0.52</td>
<td>0.60</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>56.60</td>
<td>7.28</td>
<td>4</td>
<td>11.9</td>
<td>14.3</td>
</tr>
<tr>
<td>Twigs and bark, kg/ha</td>
<td>0.53</td>
<td>0.27</td>
<td>3</td>
<td>0.23</td>
<td>0.11</td>
</tr>
<tr>
<td>Per cent of leaf litter</td>
<td>11.90</td>
<td>5.08</td>
<td>3</td>
<td>5.9</td>
<td>1.5</td>
</tr>
<tr>
<td>Per cent of annual total</td>
<td>11.7</td>
<td>27.3</td>
<td>4</td>
<td>98.4</td>
<td>1.1</td>
</tr>
</tbody>
</table>

*NS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.
sequence of K and Mg was reversed so that nutrient quantities in litter were Ca > Mg > K > P. Litterfall in spruce-fir stands contained larger quantities of each nutrient than either type of yellow birch stand but differences were not statistically significant. Deciduous litterfall generally contains larger quantities of nutrients (Chandler, 1941, 1944; Scott, 1955) and the departure from this trend in the present study as well as lack of significance among coniferous and deciduous stands resulted in part from difficulties in measuring bole and large branch litterfall. In spruce-fir stands the large quantities of nutrients indicated in these components resulted from windthrow of one large Fraser fir tree into one of the litter sampling quadrats. In general, however, this litterfall component was highly variable, and more intensive sampling over longer time periods was needed for accurate estimates. In spruce-fir stands 77 per cent and more of the annual litterfall nutrient content was indicated to be in boles and large branches due to these erratic results. In both mature and immature yellow birch stands these components were relatively unimportant in nutrient dynamics of litterfall and contributed only between 5 and 10 per cent of the litterfall Ca and Mg and 4 per cent or less of K and P.

Annual leaf litterfall, consisting of deciduous leaves, needles, reproductive components, and twigs and bark,
in spruce-fir stands contained from 9 to 39 kg/ha Ca, 9 to 25 kg/ha K, 5 to 16 kg/ha Mg, and 1.6 to 7.3 kg/ha P and means in these stands (Table XLII, page 261) generally exceeded nutrient levels in litterfall in spruce-fir stands in the Smokies (Shanks, et al., 1961), and eastern Canada (Weetman and Timmer, 1967; Damman, 1971). With the exception of P, annual leaf litterfall of yellow birch stands contained statistically significantly larger quantities of nutrients than coniferous stands. In birch stands, leaf litterfall contained 1 kg per 40-60 kg litter as compared with 1 kg per 90-100 kg litter in coniferous stands. This is the general relationship between nutrients in litterfall of hardwood and coniferous stands (Lutz and Chandler, 1946).

In yellow birch stands of the study area, Ca in annual leaf litterfall varied from 25 to 73 kg/ha, K, 12 to 22 kg/ha, Mg, 18-26 kg/ha, and P, 3 to 5 kg/ha; quantities in litter of mature and immature stands were similar. Potassium and P quantities were similar to quantities in leaf litterfall in a beech forest in the Smokies (Shanks, et al., 1961) and northeastern deciduous stands (Chandler, 1941, 1944; Scott, 1955) but quantities of Ca and Mg in yellow birch of the study area exceeded levels in other studies.

The relative contribution of each litterfall component to the total quantity of nutrients in leaf litterfall varied
between types of stands and among components within ecosystems. Also, litterfall components frequently played different roles in dry-matter (Table XV, page 160) and nutrient dynamics (Table XLII, page 261) of leaf litterfall. In yellow birch stands, deciduous leaves contained from 80 to 83 per cent of the Ca and Mg and 73 to 75 per cent of the P and K, but only 56 per cent of the dry matter. Deciduous leaves represented only 10 per cent of the dry matter but contributed more than 20 per cent of the Ca in leaf litterfall in spruce-fir stands. The significance of even small populations of deciduous trees in the nutrient dynamics of coniferous stands is suggested. Needles contained small quantities of both dry matter and nutrients in deciduous stands but were the major contributors of litterfall nutrients in coniferous stands. There they made up 67 per cent of the dry matter and contained 56 to 64 per cent of the nutrients in litterfall. In yellow birch stands, needles made up 10 per cent of the dry matter and contained between 7 and 8 per cent of the nutrients. In each system, needles were more important in dry-matter than nutrient dynamics. The relationship of reproductive components to litterfall nutrient dynamics was markedly different between ecosystems. In yellow birch stands, reproductive components constituted ca 10 per cent of the dry matter but only 3 to 4 per cent of each of Ca, K,
and Mg and 7.5 per cent of the P; in spruce-fir stands, while reproductive components contained 14 per cent of the litterfall dry matter and 9 to 13 per cent of the Ca and Mg, they contained 22 per cent or more of the K and 24 per cent of the P. This was attributed to the interaction of high production and relatively high concentrations of these nutrients in reproductive structures. These results indicate that fluctuations in both relative and absolute quantities of nutrients in annual litterfall would be associated with different phases of seed production cycles in these stands. The relationship of twig and bark components to both dry matter and nutrient dynamics of litterfall was similar in some cases (such as dry matter and P of leaf litterfall) but usually these components contributed a much larger proportion of the total dry-matter than nutrient content of litterfall.

Rodin and Basilevic (1967) concluded that litterfall was equivalent to 3 to 5 per cent of the nutrients in the plant biomass but much higher proportions occurred in stands of the study area. In spruce-fir stands nutrients in leaf litterfall equalled ca 19 per cent of the Ca, 8 per cent of K, 15 per cent of Mg, and 12 per cent of P in above-ground plant biomass (Cf. Tables XXXIX, page 243, and XLII, page 261). Litterfall Ca in mature yellow birch and P in both mature and immature yellow birch stands constituted
proportions of respective nutrient pools similar to those in coniferous stands. Calcium in leaf litterfall of immature yellow birch was only 11 per cent of the Ca pool; leaf litterfall K was 14 and 16 per cent and Mg 31 and 40 per cent, respectively, of vegetational nutrient pools in immature and mature yellow birch stands. The results showed that the role of litterfall in nutrient dynamics varied both with stand type and among nutrients. In some deciduous stands, the ratio of litterfall nutrients to plant biomass nutrients may exceed similar ratios in coniferous stands by a factor of two (Rodin and Basilevic, 1967); this relationship between deciduous and coniferous stands of the present study was typical only for two nutrients, K and Mg (Table XLII, page 261).

Quantities of nutrients in leaf litterfall generally were large in relation to quantities retained annually in perennial components of trees (Cf. Tables XLII and XL, page 251), in agreement with the usual trends (Rodin and Basilevic, 1967). Comparison of rates in stands of the present study, however, indicated that differences occurred both among nutrients within stands and between stand types when specific nutrients were considered. The greatest differences between nutrients in leaf litterfall and retention was for Ca where ratios (nutrients in leaf litterfall/nutrients retained) were 7.9, 6.0, and 12.2 kg/kg
in spruce-fir, immature yellow birch, and mature yellow birch, respectively. Other ratios were Mg 5.0, 8.7, and 3.6; K 2.8, 4.4, and 3.3; and P 3.8, 3.9, and 1.8, respectively. None of these suggest that quantities of nutrients retained annually in perennial components approaches quantities in annual litterfall as has been reported in some European beech stands (Duvigneaud and Denaeyer-DeSmet, 1970).

**Nutrient Relationships of the Forest Floor**

Concentrations of nutrients in forest floor 01 horizons (Table XLII, page 261) formed two patterns in comparison with nutrient concentrations of leaf litterfall components. In spruce-fir stands, Ca, K, and Mg and in all yellow birch stands K concentrations of 01 horizons were lower than respective concentrations in major leaf litterfall components. Conversely, P concentrations in 01 horizons of both spruce-fir and yellow birch, and Ca and Mg concentrations in 01 horizons of yellow birch stands were similar to concentration of respective nutrients in major leaf litterfall components. Calcium concentrations may increase with decay and the concentrations of both Ca and Mg in the forest floor may exceed levels in litterfall components (Kittredge, 1948; Rodin and Basilevic, 1967); however, the more usual trend in many coniferous and deciduous forests seems to be toward a
reduction in concentrations of Ca, K, Mg, and P in 01 horizons in comparison with litterfall (Rodin and Basilevic, 1967). With the exception of Ca, nutrient concentrations in bole and branch litter of the forest floor were also lower than respective concentrations in bole and branch litterfall, but relative concentrations remained the same.

In both coniferous and deciduous stands, concentrations of K and P in bole and branch litter were especially low in comparison with the concentrations in other forest floor horizons.

Nutrient concentrations in 02 horizons also formed two distinctive patterns when compared with concentrations in 01 horizons (Table XLIII). Concentrations of both Ca and Mg in 02 horizons were lower, often being only 40 per cent to 50 per cent of concentrations in 01 horizons. The reverse characterized P and K concentrations which often exceeded concentrations in 01 horizons by factors of 1.4 and more. In comparison, these concentrations approached or were within the range of nutrient concentrations of leaf litterfall components (Table XLI, page 257). Wolfe (1967) and McGinnis (1958) found trends similar to those of Ca and K concentrations between upper and lower litter horizons under both spruce-fir and beech in the Smokies; Mg concentrations, however, tended to remain more or less constant, or to increase with depth (Wolfe, 1967).
TABLE XLIII

NUTRIENT CONCENTRATIONS AND pH OF FOREST FLOOR LITTER IN SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS

<table>
<thead>
<tr>
<th>Chemical Properties</th>
<th>Spruce-Fir Horizon</th>
<th>Yellow Birch Horizon</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>bo and br&lt;sup&gt;a&lt;/sup&gt;</td>
<td>01</td>
</tr>
<tr>
<td>pH, water&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median</td>
<td>--</td>
<td>3.7</td>
</tr>
<tr>
<td>Range</td>
<td>3.2-4.1</td>
<td>3.0-3.7</td>
</tr>
<tr>
<td>n</td>
<td>(28)</td>
<td>(30)</td>
</tr>
<tr>
<td>pH, KCl&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Median</td>
<td>--</td>
<td>3.4</td>
</tr>
<tr>
<td>Range</td>
<td>2.9-3.8</td>
<td>2.8-3.2</td>
</tr>
<tr>
<td>n</td>
<td>(28)</td>
<td>(29)</td>
</tr>
<tr>
<td>Calcium (ppm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>4972</td>
<td>3292</td>
</tr>
<tr>
<td>S.E.</td>
<td>924</td>
<td>198</td>
</tr>
<tr>
<td>n</td>
<td>(8)</td>
<td>(26)</td>
</tr>
<tr>
<td>Potassium (ppm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>615</td>
<td>2274</td>
</tr>
<tr>
<td>S.E.</td>
<td>26</td>
<td>91</td>
</tr>
<tr>
<td>n</td>
<td>(8)</td>
<td>(26)</td>
</tr>
<tr>
<td>Magnesium (ppm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>3507</td>
<td>1555</td>
</tr>
<tr>
<td>S.E.</td>
<td>374</td>
<td>105</td>
</tr>
<tr>
<td>n</td>
<td>(8)</td>
<td>(26)</td>
</tr>
<tr>
<td>Phosphorus (ppm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>88</td>
<td>967</td>
</tr>
<tr>
<td>S.E.</td>
<td>18</td>
<td>52</td>
</tr>
<tr>
<td>n</td>
<td>(8)</td>
<td>(26)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Bole and branch litter ≥ 2.54 cm diameter. Smaller boles and branches were sampled with 01 horizon.

<sup>b</sup>1:1 solutions.
Considerable variation in relative concentrations of these nutrients between forest floor horizons is evident from other studies (Ovington, 1958; Lutz and Chandler, 1946; Wooldridge, 1961) which apparently results from differences in pH and nutrient concentrations of litter produced by different species and perhaps differences between soils from site to site. These studies also showed that concentrations of nutrients in litter horizons are highly variable from stand to stand and among stands of different species composition.

Calcium and P concentrations found in this study were generally within the ranges reported in other stands; concentrations of K and Mg, however, were generally higher, including litter in beech and spruce-fir stands in the Smokies (McGinnis, 1958; Wolfe, 1967).

Concentrations of nutrients would increase in forest floor horizons as organic matter decayed providing nutrients upon release were absorbed onto exchange site of mineral or organic colloids or were otherwise immobilized. High acidity especially of the 02 horizons (Table XLIII, page 271) together with high annual precipitation provides intense leaching and may account for lower concentrations of Ca and Mg in 02 as compared with 01 horizons. Several factors either singly or in combination may have resulted in increased concentrations of P in 02 horizons. These include
temporary immobilization of inorganic P by microbes (Buckman and Brady, 1969) and occurrence of P in organic forms (Black, 1968), combination with aluminum known to be readily available in similar soils (Wolfe, 1967), or iron at low pH (Black, 1968); each of these would greatly decrease the solubility P and allow accumulation in O2 horizons as organic matter decayed.

Under the extremely acidic conditions characterizing the O2 horizons, intense leaching of K leading to lower concentrations might be expected rather than the higher concentrations which were found. Organic matter determinations indicated varying degrees of mixing of organic matter in O2 horizons with mineral material from below which undoubtedly contained various K bearing minerals (Keith, 1907). Chemical determination of these horizons was for total K, a portion of which may have been derived from primary minerals. Fixation by expanding-layer silicates, apparently present in the soils (Wolfe, 1967; Keith, 1907), of K released (Black, 1968) from organic compounds upon decay may also compensate for leaching losses and permit accumulation in the O2 horizon.

Calcium was the predominant (kg/ha) nutrient in the forest floor of each ecosystem (Table XLIV). Quantities of K exceeded Mg in spruce-fir and mature yellow birch stands while the relationship was reversed in immature yellow
TABLE XLIV

NUTRIENTS OF THE FOREST FLOOR IN SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Yellow Birch</th>
<th>Significancea,b</th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
<th>Significanceb,c</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td></td>
<td>Mean</td>
<td>STD</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>STD</td>
<td></td>
</tr>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>STD</td>
<td></td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>337.62</td>
<td>233.20</td>
<td>NS</td>
<td>407.81</td>
<td>183.66</td>
<td>NS</td>
</tr>
<tr>
<td>Bole and branch litter, kg/ha</td>
<td>97.01</td>
<td>95.24</td>
<td>NS</td>
<td>162.52</td>
<td>177.34</td>
<td>2.14</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>25.17</td>
<td>16.67</td>
<td>NS</td>
<td>33.45</td>
<td>22.90</td>
<td>0.45</td>
</tr>
<tr>
<td>01, kg/ha</td>
<td>139.69</td>
<td>67.52</td>
<td>NS</td>
<td>148.34</td>
<td>55.75</td>
<td>180.95</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>47.53</td>
<td>16.16</td>
<td>NS</td>
<td>39.47</td>
<td>13.14</td>
<td>47.69</td>
</tr>
<tr>
<td>02, kg/ha</td>
<td>100.92</td>
<td>108.34</td>
<td>NS</td>
<td>96.95</td>
<td>24.11</td>
<td>197.89</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>27.30</td>
<td>11.65</td>
<td>NS</td>
<td>27.07</td>
<td>10.41</td>
<td>51.86</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>292.43</td>
<td>168.70</td>
<td>3</td>
<td>139.43</td>
<td>28.10</td>
<td>143.53</td>
</tr>
<tr>
<td>Bole and branch litter, kg/ha</td>
<td>12.00</td>
<td>11.78</td>
<td>NS</td>
<td>25.18</td>
<td>27.48</td>
<td>0.33</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>4.26</td>
<td>3.83</td>
<td>NS</td>
<td>17.65</td>
<td>16.61</td>
<td>0.22</td>
</tr>
<tr>
<td>01, kg/ha</td>
<td>101.93</td>
<td>45.49</td>
<td>4</td>
<td>29.89</td>
<td>5.27</td>
<td>26.32</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>38.48</td>
<td>13.86</td>
<td>3</td>
<td>21.92</td>
<td>4.41</td>
<td>18.14</td>
</tr>
<tr>
<td>02, kg/ha</td>
<td>176.50</td>
<td>147.22</td>
<td>2</td>
<td>84.36</td>
<td>27.78</td>
<td>116.88</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>57.26</td>
<td>13.74</td>
<td>NS</td>
<td>60.44</td>
<td>15.26</td>
<td>81.65</td>
</tr>
</tbody>
</table>
TABLE XLIV (continued)

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Spruce-Fir (n=14)</th>
<th>Immature (n=4)</th>
<th>Yellow Birch</th>
<th>Mature (n=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significancea,b</td>
<td>Mean</td>
</tr>
<tr>
<td>Magnesium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>214.80</td>
<td>110.66</td>
<td>NS</td>
<td>161.80</td>
</tr>
<tr>
<td>Bole and branch litter,</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>kg/ha</td>
<td>68.42</td>
<td>67.18</td>
<td>NS</td>
<td>73.20</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>27.52</td>
<td>18.91</td>
<td>NS</td>
<td>37.33</td>
</tr>
<tr>
<td>01, kg/ha</td>
<td>68.03</td>
<td>28.87</td>
<td>2</td>
<td>42.45</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>36.06</td>
<td>14.52</td>
<td>NS</td>
<td>30.33</td>
</tr>
<tr>
<td>02, kg/ha</td>
<td>78.34</td>
<td>61.51</td>
<td>1</td>
<td>46.14</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>36.42</td>
<td>17.36</td>
<td>NS</td>
<td>32.34</td>
</tr>
<tr>
<td>Phosphorous</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>96.14</td>
<td>37.64</td>
<td>4</td>
<td>44.70</td>
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<tr>
<td>Bole and branch litter,</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>kg/ha</td>
<td>1.72</td>
<td>1.69</td>
<td>NS</td>
<td>5.11</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>1.85</td>
<td>1.71</td>
<td>NS</td>
<td>11.93</td>
</tr>
<tr>
<td>01, kg/ha</td>
<td>41.52</td>
<td>18.76</td>
<td>4</td>
<td>11.74</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>44.51</td>
<td>12.32</td>
<td>4</td>
<td>26.28</td>
</tr>
<tr>
<td>02, kg/ha</td>
<td>52.90</td>
<td>28.34</td>
<td>3</td>
<td>27.85</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>53.64</td>
<td>12.19</td>
<td>NS</td>
<td>61.17</td>
</tr>
</tbody>
</table>

aT-test, significance of difference between means of spruce-fir and immature yellow birch stands.

bNS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.

cT-test, significance of difference between means of immature and mature yellow birch stands.
birch ecosystems, however. Phosphorus quantities were smallest and quantities were only one-third to one-half as great as the next most abundant element. Greater weights of K, P, and Mg were indicated in spruce-fir forest floor in comparison with immature yellow birch stands, although the difference between Mg quantities was not significant. These trends between ecosystems reflect the greater total weight of the forest floor of the spruce-fir ecosystem. Although not significant, a larger quantity of Ca occurred on the forest floor of deciduous stands. Although total forest floor weight was less in these stands, concentration of Ca in all forest floor litter components exceeded concentrations in spruce-fir stands. Some differences between yellow birch ecosystems were also indicated although due to high variance of forest floor weights differences were not significant excepting for P weights which were greatest in mature yellow birch stands.

Comparison of the quantity of each nutrient in the forest floor with the quantity in annual litterfall indicated definite patterns. In immature yellow birch stands, weight of each Ca, K, and Mg, in the forest floor was between 8.5 and 9.5 times the weight in annual leaf litterfall (Cf. Tables XLIV, page 274, and XLII, page 261). Slightly smaller accumulations of these nutrients were in forest floors relative to leaf litterfall nutrients in
mature stands where ratios were between 5.9 and 8.3. A much larger nutrient accumulation in the forest floor relative to annual leaf litterfall characterized spruce-fir stands. There, forest floor Ca pools exceeded Ca in leaf litterfall by a factor of 12.4 times. Even greater differences existed between K, Mg, and P quantities where respective ratios were 19.0, 18.0, and 20.9. The accumulation of P in relation to litterfall in the forest floor of mature yellow birch stands (21) was similar to spruce-fir stands; in immature stands, however, the ratio was 12 which was only slightly higher than for other nutrients in this system. Under present litter production, the accumulation of nutrients in the forest floor may represent as few as six or as many as twenty-one years addition of nutrients through leaf litterfall, depending on the specific nutrient and ecosystem.

The largest proportion of the P in the forest floor of all systems was in the 02 horizon and the proportion was especially large in mature yellow birch stands (Table XLIV, page 274). This in part was due to the greater biomass of this horizon in comparison with the immature yellow birch ecosystem but higher concentrations of P in litter components also occurred (1406 ppm P, mature compared with 1070 ppm P, immature). Generally the 02 horizon in these stands was only developed beneath mats of *Hylocomium*
which were restricted to tops of large boulders. Data from this and other studies (Tamm, 1953; Weetman and Timmer, 1967) suggest that P concentrations in litter of this species may exceed concentrations in other litter-fall components. This trend supports Ovington's (1958) conclusion that nutrient characteristics of the forest floor are primarily determined by the nutrient content of vegetation. Further differences may have resulted in that 02 horizons in other yellow birch stands were in contact with acid mineral soil rather than boulders, thus allowing for different rates in movement of nutrients between horizons.

Similar patterns characterized the distribution of K which was present in least quantities in upper horizons and largest quantities in 02 horizons. As with P, the accumulation of K in 02 horizons was greatest in mature yellow birch stands. Weight of each K and P in the 02 horizon exceeded the combined weight of the respective nutrient in bole and branch litter and 01 horizon. This relationship seems to characterize many forests (Rodin and Basilevic, 1967). Significant differences were also indicated between ecosystems in the distribution of nutrients among forest floor components. For example 01 and 02 horizons of the spruce-fir ecosystem each contained greater relative and absolute quantities of P and K; 02
horizons of mature yellow birch stands contained larger quantities of K and P than immature stands.

The distributional patterns of Ca and Mg in the forest floor were contrary to the foregoing trends. Generally the 01 horizon contained an equal or a greater quantity of each nutrient than the 02 horizon (Table XLIV, page 274). Calcium and Mg weights in 01 and 02 horizons of mature yellow birch stands were exceptions, however. These stands were distinctive in that less than 1 per cent of the forest floor pool of each nutrient was in bole and large branch components. This reflects both low dry-matter standing crop and low nutrient concentrations of these components. The distribution of Ca among forest floor components did not differ significantly when spruce-fir and immature yellow birch stands were compared, although some differences occurred between immature and mature stands with respect to distribution of both Ca and other nutrients. Forest floor horizons of mature usually contained both larger absolute and relative quantities of nutrients.

In comparison with other temperate zone forests, the total quantities of various nutrients in the forest floor of spruce-fir and yellow birch ecosystems were generally within the broad ranges reported by others. Notable exceptions were much larger quantities of Mg and P
in spruce-fir stands and large quantities of Ca in yellow
birch stands, in comparison with other beech and birch
stands. In a red spruce-balsam fir stand in Canada (Weet-
man and Webber, 1971) where the forest floor weight was
almost identical to average spruce-Fraser fir forests of
the study area, Ca weight was greater but K and P weights
each were only 54 per cent as great; in the Canadian stand,
Mg quantities were less than P and only 17 per cent as great
as in the present study area. Larger supplies of Ca but
smaller quantities of each of the other nutrients also
characterized a spruce-fir stand in the Smokies (Shanks,
et al., 1961). Yellow birch stands compared with beech in
the Smokies contained smaller amounts of forest floor Ca
and K, similar amounts of P but much larger quantities of
Mg. Comparatively low amounts of Ca and very high amounts
of Mg in the forest floors of both yellow birch and spruce-
fir ecosystems seem to be a major factor distinguishing
these from other birch and spruce-fir ecosystems.

Soil Nutrients

Low concentrations of each of the four nutrients
were indicated in soils of spruce-fir (Table XLV) and yellow
birch (Table XLVI) ecosystems. In upper horizons (A1
through A3) in spruce-fir stands, relative concentrations
(ppm) of nutrients were Ca > K > Mg > P; in lower horizons
K exceeded Ca concentrations. In all yellow birch stands,
TABLE XLV

SELECTED CHEMICAL PROPERTIES OF SOILS IN THE SPRUCE-FIR ECOSYSTEM

<table>
<thead>
<tr>
<th>Chemical Properties</th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
<th>B1</th>
<th>B2</th>
<th>B3</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH, 1:1 soil/water</td>
<td></td>
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</tr>
<tr>
<td>Mean</td>
<td>3.8</td>
<td>3.8</td>
<td>4.0</td>
<td>4.4</td>
<td>4.4</td>
<td>4.5</td>
<td>4.7</td>
</tr>
<tr>
<td>Range</td>
<td>3.5-4.4</td>
<td>3.6-4.4</td>
<td>3.6-4.5</td>
<td>3.9-4.6</td>
<td>4.0-4.6</td>
<td>4.1-4.9</td>
<td>4.3-5.2</td>
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<tr>
<td>n</td>
<td>(16)</td>
<td>(4)</td>
<td>(4)</td>
<td>(5)</td>
<td>(4)</td>
<td>(20)</td>
<td>(20)</td>
</tr>
<tr>
<td>pH, 1:1 soil/0.1M KCl solution</td>
<td></td>
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<td></td>
<td></td>
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<td>3.2</td>
<td>3.8</td>
<td>4.0</td>
<td>3.6</td>
<td>3.9</td>
<td>4.2</td>
</tr>
<tr>
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<td>3.2-4.1</td>
<td>3.8-4.2</td>
<td>3.4-3.7</td>
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<td>3.6-4.4</td>
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<td>(4)</td>
<td>(4)</td>
<td>(5)</td>
<td>(4)</td>
<td>(20)</td>
<td>(20)</td>
</tr>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Mean (meq/100 g soil)</td>
<td>0.46</td>
<td>0.77</td>
<td>0.43</td>
<td>0.06</td>
<td>0.31</td>
<td>0.07</td>
<td>0.06</td>
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<td>0.14</td>
<td>0.37</td>
<td>0.26</td>
<td>0.04</td>
<td>0.12</td>
<td>0.02</td>
<td>0.01</td>
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<tr>
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<td>(6)</td>
<td>(5)</td>
<td>(3)</td>
<td>(20)</td>
<td>(22)</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Mean (meq/100 g soil)</td>
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<td>0.40</td>
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<td>0.04</td>
<td>0.25</td>
<td>0.07</td>
<td>0.06</td>
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<td>0.02</td>
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<td>(6)</td>
<td>(6)</td>
<td>(3)</td>
<td>(19)</td>
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<td>A2</td>
<td>A3</td>
<td>B1</td>
<td>B2</td>
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<td>0.17</td>
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<td>0.04</td>
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<td>3.60</td>
<td>4.79</td>
<td>5.73</td>
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<tr>
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<td>2.74</td>
<td>2.56</td>
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<tr>
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<td>7.82</td>
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<td>28.03</td>
<td>10.18</td>
<td>7.89</td>
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<td>3.31</td>
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<td>(6)</td>
<td>(3)</td>
<td>(20)</td>
<td>(20)</td>
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282
SELECTED CHEMICAL PROPERTIES OF SOILS IN THE YELLOW BIRCH ECOSYSTEM

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<th>Chemical Properties</th>
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<th>B1</th>
<th>B2</th>
<th>B3</th>
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<td><strong>pH, 1:1 soil/water solution</strong></td>
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<td>4.6</td>
<td>4.7</td>
</tr>
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<td>(2)</td>
<td>(4)</td>
<td>(7)</td>
<td>(4)</td>
</tr>
<tr>
<td><strong>pH, 1:1 soil/0.1N KCl solution</strong></td>
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</tr>
<tr>
<td>Median</td>
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<td>4.0</td>
<td>4.2</td>
<td>4.0</td>
<td>4.3</td>
</tr>
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<td>3.9-4.2</td>
<td>4.0-4.5</td>
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<td>(2)</td>
<td>(4)</td>
<td>(7)</td>
<td>(4)</td>
</tr>
<tr>
<td><strong>Calcium</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (meq/100 g soil)</td>
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<td>0.14</td>
<td>0.07</td>
<td>0.12</td>
<td>0.08</td>
</tr>
<tr>
<td>S.E.</td>
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<td>0.001</td>
<td>0.04</td>
<td>0.02</td>
</tr>
<tr>
<td>n</td>
<td>(5)</td>
<td>(1)</td>
<td>(3)</td>
<td>(7)</td>
<td>(3)</td>
</tr>
<tr>
<td><strong>Potassium</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (meq/100 g soil)</td>
<td>0.32</td>
<td>0.17</td>
<td>0.12</td>
<td>0.12</td>
<td>0.06</td>
</tr>
<tr>
<td>S.E.</td>
<td>0.07</td>
<td>-</td>
<td>0.001</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>n</td>
<td>(5)</td>
<td>(1)</td>
<td>(3)</td>
<td>(7)</td>
<td>(3)</td>
</tr>
<tr>
<td><strong>Magnesium</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Mean (meq/100 g soil)</td>
<td>0.31</td>
<td>0.13</td>
<td>0.12</td>
<td>0.09</td>
<td>0.02</td>
</tr>
<tr>
<td>S.E.</td>
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<td>-</td>
<td>0.12</td>
<td>0.03</td>
<td>0.003</td>
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<tr>
<td>n</td>
<td>(5)</td>
<td>(1)</td>
<td>(3)</td>
<td>(7)</td>
<td>(3)</td>
</tr>
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</table>
### TABLE XLVI (continued)

<table>
<thead>
<tr>
<th>Chemical Properties</th>
<th>A1</th>
<th>A3</th>
<th>B1</th>
<th>B2</th>
<th>B3</th>
</tr>
</thead>
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<tr>
<td><strong>Phosphorus</strong></td>
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<td></td>
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</tr>
<tr>
<td>Mean (ppm)</td>
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<td>4.65</td>
<td>5.54</td>
<td>7.10</td>
<td>8.21</td>
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<tr>
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<td>2.90</td>
<td>1.33</td>
<td>2.03</td>
<td>2.17</td>
<td>3.47</td>
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<tr>
<td>n</td>
<td>(4)</td>
<td>(2)</td>
<td>(4)</td>
<td>(5)</td>
<td>(4)</td>
</tr>
<tr>
<td><strong>C.E.C.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (meq/100 g)</td>
<td>20.11</td>
<td>23.16</td>
<td>20.34</td>
<td>20.94</td>
<td>23.97</td>
</tr>
<tr>
<td>S.E.</td>
<td>4.16</td>
<td>-</td>
<td>4.47</td>
<td>3.49</td>
<td>10.44</td>
</tr>
<tr>
<td>n</td>
<td>(5)</td>
<td>(1)</td>
<td>(3)</td>
<td>(7)</td>
<td>(3)</td>
</tr>
<tr>
<td><strong>Base saturation</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Percent</td>
<td>5.94</td>
<td>1.86</td>
<td>1.65</td>
<td>1.78</td>
<td>0.87</td>
</tr>
<tr>
<td>S.E.</td>
<td>1.17</td>
<td>-</td>
<td>0.46</td>
<td>0.44</td>
<td>0.21</td>
</tr>
<tr>
<td>n</td>
<td>(5)</td>
<td>(1)</td>
<td>(3)</td>
<td>(7)</td>
<td>(3)</td>
</tr>
</tbody>
</table>
K (ppm) was most abundant nutrient in each horizon; an additional difference was that P (ppm) exceeded Mg concentrations in B2 and B3 horizons.

Comparison of these concentrations in terms of milliequivalents of extractable nutrients per 100 grams of soil (Tables XLV, page 281 and XLVI, page 283) showed that in spruce-fir stands, Ca exceeded K in upper horizons but concentrations were similar in lower horizons. Although Mg concentrations exceeded K in upper horizons (A1 through A3), K generally was more abundant than Mg in lower horizons; this relationship in lower horizons is the reverse of conditions in soils of spruce-fir stands in the Smokies (Wolfe, 1967). In soils of yellow birch stands, extractable K generally exceeded levels of both Ca and Mg. Concentrations of nutrients in soils of contrasting ecosystems in the Balsam Mountains and Smokies (Wolfe, 1967; McGinnis, 1958), as well generally showed little difference. With the exception of K, levels of extractable soil nutrients were somewhat lower than respective levels in the Smokies (Wolfe, 1967) but K levels were very similar between soils of the two areas. This caused K levels relative to other soil nutrients in the Balsam Mountains to appear high, a relationship which may reflect a difference in parent materials between the study area and those of the Smokies. Other chemical properties of the soils of the Balsam and
Great Smoky Mountains were similar, including pH, cation exchange capacity, and base saturation (per cent) (McGinnis, 1958; McCracken, et al., 1962; Wolfe, 1967).

In spruce-fir and yellow birch ecosystems of the study area, pH was lowest in the 02 horizon and gradually increased with increasing depth; although pH of upper horizons of soils in yellow birch ecosystems was higher than in spruce-fir soils, all soils were extremely acid and in deepest horizons, pH values were similar between systems. High acidity of these soils reflected in very low base saturation; again with the possible exceptions of A1 and B3 horizons, little difference was apparent between soils of the ecosystems (Tables XLV, page 281, and XLVI, page 283).

High acidity together with certain physical properties (Tables XLVII and XLVIII) explain the low nutrient status of soils of the spruce-fir and yellow birch ecosystems. Soils contained a very high percentage of sand and low percentage of clay; most horizons were sandy loams; clay content was somewhat higher in soils of yellow birch stands but the cation exchange capacity of all soils would be attributed primarily to organic matter content of soils with most exchange sites occupied by either hydrogen or aluminum. These soils were somewhat coarser in texture than those of the Smokies (Wolfe, 1967) which may account
### TABLE XLVII

SELECTED PHYSICAL PROPERTIES OF SOILS IN THE SPRUCE–FIR ECOSYSTEM

<table>
<thead>
<tr>
<th>Physical Properties</th>
<th>A1</th>
<th>A2</th>
<th>A3</th>
<th>B1</th>
<th>B2ir</th>
<th>B2</th>
<th>B3</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Thickness</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Mean (cm)</td>
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<td>9.7</td>
<td>9.3</td>
<td>18.0</td>
<td>9.1</td>
<td>19.4</td>
<td>31.3</td>
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</tr>
<tr>
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<td>1.5</td>
<td>4.0</td>
<td>2.3</td>
<td>4.6</td>
<td>1.9</td>
<td>2.4</td>
<td>3.6</td>
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</tr>
<tr>
<td>n</td>
<td>(16)</td>
<td>(3 )</td>
<td>(5 )</td>
<td>(3 )</td>
<td>(3 )</td>
<td>(18)</td>
<td>(16)</td>
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</tr>
<tr>
<td><strong>Bulk density</strong></td>
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</tr>
<tr>
<td>Mean (g/cm³)</td>
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<td>0.86</td>
<td>1.09</td>
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<td>0.09</td>
<td>0.23</td>
<td>0.10</td>
<td>-</td>
<td>-</td>
<td>0.04</td>
<td>0.04</td>
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<tr>
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<td>(3 )</td>
<td>(3 )</td>
<td>(8 )</td>
<td>(2 )</td>
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</tr>
<tr>
<td>Mean (per cent)</td>
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<td>0.0</td>
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<td>30.09</td>
<td>35.00</td>
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<td>-</td>
<td>3.70</td>
<td>5.53</td>
<td>11.83</td>
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<td>(5 )</td>
<td>(20)</td>
<td>(22)</td>
<td>(5 )</td>
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<td><strong>Fragments, &gt; 2 mm and &lt; 25.4 mm</strong></td>
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</tr>
<tr>
<td>Mean</td>
<td>6.20</td>
<td>1.23</td>
<td>5.44</td>
<td>11.44</td>
<td>-</td>
<td>10.76</td>
<td>13.85</td>
<td>14.09</td>
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<tr>
<td>S.E.</td>
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<td>0.54</td>
<td>1.70</td>
<td>3.10</td>
<td>-</td>
<td>1.59</td>
<td>2.31</td>
<td>1.77</td>
</tr>
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<td>n</td>
<td>(16)</td>
<td>(3 )</td>
<td>(5 )</td>
<td>(5 )</td>
<td>(20)</td>
<td>(22)</td>
<td>(5 )</td>
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<td><strong>Sand</strong></td>
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<td>62.27</td>
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<td>-</td>
<td>11.67</td>
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<td>2.83</td>
<td>2.40</td>
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<td>(2 )</td>
<td>(4 )</td>
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<tr>
<td><strong>Silt</strong></td>
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<td>Mean (per cent)</td>
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<td>-</td>
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<td>14.94</td>
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<td>-</td>
<td>12.14</td>
<td>-</td>
<td>2.06</td>
<td>5.33</td>
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</tr>
<tr>
<td>n</td>
<td>(5 )</td>
<td>(2 )</td>
<td>(4 )</td>
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<td>(4 )</td>
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<tr>
<td><strong>Clay</strong></td>
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<td></td>
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</tr>
<tr>
<td>Mean (per cent)</td>
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<td>-</td>
<td>-</td>
<td>4.06</td>
<td>-</td>
<td>11.17</td>
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<tr>
<td>S.E.</td>
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<td>-</td>
<td>-</td>
<td>0.48</td>
<td>-</td>
<td>4.10</td>
<td>1.34</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>(5 )</td>
<td>(2 )</td>
<td>(4 )</td>
<td></td>
<td>(3 )</td>
<td></td>
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</tr>
</tbody>
</table>

*Mean thickness not estimated; samples collected from upper 5 to 38 cm of C horizons.*
<table>
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<th>Physical Properties</th>
<th>A1</th>
<th>A3</th>
<th>B1</th>
<th>B2</th>
<th>B3</th>
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<tr>
<td><strong>Coves Without Block Fill</strong></td>
<td></td>
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<tr>
<td><strong>Thickness</strong></td>
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<td>13.1</td>
<td>8.8</td>
<td>20.0</td>
<td>27.4</td>
</tr>
<tr>
<td>Mean (cm)</td>
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<td>7.9</td>
<td>2.0</td>
<td>4.3</td>
<td>10.2</td>
</tr>
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<td>(5)</td>
<td>(2)</td>
<td>(4)</td>
<td>(5)</td>
<td>(5)</td>
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<tr>
<td><strong>Bulk density</strong></td>
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<td>0.77</td>
<td>0.81</td>
<td>0.99</td>
<td>1.14</td>
</tr>
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<td>0.05</td>
<td>0.04</td>
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<td>(3)</td>
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<td>(3)</td>
</tr>
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<td>10.0</td>
<td>2.5</td>
<td>15.0</td>
<td>23.2</td>
</tr>
<tr>
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<td>2.5</td>
<td>9.5</td>
<td>13.7</td>
</tr>
<tr>
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<td>(5)</td>
<td>(2)</td>
<td>(4)</td>
<td>(5)</td>
<td>(5)</td>
</tr>
<tr>
<td><strong>Fragments, &gt; 2 mm and &lt; 25.4 mm</strong></td>
<td>5.7</td>
<td>3.2</td>
<td>5.8</td>
<td>9.7</td>
<td>9.6</td>
</tr>
<tr>
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<td>0.4</td>
<td>2.2</td>
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<td>3.6</td>
</tr>
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<td>(5)</td>
<td>(2)</td>
<td>(4)</td>
<td>(5)</td>
<td>(5)</td>
</tr>
<tr>
<td><strong>Sand</strong></td>
<td>52.0</td>
<td>42.5</td>
<td>45.9</td>
<td>53.4</td>
<td>59.0</td>
</tr>
<tr>
<td>Mean (per cent)</td>
<td>3.8</td>
<td>10.3</td>
<td>9.0</td>
<td>5.8</td>
<td>1.8</td>
</tr>
<tr>
<td>S.E.</td>
<td>(3)</td>
<td>(2)</td>
<td>(2)</td>
<td>(3)</td>
<td>(3)</td>
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<tr>
<td><strong>Silt</strong></td>
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<td>32.2</td>
<td>40.6</td>
<td>32.0</td>
<td>30.0</td>
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<td>9.4</td>
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<td>1.2</td>
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<td>(2)</td>
<td>(2)</td>
<td>(3)</td>
<td>(3)</td>
</tr>
<tr>
<td><strong>Clay</strong></td>
<td>20.8</td>
<td>25.6</td>
<td>13.4</td>
<td>14.6</td>
<td>11.0</td>
</tr>
<tr>
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<td>0.9</td>
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<td>1.4</td>
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<td>(2)</td>
<td>(3)</td>
<td>(3)</td>
</tr>
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<tr>
<td></td>
<td>A1</td>
<td>A3</td>
<td>B1</td>
<td>B2</td>
<td>B3</td>
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<td>--</td>
<td>15.5</td>
<td>54.5</td>
<td>--</td>
</tr>
<tr>
<td>S.E.</td>
<td>15.8</td>
<td>2.5</td>
<td>13.7</td>
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</tr>
<tr>
<td>n</td>
<td>(5)</td>
<td>(2)</td>
<td>(4)</td>
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<tr>
<td><strong>Bulk density</strong></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Mean (g/cm³)</td>
<td>0.78</td>
<td>--</td>
<td>--</td>
<td>0.99</td>
<td>--</td>
</tr>
<tr>
<td>S.E.</td>
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<td>--</td>
<td>0.00</td>
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<td></td>
</tr>
<tr>
<td>n</td>
<td>(1)</td>
<td></td>
<td>(2)</td>
<td></td>
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</tr>
<tr>
<td><strong>Fragments, &gt; 25.4 mm</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (per cent)</td>
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<td>--</td>
<td>45.0</td>
<td>34.2</td>
<td>--</td>
</tr>
<tr>
<td>S.E.</td>
<td>16.6</td>
<td>5.0</td>
<td>15.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>(5)</td>
<td>(2)</td>
<td>(6)</td>
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<tr>
<td><strong>Fragments, &gt; 2 mm and &lt; 25.4 mm</strong></td>
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</tr>
<tr>
<td>Mean (per cent)</td>
<td>25.3</td>
<td>--</td>
<td>46.2</td>
<td>38.0</td>
<td>--</td>
</tr>
<tr>
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<td>1.3</td>
<td>--</td>
<td>8.2</td>
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<td></td>
</tr>
<tr>
<td>n</td>
<td>(2)</td>
<td></td>
<td>(1)</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td><strong>Sand</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Mean (per cent)</td>
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<td>--</td>
<td>--</td>
<td>75.8</td>
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</tr>
<tr>
<td>S.E.</td>
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<td>--</td>
<td>0.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>(1)</td>
<td></td>
<td>(2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Silt</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (per cent)</td>
<td>14.3</td>
<td>--</td>
<td>--</td>
<td>20.9</td>
<td>--</td>
</tr>
<tr>
<td>S.E.</td>
<td>--</td>
<td>--</td>
<td>0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>(1)</td>
<td></td>
<td>(2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Clay</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (per cent)</td>
<td>20.7</td>
<td>--</td>
<td>--</td>
<td>3.2</td>
<td>--</td>
</tr>
<tr>
<td>S.E.</td>
<td>--</td>
<td>--</td>
<td>0.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>(1)</td>
<td></td>
<td>(2)</td>
<td></td>
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</table>
for the somewhat lower base status of soils in the study area.

The volume of coarse fragments (fragments $\geq 2$ mm) and stones (fragments $\geq 25$ mm) was large and tended to increase with increasing depth in soils of spruce-fir and yellow birch ecosystems which were not located in coves with block valley fill. Volume of stones and coarse fragments was especially high in soils developed in coves with block valley fill and texture of the mineral soil fraction $< 2$ mm was coarser in lower horizons than in corresponding horizons of the other soils. Highest stone volumes in soils in block valley fill were in the upper horizons where volumes were often $\leq 80$ per cent; in some locations within these coves, voids among the large boulders further decreased the volume of mineral soil especially in the upper 60 cm. Both the volume of stones and voids decreased with increasing depth in these soils.

The volume of soil occupied by coarse fragment, stones, or voids is of significance since it is inversely related to the volume of soil minerals in which trees can effectively root. The extremely high volume of boulders in coves with block valley fill would suggest severe restrictions of effective rooting volume; however, study of the morphology of these soils showed that soil horizons were much thicker than respective horizons in other soils (Table XLVIII, page 288) and root development of trees
extended to much greater depths. These factors tended to compensate for the large volume of voids and stones.

Large standard errors (Tables XLV, page 281; XLVI, page 283; XLVII, page 287; and XLVIII, page 288) associated with the means of most physical and chemical properties indicate high variability which is typical of many forest soils (McFee and Stone, 1965; Ike and Clutter, 1968).

Soils similar to the Podzols described by Coile (1938) in areas near the present study were not found; most of the soils resembled those classified as Sols Bruns Acides (McCranken, et al., 1962) or Umbric Dystrochrepts (Wolfe, 1967) in the Smokies. There was some indication of limited development of spodic horizons in the study area but lateral transportation of iron oxides and soil disturbance by creep and windthrow (Wolfe, 1967) apparently contribute to sufficient instability to retard development of more mature soils. Data showing the annual cycle of temperature in soils in the study area at different depths in relation to elevation are given in Appendix C.

Largest soil rooting volumes occurred in immature yellow birch stands and least in mature stands (Table XLIX) but due to high variance within each stand age-class, differences were generally not significant. Within
### TABLE XLIX

WEIGHT, DRY MATTER, AND AVAILABLE CALCIUM, POTASSIUM, MAGNESIUM, AND PHOSPHORUS IN THE EFFECTIVE ROOTING ZONE OF MINERAL SOIL HORIZONS

<table>
<thead>
<tr>
<th>Horizons</th>
<th>Spruce-Fir (n=14)</th>
<th>Yellow Birch</th>
<th>Immature (n=4)</th>
<th>Mature (n=2)</th>
<th>Significancea,c</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>STD</td>
<td>Significancea,b</td>
<td>Mean</td>
<td>STD</td>
</tr>
<tr>
<td>A horizond</td>
<td>Weight of finese, t/ha</td>
<td>928.98</td>
<td>970.81</td>
<td>3</td>
<td>1937.76</td>
</tr>
<tr>
<td></td>
<td>Calcium, kg/ha</td>
<td>58.59</td>
<td>66.40</td>
<td>NS</td>
<td>106.64</td>
</tr>
<tr>
<td></td>
<td>Potassium, kg/ha</td>
<td>50.74</td>
<td>49.62</td>
<td>NS</td>
<td>147.55</td>
</tr>
<tr>
<td></td>
<td>Magnesium, kg/ha</td>
<td>17.90</td>
<td>18.53</td>
<td>NS</td>
<td>44.88</td>
</tr>
<tr>
<td></td>
<td>Phosphorus, kg/ha</td>
<td>4.35</td>
<td>4.72</td>
<td>2</td>
<td>10.41</td>
</tr>
<tr>
<td>B1 horizon</td>
<td>Weight of finese, t/ha</td>
<td>333.64</td>
<td>550.65</td>
<td>NS</td>
<td>900.52</td>
</tr>
<tr>
<td></td>
<td>Calcium, kg/ha</td>
<td>3.70</td>
<td>9.83</td>
<td>NS</td>
<td>4.13</td>
</tr>
<tr>
<td></td>
<td>Potassium, kg/ha</td>
<td>5.63</td>
<td>15.37</td>
<td>NS</td>
<td>12.46</td>
</tr>
<tr>
<td></td>
<td>Magnesium, kg/ha</td>
<td>1.41</td>
<td>3.84</td>
<td>NS</td>
<td>3.26</td>
</tr>
<tr>
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<td>Phosphorus, kg/ha</td>
<td>0.68</td>
<td>1.20</td>
<td>NS</td>
<td>2.62</td>
</tr>
<tr>
<td>B2 horizonf</td>
<td>Weight of finese, t/ha</td>
<td>1553.73</td>
<td>967.38</td>
<td>NS</td>
<td>2392.56</td>
</tr>
<tr>
<td></td>
<td>Calcium, kg/ha</td>
<td>22.23</td>
<td>34.11</td>
<td>NS</td>
<td>37.21</td>
</tr>
<tr>
<td></td>
<td>Potassium, kg/ha</td>
<td>32.24</td>
<td>46.81</td>
<td>NS</td>
<td>69.19</td>
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<tr>
<td></td>
<td>Magnesium, kg/ha</td>
<td>12.80</td>
<td>19.84</td>
<td>NS</td>
<td>16.37</td>
</tr>
<tr>
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<td>Phosphorus, kg/ha</td>
<td>4.38</td>
<td>2.34</td>
<td>NS</td>
<td>10.47</td>
</tr>
</tbody>
</table>
TABLE XLIX (continued)

aNS P < .10; 1 P > .10; 2 P > .05; 3 P > .01; 4 P > .001.

bT-test of difference between means of spruce-fir and immature yellow birch stands.

cT-test of difference between means of immature and mature yellow birch stands.

dIncludes A1, A1 and A3 horizons when present.

eSoil fraction < 2 mm diameter, including organic matter.

fIncludes B2, B21 and B22 horizons when present.
spruce-fir and immature yellow birch ecosystems largest quantities of each nutrient were in A horizons, reflecting both the large amount of soil material present and generally higher nutrient concentrations. In mature yellow birch stands A and B3 horizons contained comparable quantities of nutrients. In all excepting A horizons of spruce-fir stands, K exceeded other nutrients in absolute weight. Other nutrients in order of decreasing weights in other horizons were Ca > Mg > P. One exception was B2 horizons of mature yellow birch stands where P > Mg.

Total extractable Ca in soils of spruce-fir, immature yellow birch and mature yellow birch ecosystems averaged ca 85, 148, and 158 kg/ha, respectively (Table XLIV, page 274). Weights of other nutrients were: K ca 89, 229, and 111; Mg ca 32, 64, and 26; and P ca 9, 24, and 25 kg/ha. These levels of Ca and K in spruce-fir stands were low compared with estimates calculated from McGinnis' (1958) data from the Smokies; however, those were undoubtedly high since I could not correct soil weights for volume of coarse fragments and stones (data not given). Soil nutrient weights in a Canadian red spruce-balsam fir stand (Weetman and Webber, 1971) were similar with Ca weights in soils of the study area being slightly lower and weights of other nutrients being slightly greater. Weights of Ca and K in soils of yellow birch stands were
similar to weights of corresponding nutrients in other beech and birch stands but quantities of Mg and P were lower.

**Distribution of Dry Matter and Nutrients within Ecosystems**

Although variations occurred in the total dry matter and nutrients among ecosystems, variances were high and differences generally were not significant; the only exception was that the total weight of P in immature yellow birch stands was significantly less than in either spruce-fir or mature yellow birch ecosystems (Table L). Differences in absolute quantities, however, may be less important parameters than either circulation rates or distributional patterns of nutrients concerning functional differences between ecosystems (Delecour, 1969). Several distinct differences as well as general trends were evident when distributional patterns of dry matter and nutrients were compared both within each ecosystem and between different ecosystems. In each ecosystem soil was the largest dry matter sink. Biomass of yellow birch stands was lower and where these were on former spruce-fir sites, carry over organic matter may have associated with this distributional pattern. The spruce-fir ecosystem was distinguished by significantly greater proportions of total dry matter in both the vegetation and forest floor than in yellow birch ecosystems.
TABLE L

DISTRIBUTION OF DRY MATTER AND NUTRIENTS WITHIN ECOSYSTEMS

<table>
<thead>
<tr>
<th>Compartment</th>
<th>Spruce-Fir (n=14)</th>
<th>Significance&lt;sup&gt;a,b&lt;/sup&gt;</th>
<th>Yellow Birch</th>
<th>Significance&lt;sup&gt;a,c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Immature (n=4)</td>
<td></td>
</tr>
<tr>
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<td>Mature (n=2)</td>
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<tr>
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</tr>
<tr>
<td></td>
<td>Dry Matter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, t/ha</td>
<td>663.9 (161.8)</td>
<td>NS</td>
<td>618.6 (300.0)</td>
<td>844.7 (293.1)</td>
</tr>
<tr>
<td>Forest floor</td>
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</tr>
<tr>
<td>Per cent of total</td>
<td>27.8 (6.6) NS</td>
<td></td>
<td>19.6 (8.3) NS</td>
<td>19.8 (6.4) NS</td>
</tr>
<tr>
<td>(STD)</td>
<td>4</td>
<td></td>
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<td>NS</td>
</tr>
<tr>
<td>Vegetation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>17.6 (7.0) 2</td>
<td></td>
<td>11.8 (1.1) 2</td>
<td>7.3 (1.3) 2</td>
</tr>
<tr>
<td>(STD)</td>
<td>4</td>
<td></td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Per cent of total</td>
<td>54.7 (10.1) 4</td>
<td></td>
<td>68.6 (8.7) 4</td>
<td>72.9 (7.6) 3</td>
</tr>
<tr>
<td>(STD)</td>
<td>4</td>
<td></td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>768.5 (293.5) NS</td>
<td></td>
<td>927.0 (292.7) NS</td>
<td>752.4 (208.5) NS</td>
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<td>Vegetation</td>
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</tr>
<tr>
<td>Per cent of total</td>
<td>51.0 (16.6) NS</td>
<td></td>
<td>42.6 (17.2) NS</td>
<td>43.6 (11.9) NS</td>
</tr>
<tr>
<td>(STD)</td>
<td>2</td>
<td></td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
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<td>Spruce-Fir (n=14)</td>
<td>Significance</td>
<td>Yellow Birch</td>
<td>Immature (n=4)</td>
</tr>
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<td>----------------</td>
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<tr>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>Forest floor</strong></td>
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<tr>
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<td>39.8 - 4</td>
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<tr>
<td>Per cent of total</td>
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<td>NS</td>
<td></td>
<td>14.8 - -</td>
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<tr>
<td>(STD)</td>
<td>(10.1)</td>
<td></td>
<td></td>
<td>(13.4)</td>
</tr>
<tr>
<td><strong>Total, kg/ha</strong></td>
<td></td>
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<tr>
<td>(STD)</td>
<td>555.3 (208.7)</td>
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<td>488.1 (250.0)</td>
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<td><strong>Vegetation</strong></td>
<td></td>
<td></td>
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<tr>
<td>Per cent of total</td>
<td>36.6 - -</td>
<td>NS</td>
<td></td>
<td>31.7 -</td>
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<tr>
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<td>(12.1)</td>
<td></td>
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<td>(21.3)</td>
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<td>Per cent of total</td>
<td>50.4 - 4</td>
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<td>NS</td>
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<td>(15.8)</td>
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<td>(9.1)</td>
</tr>
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<td>Soil</td>
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<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>13.0 - -</td>
<td>NS</td>
<td></td>
<td>36.4 -</td>
</tr>
<tr>
<td>(STD)</td>
<td>(12.5)</td>
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<td>(29.0)</td>
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<td><strong>Total, kg/ha</strong></td>
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<tr>
<td>(STD)</td>
<td>317.7 (122.4)</td>
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<td>289.1 (145.5)</td>
<td>212.4 (57.7)</td>
</tr>
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<td>Compartment</td>
<td>Spruce-Fir (n=14)</td>
<td>Significance&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>Yellow Birch</td>
<td>Significance&lt;sup&gt;a,c&lt;/sup&gt;</td>
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<tr>
<td>----------------------</td>
<td>-------------------</td>
<td>-----------------------------</td>
<td>--------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Immature (n=4)</td>
<td>Mature (n=2)</td>
</tr>
<tr>
<td>Vegetation</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Per cent of total</td>
<td>27.3 - -</td>
<td>NS</td>
<td>25.8 - -</td>
<td>27.9 - -</td>
</tr>
<tr>
<td>(STD)</td>
<td>(10.6)</td>
<td></td>
<td>(12.1)</td>
<td>(9.1)</td>
</tr>
<tr>
<td>Forest floor</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>63.3 - 4</td>
<td>NS</td>
<td>55.4 - NS</td>
<td>60.0 - NS</td>
</tr>
<tr>
<td>(STD)</td>
<td>(14.4)</td>
<td></td>
<td>(7.7)</td>
<td>(10.0)</td>
</tr>
<tr>
<td>Soil</td>
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<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>9.5 - -</td>
<td>NS</td>
<td>18.8 - -</td>
<td>12.2 - -</td>
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<td>(14.3)</td>
<td>(1.0)</td>
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<tr>
<td>Phosphorus</td>
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<td>Total, kg/ha</td>
<td>142.1</td>
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<td>(17.6)</td>
<td>(3.2)</td>
</tr>
<tr>
<td>Vegetation</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>29.4 - -</td>
<td>NS</td>
<td>30.7 - -</td>
<td>21.3 - -</td>
</tr>
<tr>
<td>(STD)</td>
<td>(8.5)</td>
<td></td>
<td>(8.8)</td>
<td>(0.3)</td>
</tr>
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</tr>
<tr>
<td>Per cent of total</td>
<td>63.7 - 4</td>
<td>2</td>
<td>47.8 - 4</td>
<td>59.5 - NS</td>
</tr>
<tr>
<td>(STD)</td>
<td>(9.9)</td>
<td></td>
<td>(10.2)</td>
<td>(6.4)</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>6.9 - -</td>
<td>3</td>
<td>21.5 - -</td>
<td>19.3 - -</td>
</tr>
<tr>
<td>(STD)</td>
<td>(3.0)</td>
<td></td>
<td>(9.5)</td>
<td>(7.3)</td>
</tr>
</tbody>
</table>
TABLE L (continued)

^aNS  < P.10; 1 > P.10; 2 > P.05; 3 > P.01; 4 > P.001.

^bSignificance of difference between means of spruce-fir and immature yellow birch stands based on t-tests.

^cSignificance of difference between means of immature and mature yellow birch stands.

^dNumbers located vertically between pairs of means identified by dashes indicate probability levels of differences as defined in footnote a above.

^eIncluding all horizons A1 through B2; B3 and C horizons not included.
The major Ca sinks were the vegetation and forest floor with less than 15 per cent of the total occurring in soils. The distribution of Ca between vegetation and forest floor varied within ecosystems, however. The proportion of Ca in vegetation was significantly greater than in the forest floor in the spruce-fir ecosystem; in yellow birch stands, these two compartments contained nearly equal proportions of Ca. The distributional patterns of dry matter and Ca, as well as other nutrients, within ecosystems frequently differed from one another among the compartments. For example, vegetation contained ca 28 per cent of the total system dry matter in spruce-fir stands but 51 per cent of the total Ca. The forest floor of spruce-fir and vegetation and forest floors of yellow birch ecosystems each contained significantly larger proportions of the total Ca than dry matter. In all ecosystems, soils contained a smaller proportion of total Ca than total dry matter. Comparison of the distributions of all nutrients within the spruce-fir ecosystem showed that the vegetation contained a significantly larger proportion of the total Ca than of total K, Mg, and P; the forest floor contained significantly larger proportions of each of the other nutrients than Ca.

In the spruce-fir ecosystem, the forest floor was the largest K sink but in yellow birch ecosystems between ca
30 per cent and 40 per cent of total K occurred in each of the compartments and the differences in proportions were not significant (Table L, page 296). When compartments of different ecosystems were compared, variances were large and the proportions of K in vegetation and soils were not significantly different. The forest floor of the immature yellow birch ecosystem, however, contained a significantly smaller proportion of the total K than either the spruce-fir or mature yellow birch ecosystems. The distributions of dry matter and K within ecosystems also differed. The vegetation and forest floor in the spruce-fir ecosystem and forest floors of yellow birch ecosystems each contained a significantly larger proportion of total K than total dry matter. In each of these ecosystems the proportion of K in the soil was low as compared with the proportion of total dry matter. As compared with the distribution of Mg and P, both the vegetation and forest floor of the spruce-fir ecosystem contained a larger proportion of total K than either of the other nutrients; in the immature yellow birch ecosystem the proportion of total K in the forest floor was significantly less than the total of either Mg or P. 

In each ecosystem the major Mg sink was the forest floor (Table L, page 296). Although larger proportions of total Mg were indicated in the vegetation than in soils, the differences were only significant in the spruce-fir ecosystem.
A further similarity was that Mg was distributed among the compartments of each system in about the same way; i.e. a given compartment contained about the same proportion of Mg in each ecosystem. The proportions of total dry matter and Mg in vegetation did not differ significantly in any of the ecosystems. Proportions of total Mg were larger in the forest floor and smaller in the soil than the proportion of total dry matter in each ecosystem, however. The distributional patterns of Mg and P were similar within each system and none of the differences between respective proportions were significant.

The major P sink in each ecosystem was the forest floor. In the spruce-fir ecosystem, vegetation also contained a comparatively large proportion of total P but in yellow birch ecosystems, the differences between soil and vegetational proportions were not significant. When respective compartments among ecosystems were compared, differences were apparent (Table L, page 296). The forest floor of both spruce-fir and mature yellow birch ecosystems contained a significantly larger proportion of total P than the forest floor of immature yellow birch ecosystems. Soils and vegetation of the immature yellow birch ecosystem contained larger proportions of total P than in spruce-fir and mature yellow birch stands, respectively.
Gross, Throughfall, and Stemflow Precipitation

Average precipitation was ca 117 cm in the study area during the period June 3, 1969 through June 2, 1970. Differences between yellow birch and spruce-fir ecosystems were not apparent since both were distributed throughout the study area. Precipitation did vary within the study area between 93 cm (near Wesner Bald) and 139 cm (at Buckeye Gap); stations in gaps received more precipitation than stations at comparable elevations and precipitation tended to increase with elevation. Both phenomena occur in adjacent mountains (Stephens, 1969). These values undoubtedly are underestimations of gross precipitation of the area. Gross precipitation was 199 cm during the same period at Beech Gap located ca 3 km southeast of and at similar elevational and physiographic positions as the station at Buckeye Gap (data provided by T. Bounds, Tennessee Valley Authority Hourly Rainfall records, TVA Station No. 190). Underestimation resulted from unsatisfactory design of precipitation gauges used during the period between November 13, 1969, and June 2, 1970. Precipitation during the winter period at Buckeye Gap was indicated as 32 cm as compared with 90 cm at Beech Gap. During the winter intervals between measurements were as long as two and one-half months depending on road conditions in the study area; despite additions of oil,
evaporation from gauges undoubtedly accounted for some loss during these long intervals. General weather conditions within the study area, however, suggest that gauge design was a more important factor than evaporation in accounting for the underestimation. Comparisons of results from 3.81 gauges with 25 cm orifices with results from an 8-inch standard type Weather Bureau gauge showed that variation in orifice size did not significantly affect catch. The relative unimportance of orifice size has also been shown in other studies (Huff, 1955). Although precise estimates of the proportion of winter precipitation which falls as snow are not available, data from comparable elevations in the Smokies (Stephens, 1969) and observations of weather conditions during the study suggest that appreciable quantities of snow occur in the Balsam Mountains. Overflow of snow from the gauges probably did not occur since antifreeze was added to melt snow as it fell, but air turbulence about the orifice due to the design of the gauge may have been sufficient to reduce the catch.

Interception during the summer and autumn period was usually higher in spruce-fir than yellow birch stands, as expected (Delfs, 1967; Frechet, 1969; Nihlgard, 1969), although the differences were not significant. The high variability of throughfall within forests is well documented (Helvey and Patric, 1965) but a larger number of gauges per
stand than employed in the current study would have been required in order to compare the stand types with a high degree of precision. The throughfall and interception rates during the summer and autumn period in both spruce-fir and yellow birch ecosystems (Table LI) were in close agreement with rates reported in other coniferous (Frechette, 1969; Delfs, 1967; Rothacher, 1963; Patric, 1966) and deciduous stands (Leonard, 1961; Beall, 1934; Helvey and Patric, 1965; Nihlgard, 1969). During this period stemflow was also in close agreement with rates reported in other studies (Helvey and Patric, 1965; Zinke, 1967). The results show that stemflow resulted in only very small increases in precipitation reaching the forest floor. Similar variations between different ages of yellow birch trees were also found. Bark texture was the primary factor associated with the differences between trees. Large differences in stemflow did characterize trees of different species, however. For example, during one period with a 5.0 cm precipitation, stemflow from a red spruce 26 cm dbh, 15 m tall was 10 liters; during the same period stemflow was 42 liters from a Fraser fir 26 cm dbh, 17 m tall in the same stand and with crown morphology similar to the red spruce.

Higher rates of interception occurred in both coniferous and deciduous stands during the winter-spring period. In areas with appreciable amounts of snowfall,
### TABLE LI

GROSS, THROUGHFALL AND STEMFLOW PRECIPITATION AND INTERCEPTION IN YELLOW BIRCH AND SPRUCE-FIR ECOSYSTEMS

<table>
<thead>
<tr>
<th>Precipitation</th>
<th>Spruce-Fir (n=8)</th>
<th>Yellow Birch (n=4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6/3/69 to 11/12/69</td>
<td>6/3/69 to 11/12/69</td>
</tr>
<tr>
<td>Gross precipitation</td>
<td>11/13/69</td>
<td>6/2/70</td>
</tr>
<tr>
<td>Cm</td>
<td>95.0 ± 17.8</td>
<td>22.3 ± 3.1</td>
</tr>
<tr>
<td>STD</td>
<td>22.3 ± 3.1</td>
<td>117.3 ± 17.6</td>
</tr>
<tr>
<td>Throughfall</td>
<td>72.3 ± 10.2</td>
<td>15.9 ± 4.9</td>
</tr>
<tr>
<td>Cm</td>
<td>72.3 ± 10.2</td>
<td>15.9 ± 4.9</td>
</tr>
<tr>
<td>Stemflow</td>
<td>1.1 ± 1.1</td>
<td>5.5 ± 5.5</td>
</tr>
<tr>
<td>Per cent</td>
<td>2.8 ± 1.1</td>
<td>5.5 ± 5.5</td>
</tr>
<tr>
<td>of gross</td>
<td>2.8 ± 1.1</td>
<td>5.5 ± 5.5</td>
</tr>
<tr>
<td>STD</td>
<td>2.8 ± 1.1</td>
<td>5.5 ± 5.5</td>
</tr>
<tr>
<td>Interception</td>
<td>22.4 ± 13.0</td>
<td>33.4 ± 16.3</td>
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<tr>
<td>Apparent&lt;sup&gt;b&lt;/sup&gt;</td>
<td>22.4 ± 13.0</td>
<td>33.4 ± 16.3</td>
</tr>
<tr>
<td>per cent</td>
<td>19.6 ± 12.4</td>
<td>33.4 ± 16.3</td>
</tr>
<tr>
<td>of gross</td>
<td>19.6 ± 12.4</td>
<td>33.4 ± 16.3</td>
</tr>
<tr>
<td>STD</td>
<td>19.6 ± 12.4</td>
<td>33.4 ± 16.3</td>
</tr>
</tbody>
</table>

<sup>a</sup>Significance of difference between various precipitation means of spruce-fir and yellow birch ecosystems during the period 6/3/69 to 11/12/69 as indicated by t-tests.

<sup>b</sup>Apparent interception = [(gross precipitation - throughfall)/ gross precipitation] X 100.0 per cent.

<sup>c</sup>Adjusted interception = [(gross precipitation - throughfall + stemflow)/gross precipitation] X 100.0 per cent.
interception rates in coniferous stands would be expected to increase by small amounts during the winter (Zinke, 1967; Satterlund and Haupt, 1970) but in deciduous stands, leaf fall has little effect on interception rates (Reynolds, 1967), or rates decrease by small amounts (Leonard, 1961). The high interception rates indicated in yellow birch stands and perhaps spruce-fir stands as well seem anomalous and may be related to difficulties encountered in accurately measuring winter precipitation in this study.

It was not possible to measure stemflow during the winter-spring period. Other studies (Reynolds and Henderson, 1967) indicate slight increases may occur in deciduous stands in association with leaf fall but that changes in net precipitation are slight. In view of these results, substantial changes in the relative role of stemflow during the winter and spring seem unlikely in stands of the study area. The two-week interval at which stemflow measurements were made during the summer and autumn proved to be too long. As a result of the high stemflow capacity of Fraser fir and immature yellow birch and the high rainfall rates in the study area, providing sufficient storage capacity for a two-week interval proved to be difficult. In cases of Fraser fir trees as large as 45 cm dbh, storage capacity of 460 liters per tree proved inadequate for the largest storms encountered. During the long interval, invertebrates such
as millipedes, and litter especially on rough-barked trees tended to plug funnels and tubing connecting stemflow collars and storage barrels. An additional parameter particularly important in determining stemflow and throughfall volume is storm intensity (Leonard, 1961) which could not be measured in the study area as a result of high storm frequency during most two-week periods.

Fog interception proved to be an additional variable affecting throughfall and stemflow. Fog often increases at high elevations (Stephens, 1969; Vogelmann, et al., 1968) and interception by conifers may significantly augment precipitation received from rain showers (Vogelmann, et al., 1968). Although it was not possible to measure the magnitude of stemflow and throughfall attributed to fog interception in the present study, stemflow from Fraser fir and immature yellow birch trees and throughfall in coniferous stands were observed on numerous occasions in association with fog.

Other difficulties encountered in the precipitation study included vandalism and theft of gauges by people traveling along the Blue Ridge Parkway (despite attempts to conceal gauges); destruction of stemflow collars by deer, rodents, and people; destruction of stemflow containers by gnawing rodents; and overturning of rain gauges by wild hogs. Stemflow and precipitation studies are
expensive to conduct, both in terms of labor and monetary requirements. Difficulties encountered show that in order to justify studies of this type, either in terms of reliability of data collected or monetary and labor considerations, investigations must be carefully designed and intensive maintenance of equipment provided; this latter stipulation requires that sites be chosen to provide convenient and continual access at all seasons of the year.

**Nutrient Concentration in Precipitation**

Average nutrient concentrations of gross precipitation, throughfall and stemflow by dates were highly variable. Nutrient concentrations seemed to vary at random in relation to season as found in New Hampshire (Likens, *et al.*, 1967) but seasonal trends which may occur (Denaeyer-Desmet, 1966) could have been obscured by high variance in the present study.

In spite of numerous problems encountered, any of which could have seriously affected the validity of nutrient analyses, several definite trends seemed to characterize precipitation nutrient concentrations (Table LII). The nutrient in highest concentration in gross precipitation was Ca followed in decreasing order by K and Mg; together with ranges of each nutrient, means were in close agreement with concentrations reported elsewhere throughout the Eastern United States and Canada (Weetman and Timmer, 1967; Gambell
### TABLE LII

**NUTRIENT CONCENTRATIONS IN PRECIPITATION**

<table>
<thead>
<tr>
<th>Precipitation Source</th>
<th>Nutrient</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>P</th>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gross Precipitation</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. Mean (ppm)</td>
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<td>0.65</td>
<td>0.45</td>
<td>0.06</td>
<td>1.06</td>
</tr>
<tr>
<td>B. Range&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.05-1.88</td>
<td>0.05-1.88</td>
<td>0.02-0.16</td>
<td>0.19-2.56</td>
<td></td>
</tr>
<tr>
<td>C. n</td>
<td>(51)</td>
<td>(51)</td>
<td>(51)</td>
<td>(51)</td>
<td></td>
</tr>
<tr>
<td>Throughfall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce-fir</td>
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<td></td>
</tr>
<tr>
<td>D. Mean (ppm)</td>
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<td>1.05</td>
<td>1.77</td>
<td>0.21</td>
<td>1.42</td>
</tr>
<tr>
<td>E. Range&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.25-4.22</td>
<td>0.34-5.5</td>
<td>0.06-0.70</td>
<td>0.23-4.32</td>
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</tr>
<tr>
<td>F. n</td>
<td>(74)</td>
<td>(80)</td>
<td>(72)</td>
<td>(70)</td>
<td></td>
</tr>
<tr>
<td>Ratio: (D)/(A)</td>
<td>1.6</td>
<td>3.9</td>
<td>3.7</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>Yellow birch</td>
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<tr>
<td>G. Mean (ppm)</td>
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<td>0.83</td>
<td>1.61</td>
<td>0.21</td>
<td>1.26</td>
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<tr>
<td>H. Range&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.15-3.24</td>
<td>0.25-3.60</td>
<td>0.07-0.67</td>
<td>0.11-4.34</td>
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</tr>
<tr>
<td>I. n</td>
<td>(43)</td>
<td>(40)</td>
<td>(39)</td>
<td>(41)</td>
<td></td>
</tr>
<tr>
<td>Ratio: (G)/(A)</td>
<td>1.3</td>
<td>3.6</td>
<td>3.7</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Stemflow</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Abies fraseri</td>
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<tr>
<td>J. Mean (ppm)</td>
<td></td>
<td>1.65</td>
<td>2.92</td>
<td>0.80</td>
<td>1.11</td>
</tr>
<tr>
<td>K. Range&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.24-6.50</td>
<td>0.52-7.93</td>
<td>0.14-2.50</td>
<td>0.29-4.44</td>
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<tr>
<td>L. n</td>
<td>(62)</td>
<td>(63)</td>
<td>(53)</td>
<td>(58)</td>
<td></td>
</tr>
<tr>
<td>Ratio: (J)/(A)</td>
<td>2.5</td>
<td>6.4</td>
<td>14.3</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td>Ratio: (J)/(D)</td>
<td>1.6</td>
<td>1.6</td>
<td>3.9</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Picea rubens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. Mean (ppm)</td>
<td></td>
<td>2.51</td>
<td>2.63</td>
<td>4.10</td>
<td>1.47</td>
</tr>
<tr>
<td>N. Range&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.89-7.74</td>
<td>1.05-5.25</td>
<td>0.67-11.15</td>
<td>0.31-3.43</td>
<td></td>
</tr>
<tr>
<td>O. n</td>
<td>(60)</td>
<td>(57)</td>
<td>(52)</td>
<td>(56)</td>
<td></td>
</tr>
<tr>
<td>Ratio: (M)/(A)</td>
<td>3.9</td>
<td>5.8</td>
<td>73.2</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>Ratio: (M)/(D)</td>
<td>2.4</td>
<td>1.5</td>
<td>20.0</td>
<td>1.0</td>
<td></td>
</tr>
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TABLE LII (continued)

<table>
<thead>
<tr>
<th>Precipitation Source</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betula lutea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. Mean (ppm)</td>
<td>1.43</td>
<td>2.55</td>
<td>2.55</td>
<td>1.04</td>
</tr>
<tr>
<td>Q. Range(^a)</td>
<td>.48-4.86</td>
<td>.93-4.85</td>
<td>.21-9.80</td>
<td>.21-3.87</td>
</tr>
<tr>
<td>R. n</td>
<td>(62)</td>
<td>(54)</td>
<td>(48)</td>
<td>(54)</td>
</tr>
<tr>
<td>Ratio: (P)/(A)</td>
<td>2.2</td>
<td>5.6</td>
<td>45.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Ratio: (P)/(G)</td>
<td>1.7</td>
<td>1.6</td>
<td>12.4</td>
<td>0.8</td>
</tr>
</tbody>
</table>

\(^a\)Range of means of nutrient concentrations calculated for each collecting interval.
and Fisher, 1966; Likens, et al., 1967; Fisher, et al., 1968). Only P concentrations were anomalous averaging about 1 ppm in the study area as compared with concentrations of 0.08 ppm and less elsewhere (Madgwick and Ovington, 1959; Weetman and Timmer, 1967). Factors associated with the collection, storage, and analysis of precipitation which may affect P concentrations of samples include uptake by algae growing in rain gauges (Carlisle, et al., 1967) absorption of P by polyethylene (Nihlgard, 1970), and leaching of arsenate from analytical glassware and P from glass storage containers (Jackson, 1958). Although the exact magnitude of each of the above could not be estimated, leaching of P from storage containers probably accounted for high concentrations.

Augmentation of nutrient content of precipitation as it passed over plant surfaces within the forest canopy was indicated by the results of the present study and is well known in other studies (Madgwick and Ovington, 1959; Nihlgard, 1970). In both yellow birch and spruce-fir ecosystems, throughfall concentrations in decreasing order were K > Ca > Mg; as in gross precipitation P concentrations were anomalous (Table LII, page 310). Concentrations were slightly higher in throughfall in the spruce-fir ecosystem as compared with concentrations in yellow birch stands. In addition to leaching and washoff, these concentrations
must also reflect leaching of litter which often accumulated in funnels during intervals between sample collection; concentrations of K would have been affected most (Edwards, et al., 1971).

Greater enrichment of K in throughfall is usual in forests (Mina, 1965; Nihlgard, 1970) although Ca may exceed K in some birch stands (Mina, 1965). In the present study, K concentration averaged 3.9 times higher in throughfall than gross precipitation in the spruce-fir ecosystem and 3.6 times higher in yellow birch ecosystems (Table LII, page 310); in some collections, increases as much as 15 fold were recorded. Greatest augmentation of K and other nutrients as well in the spruce-fir ecosystem was probably attributed to greater biomass of foliage and branches (Madgwick and Ovington, 1959) and more intensive leaching due to low pH of throughfall (Nihlgard, 1970). In the current study median pH of throughfall was 4.5 (n=50) in spruce-fir stands as compared with 4.8 (n=28) in yellow birch ecosystems.

Calcium concentration in throughfall averaged slightly higher in spruce-fir than yellow birch ecosystems and represented increases of 1.6 and 1.3 times over concentrations in bulk precipitation, respectively (Table LII). On specific dates Ca concentrations in throughfall exceeded concentrations in gross precipitation by factors up to 6 times in spruce-fir stands and in throughfall of yellow birch
stands by factors up to 5 times.

Average Mg concentrations in throughfall were similar in both types of ecosystems and represented a 3.7 fold increase over concentrations of bulk precipitation. On particular dates, ratios of throughfall/bulk precipitation were as high as 8.7 in spruce-fir stands and 4.4 in yellow birch stands. Similar results have been reported in other studies and typically augmentation of nutrients increases in the order Ca < Mg < K (Madgwick and Ovington, 1959; Nihlgard, 1970), as in the present stands.

Throughfall P concentrations appeared high in relation to other studies (Madgwick and Ovington, 1959; Weetman and Timmer, 1967) but the increases in relation to bulk precipitation were not unrealistic either in terms of absolute changes in concentrations or relative increases in relation to other nutrients (Madgwick and Ovington, 1959).

Nutrient concentrations in stemflow of Fraser fir, red spruce, and yellow birch varied randomly throughout the sampling period. Generally, K concentrations exceeded concentrations of other nutrients although the concentrations of Mg in red spruce and yellow birch stemflow equalled or exceeded K levels (Table LII, page 310). When species were compared, stemflow from red spruce usually contained highest nutrient concentrations and yellow birch lowest although an exception was that highest mean concentration
of K occurred in stemflow of Fraser fir. Concentrations of nutrients, excluding P, were higher in stemflow than throughfall or in gross precipitation. Magnesium concentrations increased most in stemflow of red spruce where concentrations averaged 70 times higher than in gross precipitation and up to 20 times higher than throughfall (Table LII, page 310). Increases of 5.6 to 6.4 times in K and 2.2 to 3.9 times in Ca concentrations occurred compared to gross precipitation.

Phosphorus concentrations in stemflow showed little difference from concentrations in either throughfall or gross precipitation and in some cases, concentrations were lower (Table LII). Decreases in P concentration in throughfall below concentrations in gross rainfall have been found in other spruce stands (Weetman and Timmer, 1967); in the present study the apparent disappearance may reflect difficulties with sampling or perhaps resulted from uptake by epiphytes.

Acidity of stemflow, solubility of nutrients, and bark texture are principal factors which affect nutrient content of stemflow (Nihlgard, 1970; Mina, 1965) and the results of the current study suggest that the importance of each varies from nutrient to nutrient. The forms in which Ca occurs are apparently least soluble of the four nutrients (Nihlgard, 1970) and comparisons among the three
tree species in the present study indicated that intensive leaching due to low pH (median 4.4, n=43) from the relatively large surface provided by rough bark texture resulted in high concentrations in red spruce stemflow. Slightly higher pH (median 4.6, n=39) and smooth bark texture of Fraser fir resulted in less intensive leaching. Despite rough textured bark of some yellow birch trees in the sample, Ca concentrations were relatively low and high pH of stemflow (median 5.5, n=43) apparently was the principal factor regulating leaching intensity and nutrient concentrations; Ca concentration of stem bark apparently was not an important factor since concentrations of yellow birch bark were up to 2 or more times greater than bark of conifers.

Potassium is very soluble in plant tissues (Tukey, et al., 1958) and in the current study concentrations in stemflow apparently were not highly dependent upon stemflow pH, bark texture or nutrient concentration of stem bark; further augmentation of K in stemflow of Fraser fir may have resulted from leaching from epiphytic mosses which formed dense mats on several of the larger sample trees.

High solubility of Mg was indicated by the extremely high ratios of Mg in stemflow to bulk precipitation. Concentrations were also dependent upon bark texture and pH of stemflow. Mina (1965) found similar patterns of changes in concentrations of both Mg and K in stemflow of spruce and birch.
Input and Transfer of Nutrients Via Precipitation

The quantities of P (kg/ha/yr) contained in bulk precipitation (Table LIII) far exceeded quantities of 0.5 kg/ha/yr generally reported in the Northeastern United States and Eastern Canada (Likens, et al., 1967; Weetman and Timmer, 1967) and further illustrate that the techniques employed in this study were not suitable for measuring the P contents of precipitation. Annual input of each of the other nutrients was well within ranges reported (Likens, et al., 1967; Weetman and Timmer, 1967; Weetman and Webber, 1971) and were limited to a few kilograms per year. These nutrients in order of decreasing quantities were Ca > K > Mg. As compared with the total nutrient content supplied at the forest floor from all sources of precipitation, bulk precipitation contributed approximately one-half to two-thirds of the Ca, one-fifth to one-fourth of the K, and one-fourth of the Mg. Bulk precipitation supplied somewhat lower proportions of these nutrients in other forests but gross precipitation was more significant in Ca dynamics than in either Mg or K (Madgwick and Ovington, 1959; Nihlgard, 1970).

Nutrient input in the study area through bulk precipitation may exceed values shown in Table LIII by a factor of up to 1.4 times due to the degree to which annual precipitations apparently was underestimated. Making this
### TABLE LIII

**NUTRIENTS IN GROSS PRECIPITATION, THROUGHFALL, AND STEMFLOW IN SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS**

<table>
<thead>
<tr>
<th>Sources of Nutrient</th>
<th>Spruce-Fir (n=8)</th>
<th>Yellow Birch (n=4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6/3/69 to 11/12/69</td>
<td>11/12/69 to 6/2/70</td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>10.7 3.3 14.0</td>
<td>10.9 2.7 13.6</td>
</tr>
<tr>
<td>STD</td>
<td>3.6 1.8 4.6</td>
<td></td>
</tr>
<tr>
<td>Gross, kg/ha</td>
<td>5.1 1.1 6.3</td>
<td>6.4 1.5 7.8</td>
</tr>
<tr>
<td>STD</td>
<td>0.5 .9 0.5</td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>51.9 39.3 49.2</td>
<td>69.0 55.9 65.9</td>
</tr>
<tr>
<td>STD</td>
<td>14.0 22.4 15.7</td>
<td></td>
</tr>
<tr>
<td>Throughfall, kg/ha</td>
<td>5.1 2.1 7.3</td>
<td>4.1 1.2 5.3</td>
</tr>
<tr>
<td>STD</td>
<td>3.0 1.9 4.5</td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>44.0 60.7 47.7</td>
<td>26.4 44.1 30.5</td>
</tr>
<tr>
<td>Stemflow, kg/ha</td>
<td>0.4 -- --</td>
<td>0.5 -- --</td>
</tr>
<tr>
<td>STD</td>
<td>0.2 -- --</td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>4.0 -- --</td>
<td>4.6 -- --</td>
</tr>
<tr>
<td>STD</td>
<td>4.0 -- --</td>
<td></td>
</tr>
<tr>
<td>Fir, kg/ha</td>
<td>0.2 -- --</td>
<td>0.004 -- --</td>
</tr>
<tr>
<td>STD</td>
<td>0.2 -- --</td>
<td></td>
</tr>
<tr>
<td>Sources of Nutrient</td>
<td>Spruce-Fir (n=8)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6/3/69 to 11/12/69</td>
<td>11/12/69 to 6/2/70</td>
</tr>
<tr>
<td>Spruce, kg/ha</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>STD</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Otherb, kg/ha</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>STD</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total, kg/ha</td>
<td>16.8</td>
<td>4.8</td>
</tr>
<tr>
<td>STD</td>
<td>5.8</td>
<td>3.3</td>
</tr>
<tr>
<td>Gross, kg/ha</td>
<td>3.2</td>
<td>0.9</td>
</tr>
<tr>
<td>STD</td>
<td>0.8</td>
<td>0.4</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>20.6</td>
<td>26.4</td>
</tr>
<tr>
<td>STD</td>
<td>6.3</td>
<td>19.6</td>
</tr>
<tr>
<td>Throughfall, kg/ha</td>
<td>12.9</td>
<td>3.9</td>
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<td>STD</td>
<td>5.3</td>
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<td>Per cent of total</td>
<td>75.3</td>
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<td>STD</td>
<td>6.1</td>
<td>19.6</td>
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<tr>
<td>Stemflow, kg/ha</td>
<td>0.7</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.3</td>
<td>--</td>
</tr>
<tr>
<td>Per cent of total</td>
<td>4.1</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>1.7</td>
<td>--</td>
</tr>
<tr>
<td>Sources of Nutrient</td>
<td>Spruce-Fir (n=8)</td>
<td>Yellow Birch (n=4)</td>
</tr>
<tr>
<td>---------------------</td>
<td>------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td></td>
<td>6/3/69 to 11/12/69</td>
<td>11/13/69 to 6/2/70</td>
</tr>
<tr>
<td>Fir, kg/ha</td>
<td>0.4 - - - - 1.0</td>
<td>0.01 - - - - 1.0</td>
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<tr>
<td>STD</td>
<td>0.3 - - - - 1.0</td>
<td>0.01 - - - - 1.0</td>
</tr>
<tr>
<td>Spruce, kg/ha</td>
<td>0.2 - - - - 1.0</td>
<td>0.1 - - - - 1.0</td>
</tr>
<tr>
<td>STD</td>
<td>0.1 - - - - 1.0</td>
<td>0.1 - - - - 1.0</td>
</tr>
<tr>
<td>Others&lt;sup&gt;b&lt;/sup&gt;, kg/ha</td>
<td>0.1 - - - - 1.0</td>
<td>1.0 - - - - 1.0</td>
</tr>
<tr>
<td>STD</td>
<td>0.2 - - - - 1.0</td>
<td>1.0 - - - - 1.0</td>
</tr>
</tbody>
</table>

**Magnesium**

<table>
<thead>
<tr>
<th></th>
<th>Spruce-Fir (n=8)</th>
<th>Yellow Birch (n=4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total, kg/ha</td>
<td>2.5 0.7 3.2 NS 4.3 1.1 5.4</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>0.8 0.4 1.1 2.4 0.8 3.0</td>
<td></td>
</tr>
<tr>
<td>Gross, kg/ha</td>
<td>0.6 0.3 0.9 NS 0.6 0.4 1.0</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>0.1 0.2 0.2 0.02 0.1 0.1</td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>25.2 44.1 29.1 NS 18.2 60.1 22.9</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>9.4 20.9 8.9 11.3 42.5 9.4</td>
<td></td>
</tr>
<tr>
<td>Throughfall, kg/ha</td>
<td>1.4 0.4 1.8 NS 2.1 0.6 2.7</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>0.6 0.3 0.9 0.8 0.8 1.4</td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>52.8 55.9 53.2 NS 52.3 39.9 52.3</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>9.4 20.9 10.0 13.0 42.5 12.2</td>
<td></td>
</tr>
<tr>
<td>Stemflow, kg/ha</td>
<td>0.6 - - - - 1.7</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>0.1 - - - - 1.7</td>
<td></td>
</tr>
<tr>
<td>Per cent of total</td>
<td>25.2 - - - - 29.5</td>
<td></td>
</tr>
<tr>
<td>STD</td>
<td>9.4 - - - - 23.2</td>
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</table>
TABLE LIII (continued)

<table>
<thead>
<tr>
<th>Sources of Nutrient</th>
<th>Spruce-Fir (n=8)</th>
<th>Yellow Birch (n=4)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>6/3/69 to 11/12/69</td>
<td>11/13/69 to 6/2/70</td>
</tr>
<tr>
<td>Fir, kg/ha</td>
<td>0.1</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.1</td>
<td>--</td>
</tr>
<tr>
<td>Spruce, kg/ha</td>
<td>0.3</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.2</td>
<td>--</td>
</tr>
<tr>
<td>Othersb, kg/ha</td>
<td>0.2</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.3</td>
<td>--</td>
</tr>
</tbody>
</table>

Phosphorus

| Total, kg/ha        | 13.6             | 3.9              | 17.5             | NS                | 12.8              | 5.2             | 18.0             |
| STD                 | 6.1              | 2.6              | 5.8              |                   | 6.0              | 2.0             | 6.6              |
| Gross, kg/ha        | 8.2              | 4.3              | 12.5             | NS                | 10.8             | 5.5             | 16.3             |
| STD                 | 2.1              | 1.4              | 2.7              |                   | 3.9              | 1.4             | 3.4              |
| Per cent of total   | 74.3             | --               | --               |                   | --               | --              | --               |
| STD                 | 47.0             | --               | --               |                   | --               | --              | --               |
| Throughfall, kg/ha  | 5.2              | -0.4             | 4.8              | NS                | 1.8              | -0.4            | 1.4              |
| STD                 | 6.5              | 2.4              | 5.9              |                   | 8.5              | 1.0             | 9.1              |
| Per cent of total   | 24.3             | --               | --               |                   | --               | --              | --               |
| STD                 | 47.4             | --               | --               |                   | --               | --              | --               |
| Stemflow, kg/ha     | 0.2              | --               | --               | NS                | 0.3              | --             | --               |
| STD                 | 0.1              | --               | --               |                   | 0.3              | --             | --               |
| Per cent of total   | 1.5              | --               | --               | NS                | 3.2              | --             | --               |
| STD                 | 0.7              | --               | --               |                   | 4.4              | --             | --               |
### TABLE LIII (continued)

<table>
<thead>
<tr>
<th>Sources of Nutrient</th>
<th>Spruce-Fir (n=8)</th>
<th>Yellow Birch (n=4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6/3/69 to 11/12/69</td>
<td>11/13/69 to 6/2/70</td>
</tr>
<tr>
<td>Fir, kg/ha</td>
<td>0.1</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.1</td>
<td>--</td>
</tr>
<tr>
<td>Spruce, kg/ha</td>
<td>0.1</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.05</td>
<td>--</td>
</tr>
<tr>
<td>Othersb, kg/ha</td>
<td>0.04</td>
<td>--</td>
</tr>
<tr>
<td>STD</td>
<td>0.05</td>
<td>--</td>
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<tr>
<td></td>
<td>0.001</td>
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<td>0.03</td>
<td>--</td>
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<tr>
<td></td>
<td>0.3</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>0.3</td>
<td>--</td>
</tr>
</tbody>
</table>

*a* Includes all deciduous species; estimates based on yellow birch regression equations.

*b* Estimates based on nutrient analyses of stemflow from yellow birch.
correction indicates annual inputs of < 11 kg/ha Ca, < 8 kg/ha K, and < 1.4 kg/ha Mg. In any case, the results indicate that annual input of nutrients through gross precipitation closely approximated annual accumulations in perennial components of vegetation in the ecosystems in the study area. Madgwick and Ovington (1959) in a study of precipitation nutrient dynamics of several forest types and Weetman and Webber (1971), in a study concerning black spruce and red spruce-balsam fir stands drew similar conclusions.

Similar or smaller quantities of Ca and larger quantities of K and Mg were leached from crowns of trees than were supplied in gross precipitation in spruce-fir and yellow birch ecosystems (Table LIII, page 318). Total nutrient content reaching the forest floor was far greater than outside forests in the study area despite the significant reduction in precipitation due to interception loss. Nutrients in order of decreasing quantities in throughfall were K > Ca > Mg which together with absolute quantities are similar to results from other studies (Mina, 1965). Nutrient quantities in throughfall of deciduous stands are often lower than in coniferous stands due to their greater acidity and crown biomass (Nihlgard, 1970) but this trend was only apparent in Ca in Balsam Mountain stands; species differences, acting through bark texture and relative availability of soluble acidic compounds in tissues, affect
quantities of nutrients leached, and the direction of trends between different series of species vary. The principal source of nutrients of mosses is throughfall, not absorption or humus from soil (Tamm, 1953) and results of the present study indicated that more than adequate supplies of Ca, K, and Mg to balance annual uptake were contained in throughfall in these ecosystems.

In spite of the high concentrations of nutrients in stemflow relative to concentrations of other sources, quantities of nutrients were small and accounted for 5 percent or less of the total reaching the forest floor through precipitation (Table LIII, page 318). As in throughfall, nutrients in order of decreasing quantities were K > Ca > Mg. Fraser fir was the major supplier of nutrients in stemflow in spruce-fir stands even though concentrations of most nutrients were lower than in stemflow of red spruce. Both the larger volume of stemflow associated with the smooth-barked fir and the higher density of fir in the coniferous ecosystem were the principal contributing factors determining relative importance of each species in these stands. Red spruce contributed nearly as much Ca to stemflow as yellow birch in yellow birch ecosystems which emphasizes the intensity of leaching of less soluble nutrients which may occur with a combination of rough bark texture and acidic stemflow.
The small contribution both to the total hydrologic and nutrient cycles of stemflow probably obscures its real significance in the ecosystems of the study area. The concentration of water and nutrients, albeit the small quantity in relation to total water and nutrients of precipitation, may affect root development (Leonard, 1961) or alter numerous chemical properties of the surrounding soil (Gersper and Holowaychuk, 1971), the effects of which may persist for years even after trees have fallen or been removed (Mina, 1967). The implications are apparent; stemflow is a major factor which could contribute to high degrees of variability which characterized the soils of the study area, and the localization of water and nutrients within small areas must affect both tree growth and contribute to the highly variable and non-random distributional patterns of many understory species in the study area.

**Intensity of Nutrient Cycles**

The magnitude of annual nutrient flux in relation to the quantity of nutrients in the donor pool provides a measure by which the relative intensity of nutrient cycles may be compared, both within and between ecosystems. The transfer coefficients in Table LIV represent these ratios for various phases of nutrient cycles of the spruce-fir and yellow birch ecosystems and indicate that flux rates between vegetation and the forest floor-soil system ($R_{v-fs}$ and $U_{fs-v}$
### TABLE LIV

ESTIMATES OF ANNUAL TRANSFER COEFFICIENTS OF NUTRIENTS BETWEEN COMPARTMENTS OF SPRUCE-FIR AND YELLOW BIRCH ECOSYSTEMS

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Pathway(^b)</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LF(_{v-fs})(^c)</td>
<td>PR(_{v-fs})(^d)</td>
<td>R(_{v-fs})</td>
<td>ACC(_{fs-v})(^e)</td>
<td>U(_{fs-v})</td>
</tr>
<tr>
<td>Spruce-fir</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>.0823</td>
<td>.0214</td>
<td>.1037</td>
<td>.0211</td>
<td>.1097</td>
</tr>
<tr>
<td>K</td>
<td>.0829</td>
<td>.0924</td>
<td>.1753</td>
<td>.0142</td>
<td>.1013</td>
</tr>
<tr>
<td>Mg</td>
<td>.1744</td>
<td>.0377</td>
<td>.2121</td>
<td>.0092</td>
<td>.0745</td>
</tr>
<tr>
<td>P</td>
<td>.1159</td>
<td>-f</td>
<td></td>
<td>.0114</td>
<td>.0547</td>
</tr>
<tr>
<td>Immature yellow birch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>.1187</td>
<td>.0154</td>
<td>.1341</td>
<td>.0120</td>
<td>.1028</td>
</tr>
<tr>
<td>K</td>
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<td>.1498</td>
<td>.2862</td>
<td>.0100</td>
<td>.1028</td>
</tr>
<tr>
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<td>.3041</td>
<td>.0701</td>
<td>.3742</td>
<td>.0097</td>
<td>.1135</td>
</tr>
<tr>
<td>P</td>
<td>.1211</td>
<td>-f</td>
<td></td>
<td>.0147</td>
<td>.0718</td>
</tr>
<tr>
<td>Mature yellow birch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
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<td>.0183</td>
<td>.2225</td>
<td>.0116</td>
<td>.1725</td>
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<tr>
<td>K</td>
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<td>.1682</td>
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<td>.1603</td>
</tr>
<tr>
<td>Mg</td>
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<td>.0780</td>
<td>.5124</td>
<td>.0391</td>
<td>.2091</td>
</tr>
<tr>
<td>P</td>
<td>.1306</td>
<td>-f</td>
<td></td>
<td>.0192</td>
<td>.0545</td>
</tr>
</tbody>
</table>

\(^a\)Transfer coefficients represent the ratio of annual nutrient flux (kg/ha) to nutrient pool (kg/ha); for example, LF\(_{calcium}\) \(\div\) V\(_{calcium}\).

\(^b\)Symbol denotes transfer pathway or process and subscripts identify donor and recipient compartments, respectively, where LF = annual litterfall, PR = throughfall + stemflow, R = LF\(_{v-fs}\) + PR\(_{v-fs}\), ACC = accumulation in aboveground perennial components of vegetation, U = uptake estimated as the sum P\(_{v-fs}\) + ACC\(_{fs-v}\), v = above-ground vegetation, and fs = combined forest floor-soil compartment.
| TABLE LIV (continued) |

<table>
<thead>
<tr>
<th>c</th>
<th>Ratios based on eleven spruce-fir stands; data from two stands were excluded due to atypically large quantities in annual litterfall. Litterfall transfer rates were based on four immature and two mature yellow birch stands.</th>
</tr>
</thead>
<tbody>
<tr>
<td>d</td>
<td>( d_n = ) eight spruce-fir and four yellow birch stands. Data from one mature and three immature yellow birch stands were combined; resulting means of nutrients transferred via precipitation were used in calculating transfer coefficients in both yellow birch ecosystems.</td>
</tr>
<tr>
<td>e</td>
<td>( e_n = 14 ) spruce fir, four immature yellow birch, two mature yellow birch stands.</td>
</tr>
<tr>
<td>f</td>
<td>Could not be estimated due to aberrant data.</td>
</tr>
</tbody>
</table>
in Table LIV, page 326) were most intense in mature yellow birch stands. This means that, in the mature yellow birch ecosystem, larger proportions of the nutrients in each pool were incorporated in annual cycles than in either immature yellow birch or spruce-fir ecosystems. Several factors, all associated to some degree with the relative maturity of these stands, seem to account for the greater intensity of nutrient cycles. As ecosystems develop and progress toward more mature stages, nutrient distribution shifts from extrabiotic to intrabiotic pools and nutrient cycles tend to become more closed (Odum, 1969). Although the differences between immature and mature yellow birch ecosystems were often small, the distribution of nutrients among components within the two as shown in Table L, page 296, suggests that similar trends might exist; a smaller proportion of the nutrients of the mature system was in the soil and intrabiotic storage was of greater importance than in immature. The nutrients in annual uptake represented a greater fraction of the soil nutrient pool which increased the intensity of the soil-vegetation phase of the nutrient cycle.

Shifts in the distribution of annual dry-matter increment and consequently of nutrients occurred between immature and mature yellow birch ecosystems (Table XXII, page 181). A smaller fraction of the annual net primary
production was in perennial components of trees and an increasing fraction in foliage in the mature stands; the result was that smaller proportions of nutrients accumulated annually in the tree biomass and a greater proportion was incorporated in annual litterfall. The relatively high rates at which both K and Mg accumulated in mature stands in comparison with immature stands (Cf. transfer coefficients of ACC\textsubscript{fs-v}, Table LIV, page 326) seem contradictory to the trend of decreasing accumulation of nutrients in biomass; however, they reflect the striking increase in importance of bryophytes which accounted for 90 per cent or more of the estimated annual uptake of K, Mg, and P in mature stands (Table XL, page 251). In these stands, the fraction of each of the above nutrients which accumulated annually in perennial tree components was very small.

More intense nutrient cycles between vegetation and forest floor-soil compartment were indicated in immature yellow birch stands than in spruce-fir stands (Cf. R\textsubscript{v-fs}, Table LIV). The principal factor accounting for this was the complete turnover of comparatively nutrient-rich foliage of the deciduous species in these stands. The rates at which nutrients accumulated in perennial components in the immature yellow birch stands were similar to or occasionally less than corresponding rates in spruce-fir stands. These rates reflect both slightly lower
quantities of nutrients which accumulated annually in perennial components and the larger nutrient pool in the forest floor-soil compartment of immature yellow birch stands. Flux rates of P varied from rates of other nutrients in that little difference was indicated between stands and about the same intensity of cycling characterized each ecosystem.

The transfer coefficients (Table LIV, page 326) also indicated that the principal pathway along which flux occurred varied according to the nutrient. Precipitation (throughfall + stemflow) was equally or more important than litterfall as a pathway in K transfer. This reflects the solubility of K in plant tissues. Calcium and Mg each was transferred from plants to the forest floor-soil compartment primarily through litterfall but precipitation was somewhat more important in transferring Mg than Ca. Different cycling rates were also indicated among nutrients within ecosystems. The flux of Ca was least intensive and flux of Mg most intensive between vegetation and forest floor-soil compartments in each system.

Higher rates of annual transfer of nutrients from vegetation (\(R_{V-fs}\)) than estimated annual uptake rates (\(U_{fs-v}\)) are indicated in Table LIV; these differences do not necessarily indicate losses from the ecosystems but rather suggest that a larger proportion of the nutrients in the
vegetation pool are incorporated in annual cycles than nutrients of the forest floor-soil pool.
VI. SUMMARY AND CONCLUSIONS

Current stands of red spruce and Fraser fir in the study area developed from remaining advanced regeneration and from seedlings which were established after extensive clearcutting during the 1920's. Many of the yellow birch stands occupied former spruce-fir sites which burned after clearcutting or where logging practices and pulping operations destroyed advanced regeneration or residual trees. Present spruce-fir stands occupied a much smaller proportion of the high elevation areas in the Balsam Mountains and are composed of a greater proportion of Fraser fir than the pre-logging forests. Both spruce-fir and immature yellow birch stands were between 40 and 50 years old at dbh and were essentially even-aged stands although age-structure was complicated by occasional residual trees which remain from pre-logging periods.

Mature yellow birch stands which were sampled included trees as old as 265 years and occupied block fields in steep, northeast facing coves. These stands were distinct with respect to site, species composition, and community structure from other high elevation deciduous stands previously studied in the mountains of North Carolina and Tennessee.
Wide variations in total weight of dry matter occurred among stands within each ecosystem but apparently maximum weights of each system may be of the same order of magnitude. Differences between ecosystems were apparent, however, in the proportions of dry matter in each compartment. Soil contained about 70 per cent of total dry matter of each yellow birch ecosystem and was a more important sink than in the spruce-fir ecosystem where approximately 55 per cent of the dry matter was in soil; the proportion of dry matter in both vegetation (28 per cent) and forest floor (18 per cent) of the spruce-fir ecosystem exceeded that in the yellow birch ecosystems (20 per cent and < 12 per cent in each compartment, respectively).

The larger proportion of dry matter in the vegetation of the spruce-fir ecosystem reflected the significantly larger biomass of trees and tall shrubs, which averaged 180 t/ha. In all ecosystems biomass of understory strata was small. Larger tree-tall shrub biomass in spruce-fir stands was attributed to greater bole and foliage biomass which averaged 138 t/ha and 15.5 t/ha, respectively, and exceeded biomass of corresponding components in immature yellow birch stands by factors of 2 and 4. The significance of differences in crown morphology as a factor affecting biomass of these stands was illustrated by the large branch biomass in yellow birch ecosystem where mean branch biomass (24 t/ha) equalled
mean branch biomass in spruce-fir stands. Biomass of mature yellow birch stands (mean 154 t/ha) exceeded biomass of immature stands (mean 103 t/ha) in the study area which is similar to the relationship between mature and immature stands in the Smokies (Whittaker, 1966). The smaller biomass of spruce-fir and immature yellow birch stands in the study area as compared with high elevation forests in the Smokies (Shanks and Clebsch, 1962; Whittaker, 1966) apparently is attributable to less age. Leaf area index was as high as 7 or more in immature yellow birch stands where scattered red spruce occurred but was usually about 4 in unmixed stands. Large leaf areas were indicated in spruce-fir stands where the mean was ca 21 but ranged as high as 36 and suggests that estimates of leaf area in spruce-fir stands in the Smokies (Whittaker, 1966) may be low.

Biomass of stands was closely related to stand structure and species composition in the study area, but not to soil and site parameters. In all stands basal area was directly correlated with total biomass and also with the biomass of boles, branches, and foliage; increased density of yellow birch in spruce-fir stands caused a decrease in stand biomass. Foliage biomass of yellow birch trees in these stands was independent of basal area which means that foliage biomass was independent of stocking rates (stand basal area, density). The presence of red
spruce in these stands, however, resulted in correlation of foliage biomass with basal area. Total stand density was not related to stand biomass in spruce-fir ecosystems of the study area but the opposite was true of stands of similar aged balsam fir in eastern Canada (Baskerville, 1965).

The low biomass of understory strata apparently was related to low light intensities, or intense competition with the dense overstory for soil moisture, or perhaps their interaction. Both biomass and species diversity were greater in immature yellow birch stands where presumably there is less competition due to much lower crown biomass. The biomass of bryophytes averaged 3.7 t/ha in mature yellow birch stands and was nearly four times greater than in the other ecosystems. The ground surface in these stands was covered with large boulders which are particularly favorable habitats for bryophytes. Lower biomass in other stands probably reflected the lack of suitable habitats more than competition for light and throughfall nutrients.

Within stands of each ecosystem forest floor, weights were highly variable, which may be attributed to differential distribution of annual litterfall due to production rates, wind patterns, pit-mound microtopography, and disruption of litter horizon by windthrow. In mature and immature yellow birch stands, forest floor weights were only 50-60 per cent as great as in spruce-fir stands where
mean weight was 120 t/ha. The weights were equivalent to approximately 20 years' accumulation of annual litterfall in spruce-fir stands, 16 years in immature yellow birch stands, and 11 years in mature yellow birch stands which suggests a nearly two-fold difference between decay rates in the ecosystems. Compared with other deciduous forests, forest floor weight in immature yellow birch stands was high which may indicate a combination of slower decay rates due to the higher elevation, differences in chemical composition, and perhaps carry-over from previous spruce-fir stands. Variations among stands were not correlated with topographic features but weights tended to decrease in spruce-fir stands as the proportion of deciduous species increased. Higher nutrient status and lower acidity of deciduous litter would increase decay rates.

Bole volume increment of 6.8 m³/ha/yr in spruce-fir stands was significantly greater than in immature yellow birch (3.8 m³/ha/yr) and mature yellow birch (1.0 m³/ha/yr) stands. Above-ground net primary ecosystem production ranged between 5 and 10 t/ha/yr and tended to decrease in the sequence spruce-fir > immature yellow birch > mature yellow birch, although differences between mean rates of productivity were statistically insignificant. Net production in coniferous stands was similar to rates in mature spruce-fir stands but only about one-half the rates
in an immature stand in the Smokies (Whittaker, 1966); differences in species composition, ages of stands, or perhaps methods of estimating production are indicated. As with biomass, net production of understory strata in spruce-fir and immature yellow birch stands was trivial compared with production by trees and tall shrubs. However, each understory stratum contributed from 3-10 times more to ecosystem productivity than to ecosystem biomass; the trend was especially apparent in mature yellow birch stands where bryophytes comprised about 2 per cent of the biomass but 20 per cent of the total ecosystem production.

Tree-tall shrub strata of the ecosystems were more clearly differentiated by distribution of net production than by absolute rates. In both immature yellow birch and spruce-fir ecosystems, foliage constituted approximately one-half and boles one-third of the net production. However, branch production was approximately 12 per cent of total production in immature yellow birch stands but only 6 per cent in the other ecosystems. Reproductive structures were a major proportion of production in spruce-fir stands (13.6 per cent) but minor in other stands (< 6 per cent). In mature yellow birch stands, bole and branch production was very low (ca 15 per cent) and foliage was nearly three-fourths of total production. Although bole volume increment in spruce-fir stands was nearly double rates in
immature yellow birch stands, dry-matter production rates were not significantly greater due to the higher specific gravity of yellow birch wood.

Net production of foliage and reproductive components in coniferous stands decreased toward higher elevations on steeper, northeast slopes. In immature yellow birch stands foliage production decreased toward higher elevations but together with other components in other systems net production was generally not related to soil or site conditions. In the Smokies total net production and biomass were correlated with elevation (Whittaker, 1966) but both the range of elevation and forest types were more inclusive than in the study area.

Net production was correlated with stand structure but the relationship varied between ecosystems. In spruce-fir stands, net production was not greatest at any particular basal area nor was it correlated with stand biomass, foliage biomass, or leaf area; neither the theories of Assmann (cited in Wegge, 1966) nor Baskerville (1965) describe the relationship between stand structure and production in these stands. Production was more or less constant across the range of these parameters encountered in spruce-fir stands of the study area which is similar to Möller's (1947, 1954) findings. However, implicit in Möller's theory is constancy of foliage biomass over a broad range of stand stocking rates
whereas foliage biomass in spruce-fir stands in this study area increased as stand basal area and biomass increased. In the current stands, net production remained constant with increased basal area and biomass because net assimilation rates (or leaf efficiency) of foliage decreased with increasing foliage biomass counteracting any tendency for net production to increase as foliage biomass increased. Foliage biomass was independent of stand density and both average foliage biomass per tree and the ratio of nonphotosynthetic to photosynthetic tissue (NPS/PS) decreased as stand density increased; higher production in denser stands was attributed to a more favorable ratio of NSP/PS tissue and perhaps more effective light penetration in smaller crowns of denser stands. Mutual shading of needles may also be less limiting in these smaller crowns.

In immature yellow birch stands, bole volume and bole and branch dry-matter production all increased as stand density, stand basal area, stand biomass, foliage biomass, and leaf area increased. Variations of these structural parameters and of net production were positively correlated in these stands. This supports Baskerville's (1965) conclusions concerning the relationship between structural parameters and net production of trees. In mature yellow birch stands however, the relationship between these structural parameters and net production was not significant and
similar to the relationship in spruce-fir stands of the study area and probably reflected an increasing ratio of nonphotosynthetic to photosynthetic tissue with increasing stand biomass and age.

Annual leaf litterfall was equivalent to approximately 3-4 per cent of tree-shrub biomass in each ecosystem and 63 per cent and 72 per cent of above-ground net primary production in immature yellow birch and spruce-fir stands, respectively. In mature yellow birch stands annual leaf litterfall and net primary production were nearly equal which, together with very low rates of bole and branch production, indicates that these stands are near maximum biomass under present structural and site conditions. Production of several litterfall components was correlated with annual above-ground net primary production of combined tree and shrub strata and when applied in combination through multiple regression techniques served as an index of production in immature yellow birch and spruce-fir ecosystems. Bole and branch contribution to litterfall was apparently < 10 per cent of annual litterfall in these ecosystems but was highly variable and would require sampling from larger plots and over longer time intervals than employed in this study to improve reliability of estimates.

Except for P, the absolute weights of nutrients, like dry matter, did not vary greatly between the ecosystems in
this study. Phosphorus occurred in significantly larger quantities in both spruce-fir and mature yellow birch ecosystems than in immature yellow birch ecosystems. The distribution of nutrients among compartments varied in relation to one another, however, and frequently the proportion of a nutrient in a compartment in relation to the total pool differed considerably from the proportion of dry matter.

Vegetation and forest floor were the major nutrient sinks and the proportion in the soil was generally very low. In the spruce-fir ecosystem, vegetation contained 51 per cent of the Ca and the forest floor contained 50 per cent K and about 64 per cent of both Mg and P. In both yellow birch ecosystems, vegetation and forest floor were of about equal importance as Ca and K sinks; also in these ecosystems, K was more or less evenly distributed among vegetation-forest floor-soil compartments which distinguishes the distribution of K from other nutrients and the yellow birch from spruce-fir ecosystems. As in the spruce-fir ecosystem, the forest floor was the principal sink for Mg and P in both yellow birch ecosystems but the proportions of total pools were slightly smaller than in spruce-fir forest floor.

Relative pool sizes of nutrients in above-ground vegetation in order of decreasing quantities were Ca>K>Mg>P of which trees and tall shrubs contained > 94 per cent of each.
Saplings, low shrubs and tree and shrub regeneration each usually contained < 1.0 per cent of each nutrient. Herbs and bryophytes also contained small quantities, but in relation to the distribution of biomass among vegetational strata, each of these was from 2-10 times more important as a nutrient sink than as a dry-matter sink. In immature yellow birch stands, herbs contained ≤ 7.5 per cent of total K in vegetation as compared with only ≤ 0.3 per cent of vegetational dry matter. Bryophytes were especially significant sinks of nutrients in mature yellow birch stands where they contained as much as 30 per cent of the total vegetational nutrient pool as compared with only 3 per cent of the total dry matter. Tree branches and foliage each contained from 17-25 per cent of vegetational nutrient pool as compared with 14 per cent and 8.5 per cent, respectively, of biomass in spruce-fir stands. In yellow birch stands, these components contained as much as 49 per cent and 25 per cent, respectively, of vegetational nutrients.

Only 5-9 kg/ha Ca, 4-6 kg/ha K, 2-6 kg/ha Mg and < 2 kg/ha P accumulated annually in perennial above-ground components of vegetation which were small amounts when compared with those of nutrients lost in annual litterfall or that moved in annual nutrient uptake from the soil-forest floor compartments. In mature yellow birch stands, quantities of each nutrient which accumulated in boles and branches
of trees was < 40 per cent compared with bryophytes where 56 per cent of the Ca and 89 per cent or more of each of the other nutrients accumulated annually.

Despite approximately 20 per cent greater leaf litter-fall in spruce-fir than in yellow birch stands, the quantity of nutrients contained in litterfall in the ecosystems was similar because of the much higher nutrient concentrations in deciduous litter. In fact, nutrients were returned at about the rate of 1 kg/40-60 kg litterfall in yellow birch stands compared with rates of 1 kg/90-100 kg litterfall in spruce-fir stands. Quantities of Ca were largest and P smallest in litterfall of all stands but Mg > K in deciduous stands and K > Mg in spruce-fir stands. In each ecosystem, foliage contained 75 per cent or more of the nutrients in annual litterfall; even small quantities of deciduous leaves significantly increased nutrients in litterfall of spruce-fir stands. Reproductive components in spruce-fir stands contained 24 per cent of P in leaf litterfall which indicates that in years of average or below average seed production, shifts occur in the nutrient cycles of these stands.

Calcium was most abundant (335-400 kg/ha) and P least abundant (45-96 kg/ha) of nutrients in the forest floor in each ecosystem; in the spruce-fir ecosystem K > Mg but the order was reversed in yellow birch ecosystems as above. Within the forest floor, distributional patterns varied
among nutrients. Bole and branch litter and smaller components of the 01 horizon in spruce-fir and immature yellow birch stands contained quantities > 72 per cent of Ca and > 62 per cent of Mg whereas 55-85 per cent K and P accumulated in the 02 horizon. These differences apparently reflect intensive leaching of Ca and Mg and the formation of insoluble compounds of P with Al and/or Fe under the very acid conditions of the 02 horizon, fixation of P in organic compounds, fixation of K by expanding layer silicates, and perhaps immobilization of each by microbes. Forest floor nutrient pools were equivalent to the nutrients contained in 6 to 21 years annual litterfall and generally Ca represented quantities equivalent to longest periods of accumulations and P the least.

Potassium quantities increased with increasing depth within the soils and exceeded quantities of Ca in some cases. This suggested release of K by weathering of biotite and other K bearing primary minerals present in these soils. Coarse texture and high acidity were correlated with low Ca and Mg status of these soils. Additional sources of K available to plants apparently included nonexchangeable K from biotite, muscovite, and perhaps organic matter; appreciable quantities may exist in these soils which would significantly alter the distributional patterns of K, especially in the yellow birch ecosystems. The results
which showed little relationship between soil properties and
vegetational parameters, either structural or functional,
raise serious questions concerning the validity of the
standard chemical analysis methods used to measure availa-
ibility of soil nutrients to trees in the study area. Evi-
dence is increasing that direct uptake of nutrients via
mycorrhizae occurs (Went and Stark, 1968). This suggests
that in the study area soil nutrients upon which trees are
most dependent are in nonexchangeable forms in soil organic
matter rather than exchangeable nutrients which might be
measured by the tests used. Clearer study of the role of
mycorrhizae in the nutrition of these species in soils of
the study area is needed; when the sources of nutrients
have been identified, then tests can be developed for valid
assessment of nutrient status of these soils and the rela-
tionship between vegetational dynamics and soil nutrients
determined.

Variations in the distribution of litter on the forest
floor, soil creep, concentration of nutrients about tree
bases by stemflow, and disruption of soils by windthrow
contributed to high degrees of variability within the soils
of the study area. Results suggested that insufficient
numbers of soil samples were analyzed to accurately char-
acterize these soils and limited sampling in this study may
have further obscured soil-vegetational relationships.
Nutrient input of Ca, K, and Mg via gross precipitation is equivalent to annual accumulation of each nutrient in perennial components of vegetation. Methods used in this study were not adequate for analysis of P concentrations in precipitation. Annual net precipitation was approximately 75 per cent and 80 per cent of gross precipitation in spruce-fir and yellow birch ecosystems, respectively, in the study area; despite this reduction, throughfall contained larger quantities of nutrients than gross precipitation as the result of leaching and/or washoff of nutrients from plant surfaces. Concentrations in throughfall was Ca - 1.3-1.6 times concentrations in gross rainfall; K - 3.9 times; and Mg 3.6 times. Relative to nutrients in annual litterfall, only small quantities of Ca (< 7 kg/ha) and Mg (< 3 kg/ha) were transferred annually in precipitation from plants to the forest floor, but annual transfer of K (17 kg/ha) from plants via leaching and/or washoff was slightly greater than that via litterfall. Stemflow contributed < 6 per cent of total precipitation, Ca, and K reaching the forest floor annually. Nutrient enrichment of stemflow varied with species apparently in relation to solubility of the nutrient, bark texture, and pH of stemflow but quantities were in the order Mg > K > Ca. Because of the leaching of Mg from bark of red spruce and yellow birch, stemflow contributed between 25 and 30 per cent of the total magnesium reaching the forest floor via precipitation.
Stemflow may be of greater significance in these ecosystems than absolute quantities of water and nutrients indicate, because of their concentration at the base of trees. Variations in the distribution of understory vegetation as well as in soil properties may result; the role of both throughfall and stemflow in the dynamics of these stands requires further study.

The intensity of nutrient cycles as determined by the relative quantity of ecosystem nutrients involved in annual cycles, decreased between ecosystems in the order mature yellow birch > immature yellow birch > spruce-fur. Intensity of cycles also varied among nutrients generally in decreasing order Mg > P > K > Ca. These and the other results showed that the three ecosystems studied in the Balsam Mountains were better characterized and distinguished by distributional patterns of dry matter and by dry-matter production and nutrient cycling rates than by absolute quantities of either in the ecosystems. More rapid transfer rates of nutrients from vegetation to the forest floor - soil compartment than uptake rates by vegetation were indicated. These differences do not necessarily indicate annual mineral input into the ecosystems but rather suggest that a large proportion of the nutrients in the vegetation are incorporated in annual cycles to the forest floor - soil compartment, but a smaller proportion of the soil nutrients are incorporated in annual uptake by plants.
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APPENDICES
APPENDIX A

TABLE LV

TOPOGRAPHIC ATTRIBUTES OF STANDS

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a\(\text{U}\) = uniform slope; Co = concave slope; Cv = convex slope.

bElevation of ridge upslope from plot minus plot elevation.
TABLE LVI

DISTRIBUTION OF STEMS > 2.54 CM DIAMETER AT BREAST HEIGHT BY DIAMETER CLASS

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TABLE LVII

SPECIFIC GRAVITY OF BOLES (WOOD AND BARK)
OF TREES HARVESTED DURING 1969

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^aDenotes total number of bole sections in sample; sections were distributed among one to four trees, depending on species.
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\(^a\)H. R. DeSelms, unpublished data. Based on trees harvested from Blue Ridge Parkway right-of-way in study area in 1959.
TABLE LVIX

REGRESSION CONSTANTS OF EQUATIONS FOR ESTIMATING BOLE VOLUME AND BIOMASS, BRANCH BIOMASS, FOLIAGE BIOMASS AND 1965 DIAMETER OF TREES

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<th>Independent Variable</th>
<th>Regression Coefficient</th>
<th>Y-Intercept (Constant)</th>
<th>Standard Error of Estimate</th>
<th>Multiple R</th>
<th>N</th>
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TABLE LVIX (continued)

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**Prunus pensylvanica**

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| 1Bo                             | 1DBH                              | 1.0984                  | +0.2780                | -                                      | -         | 2  |
| 1Bo                             | 1D46                              | 0.6907                  | +0.6614                | -                                      | -         | 2  |

**Quercus rubra**

| 1Bv                             | 1DBH                              | 2.5908                  | +2.1698                | -                                      | -         | 2  |
| 1Bo                             | 1DBH                              | 0.9583                  | +0.4518                | -                                      | -         | 2  |
| 1Br                             | 1DBH                              | 3.8598                  | -3.2742                | -                                      | -         | 2  |
| 1F                              | 1DBH                              | 3.5458                  | -3.3398                | -                                      | -         | 2  |
| DBH65                           | DBH69                             | 0.9147                  | +0.0407                | 0.0264                                 | .999      | 3  |
| 1Bo                             | 1D46                              | 2.4028                  | -0.4047                | -                                      | -         | 2  |
| 1Br                             | 1D46                              | 3.5895                  | -3.2446                | -                                      | -         | 2  |
| 1F                              | 1D46                              | 3.2954                  | -3.3104                | -                                      | -         | 2  |

**Rhododendron spp.**

| 1Bv                             | 1DBH                              | 2.3740                  | +2.0934                | 0.0504                                 | .992      | 5  |
| 1Bo                             | 1DBH                              | 3.1548                  | -1.7136                | 0.1247                                 | .990      | 6  |
| 1Br                             | 1DBH                              | 3.0413                  | -1.9457                | 0.1862                                 | .977      | 6  |
| 1F                              | 1DBH                              | 1.5240                  | -1.3281                | 0.1229                                 | .961      | 6  |
| 1Bo                             | 1D46                              | 4.6474                  | -3.0168                | 0.2515                                 | .974      | 6  |
| 1Br                             | 1D46                              | 2.8954                  | -2.0476                | 0.0750                                 | .994      | 6  |
| 1F                              | 1D46                              | 1.8758                  | -1.6847                | 0.0852                                 | .981      | 6  |

**Sorbus americana**

<p>| 1Bv                             | 1DBH                              | 1.6589                  | +2.9793                | 0.0904                                 | .982      | 3  |
| 1Bo                             | 1DBH                              | 2.1842                  | -0.8269                | 0.1358                                 | .998      | 4  |
| 1Br                             | 1DBH                              | 2.0270                  | -1.3485                | 0.4887                                 | .971      | 4  |</p>
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<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>1Bo</td>
<td>1DBH</td>
<td>2.0124</td>
<td>-0.9484</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>1Br</td>
<td>1DBH</td>
<td>2.6907</td>
<td>-1.6086</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>1F</td>
<td>1DBH</td>
<td>1.7529</td>
<td>-2.2759</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>1Bo</td>
<td>D46</td>
<td>1.5057</td>
<td>-0.7410</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>1Br</td>
<td>D46</td>
<td>2.0148</td>
<td>-1.3326</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>1F</td>
<td>D46</td>
<td>1.3116</td>
<td>-2.0954</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
</tbody>
</table>

<sup>a</sup>Bv = bole volume (cm<sup>3</sup>), Bo = bole biomass (kg), Br = branch biomass (kg), F = foliage biomass (kg), l = log<sub>10</sub>.

<sup>b</sup>DBH = bole diameter at breast height (cm); D46 = bole diameter (cm) at height of 46 cm; DBH69 = bole diameter at breast height (inches).

<sup>c</sup>Standard error of estimate of \( \hat{Y} \) at \( \bar{X} \).
TABLE LX

RATIO OF 1965 BOLE DIAMETER/1969 BOLE DIAMETER\(^a\) (AT 46 CM)
FROM WHICH DIAMETER INCREMENTS OF CERTAIN WOODY SPECIES
WERE ESTIMATED

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>S.E. (^b)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies fraseri</td>
<td>0.903</td>
<td>0.055</td>
<td>12</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td></td>
<td>.c</td>
<td></td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>0.774</td>
<td>0.072</td>
<td>7</td>
</tr>
<tr>
<td>Aesculus octandra</td>
<td>0.922</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Amelanchier arborea</td>
<td>0.776</td>
<td>0.061</td>
<td>4</td>
</tr>
<tr>
<td>Betula lutea</td>
<td>0.907</td>
<td>0.018</td>
<td>12</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>0.934</td>
<td>0.014</td>
<td>6</td>
</tr>
<tr>
<td>Picea rubens</td>
<td>0.934</td>
<td>0.016</td>
<td>16</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>0.744</td>
<td>0.079</td>
<td>2</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>0.558</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Rhododendron spp.</td>
<td>0.586</td>
<td>0.083</td>
<td>5</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>0.759</td>
<td>0.101</td>
<td>3</td>
</tr>
<tr>
<td>Vaccinium spp.</td>
<td>0.721</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>0.754</td>
<td>0.130</td>
<td>2</td>
</tr>
</tbody>
</table>

\(^a\)Based on measurements of radial increments made from cross-sectional discs from boles at 46 above stem base.

\(^b\)Standard error of mean.

\(^c\)Acer spicatum ratio assumed.
TABLE LXI

RATIOS FROM WHICH BIOMASS OF COMPONENTS AND DIAMETER INCREMENTS OF SMALL SAPLINGS AND SHRUBS WERE ESTIMATED

<table>
<thead>
<tr>
<th>Species</th>
<th>kg/cm&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Ratio&lt;sup&gt;b&lt;/sup&gt;</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bole</td>
<td>Twigs</td>
<td>Foliage</td>
</tr>
<tr>
<td><strong>Acer saccharum</strong></td>
<td>0.0407</td>
<td>0.0254</td>
<td>0.0240</td>
</tr>
<tr>
<td><strong>Cornus alternifolia</strong></td>
<td>0.0163</td>
<td>0.0045</td>
<td>0.0052</td>
</tr>
<tr>
<td><strong>Crataegus sp.</strong></td>
<td>0.0525</td>
<td>0.0170</td>
<td>0.1030</td>
</tr>
<tr>
<td><strong>Prunus pensylvanica</strong></td>
<td>-</td>
<td>0.2421</td>
<td>0.0198</td>
</tr>
<tr>
<td><strong>Ribes rotundifolium</strong></td>
<td>0.0240</td>
<td>0.0062</td>
<td>0.0059</td>
</tr>
<tr>
<td><strong>Rubus allegheniensis</strong></td>
<td>0.0130</td>
<td>-d</td>
<td>0.0740</td>
</tr>
<tr>
<td><strong>Sambus pubens</strong></td>
<td>0.0567</td>
<td>0.2894</td>
<td>0.0380</td>
</tr>
<tr>
<td><strong>Viburnum alnifolium</strong></td>
<td>0.0023</td>
<td>0.1350</td>
<td>0.0226</td>
</tr>
</tbody>
</table>

<sup>a</sup>Ratio of component weight (kg)/stem diameter (cm) at 46 cm height harvested samples. Component biomass of stems encountered in plot tally was estimated as the product of the appropriate ratio multiplied by stem diameter at 46 cm height of each stem tallied.

<sup>b</sup>Ratio of stem diameter at 46 cm height in 1965 to diameter 1969. Diameter in 1965 was estimated from measurements of radial increment at 46 cm height during the interval 1965-1969. Biomass was calculated from 1965 diameter and net production estimated as (1969 biomass - 1965 biomass)/(5.0).

<sup>c</sup>Ratio estimated at 46 cm height assumed.

<sup>d</sup>All perennial components treated as stems.

<sup>e</sup>Stems were all first-year.
<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Blades or Needles</th>
<th>Leaf Area Per Unit Leaf Weight cm²/g</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies fraseri</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 year needles</td>
<td>105</td>
<td>179.6</td>
<td>20.0</td>
</tr>
<tr>
<td>2 years</td>
<td>105</td>
<td>132.4</td>
<td>10.0</td>
</tr>
<tr>
<td>3 years</td>
<td>105</td>
<td>115.6</td>
<td>11.6</td>
</tr>
<tr>
<td>4 years and older</td>
<td>105</td>
<td>92.6</td>
<td>10.0</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td>15</td>
<td>337.1</td>
<td>22.9</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>51</td>
<td>390.8</td>
<td>11.4</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>91</td>
<td>292.9</td>
<td>88.2</td>
</tr>
<tr>
<td>Aesculus octandra</td>
<td>84</td>
<td>306.1</td>
<td>83.4</td>
</tr>
<tr>
<td>Amelanchier arborea</td>
<td>67</td>
<td>202.6</td>
<td>16.0</td>
</tr>
<tr>
<td>Betula lutea</td>
<td>138</td>
<td>246.0</td>
<td>75.6</td>
</tr>
<tr>
<td>Cornus alternifolia</td>
<td>10</td>
<td>417.0</td>
<td>82.2</td>
</tr>
<tr>
<td>Crataegus sp.</td>
<td>35</td>
<td>672.9</td>
<td>132.2</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>72</td>
<td>261.6</td>
<td>30.1</td>
</tr>
<tr>
<td>Picea rubens</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 year needles</td>
<td>25</td>
<td>154.2</td>
<td>15.8</td>
</tr>
<tr>
<td>2 years</td>
<td>25</td>
<td>150.0</td>
<td>13.0</td>
</tr>
<tr>
<td>3 years</td>
<td>25</td>
<td>149.3</td>
<td>11.1</td>
</tr>
<tr>
<td>4 years and older</td>
<td>25</td>
<td>135.7</td>
<td>7.2</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>42</td>
<td>196.8</td>
<td>15.3</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>20</td>
<td>143.9</td>
<td>17.2</td>
</tr>
<tr>
<td>Rhododendron catawbiense</td>
<td>75</td>
<td>98.5</td>
<td>4.9</td>
</tr>
<tr>
<td>Rhododendron maximum</td>
<td>35</td>
<td>86.2</td>
<td>18.2</td>
</tr>
<tr>
<td>Ribes glandulosum</td>
<td>10</td>
<td>211.4</td>
<td>132.1</td>
</tr>
<tr>
<td>Ribes rotundifolium</td>
<td>10</td>
<td>399.4</td>
<td>-</td>
</tr>
<tr>
<td>Rubus allegheniensis</td>
<td>38a</td>
<td>313.1</td>
<td>32.3</td>
</tr>
<tr>
<td>Rubus idaeus var. canadensis</td>
<td>57b</td>
<td>489.9</td>
<td>132.2</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>69c</td>
<td>377.8</td>
<td>14.8</td>
</tr>
</tbody>
</table>
### TABLE LXII (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Blades or Needles</th>
<th>Leaf Area Per Unit Leaf Weight cm²/g.</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorbus americana</td>
<td>768d</td>
<td>144.3</td>
<td>22.6</td>
</tr>
<tr>
<td>Vaccinium constablaei</td>
<td>98</td>
<td>277.9</td>
<td>36.4</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>15</td>
<td>100.8</td>
<td>10.1</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>29</td>
<td>231.5</td>
<td>27.0</td>
</tr>
</tbody>
</table>

*a* Leaflets from ca 8 leaves.

*b* Leaflets from ca 12 leaves.

*c* Leaflets from ca 6 leaves.

*d* Leaflets from ca 50 leaves.
APPENDIX B

SOILS

Pedon 8-1

Location: plot 8 near Buckeye Gap east of Parkway within one meter of an intermittent stream in a cove with an immature yellow birch stand. Red spruce dominated slopes on either side of cove.

Slope 31 per cent; Azimuth 38°; elevation 1600 m.

Rock outcrops and boulders: biotite schist and quartz-feldspar biotite gneiss; Quartzite.

Collected: August 8, 1969.

01 8-2 cm; deciduous leaf litter.

02 2-0 cm.

A1 0-20 cm; dark reddish brown (5YR 2/2, moist) to weak red (10R 5/2, dry) sandy clay loam; granular to weak subangular blocky; friable; stones 25% by volume; many fine roots; pH 4.2 (water), 3.7 (KCl).

B2 20-41 cm; yellowish brown (10YR 5/8, moist) to pale brown (10YR 6/3, dry) sandy loam; weak subangular blocky; friable; stones 50%; many roots to 0.6 cm diameter; pH 4.5 (water), 4.0 (KCl).

B3 41-51 cm; yellowish brown (10YR 5/6, moist) to light reddish brown (2.5YR 6/4, dry) sandy loam; stones 75%; no roots; pH 4.7 (water), 4.5 (KCl).

Pedon 8-2

Location: plot 8 near Buckeye Gap east of Parkway in an immature yellow birch stand. Red spruce dominated slopes on either side of cove.

Slope 31%; Azimuth 38°; elevation 1600 m.
Rock outcrops and boulders: biotite schist, quartz-feldspar biotite gneiss, and quartzite.

Collected: August 8, 1969

01 6-3 cm; deciduous litter.

02 3-0 cm; many fine roots.

A1 0-10 cm; dark reddish brown (5YR 2/2, moist) to weak red (10R 5/3, dry) sandy clay loam; granular; friable; stones 10%; roots up to 1.7 cm diameter abundant; pH 3.8 (water), 3.5 (KCl).

A3 10-15 cm; dark brown (7.5YR 3/2, moist) to reddish brown (2.5YR 5/4, dry) sandy clay loam; granular to weak subangular blocky; friable; stones 10%; moderate number of roots to 1.7 cm diameter; pH 4.2 (water), 3.6 (KCl).

B1 15-23 cm; dark brown (10YR 3/3, moist) to reddish brown (2.5YR 5/4) sandy loam; weak subangular blocky to granular; friable; no stones; roots few; pH 4.3 (water), 4.0 (KCl).

B2 23-36 cm; yellowish brown (10YR 5/6, moist) to yellow (10YR 7/6, dry) sandy loam; weak subangular blocky, firm, stones absent; roots scarce; pH 4.7 (water), 4.2 (KCl).

B3 36-31+ cm; strong brown (7.5YR 5/8, moist, to 2.5YR 7/4, dry) sandy loam; weak subangular blocky; firm; stones and roots absent; pH 4.6 (water), 4.3 (KCl).

Pedon 38-1

Location: plot 38 at Deep Gap; uniform microtopography in a cove dominated by immature yellow birch and with occasional Quercus rubra.

Slope 36%; Azimuth 259°; elevation 1585 m.

Rock outcrops and boulders: calc-silicate rock, garnet mica schist, muscovite feldspar quartz gneiss.

Collected: August 11, 1969.
01 4-1 cm; yellow birch leaf and branch litter; many fine roots.

02 1-0 cm; many fine roots.

A1 0-8 cm; black (10YR 2/1, moist) to dark gray brown (10YR 4/2, dry) sandy clay loam; granular; very friable, gradual boundary; stones 10%; many fine roots; pH 4.4 (water), 4.1 (KCl).

A3 8-29 cm; very dark gray brown (10YR 3/2, moist) to dark gray brown (10YR 4/2, dry) clay loam; weak subangular blocky; friable, gradual boundary; stones 10%; many roots to 0.6 cm diameter; pH 4.7 (water), 4.4 (KCl).

B1 29-41 cm; dark yellowish brown (10YR 3/4, moist) to light yellowish brown (10YR 6/4, dry) loam; weak subangular blocky; friable; clear boundary; stones 10%; roots occasional; pH 4.9 (water), 4.1 (KCl).

B2 41-61 cm; yellowish brown (10YR 5/8, moist) to pale yellow (2.5YR 7/4, dry) loam; weak subangular blocky; friable; gradual boundary; stones 20%; roots occasional; pH 4.9 (water), 3.9 (KCl).

B3 61-124+ cm; brownish yellow (10YR 6/8, moist) to pale yellow (2.5YR 8/4, dry) sandy loam; coarse granular, friable, gradual boundary, stones 20%; no roots; pH 5.3 (water), 4.0 (KCl).

Pedon 53-1

Location: plot 53, near Wesner Bald on block field in bottom of large cove; vegetation consisted of mature yellow birch with a sparse understory of mountain maple. Boulders covered with dense mat predominated by Hylocomium splendens.

Slope 49%; Azimuth 18°; elevation 1570 m.

Rock outcrops and boulders: quartz feldspar biotite gneiss and quartzite.

01 4-1 cm; deciduous leaf litter in depressions between boulders; absent from boulder.

02 1-0 cm; poorly developed beneath deciduous leaf litter in depressions; formed a continuous layer beneath Hylocomium splendens on boulders.

A1 0-64 cm; black (N2/, moist) loamy sand, granular; very friable; clear boundary; stones 85%; voids 10%; roots, many to 1.7 cm diameter.

B1 64-76 cm; dark reddish brown (5YR 2/2, moist) sandy loam; granular, very friable, clear boundary; stones 40%; no voids; roots, several to 0.6 cm diameter.

B2 76-87 cm; dark reddish brown (5YR 3/3, moist) sandy loam; granular, very friable; clear boundary; stones 25%; no voids; roots, several to 0.6 cm diameter.

Pedon 10-2

Location: plot 10 on Big Bear Trail Ridge ca 50 meters east of Blue Ridge Parkway in a dense Fraser fir stand; uniform microtopography.

Slope 50%; Azimuth 182°; elevation 1768 m.

Rock outcrops and boulders: biotite gneiss, garnet biotite gneiss, and biotite schist.


01 17-13 cm; litter of Fraser fir needles and branches.

02 13-0 cm; black (N2/, moist) to dark reddish gray (10R 3/1, dry) muck; clear boundary; many fine roots; pH 3.6 (water), 3.1 (KCl).

A1 0-18 cm; very dusky red (10R 2/2, moist) to dark reddish gray (10R 4/1, dry) loamy sand; granular; friable; clear boundary; stones absent; many roots; pH 3.8 (water), 3.3 (KCl).

A3 18-29 cm; black (N2/, moist) to dark gray (5YR 4/1, dry) sandy loam; subangular blocky; friable; clear boundary stones absent; roots occasional.
B  29-41 cm; dark reddish brown (2.5YR 2/4, moist) to weak red (2.5YR 4/2, dry) loamy sand; granular; friable; clear boundary; stones absent; roots occasional; pH 3.9 (water), 3.5 (KCl).

R  41+ cm.

Pedon 12-1

Location: plot 12 on Reinhart Knob in Fraser fir stand with occasional red spruce and yellow birch, microtopography uniform.

Slope 13%; Azimuth 266°; elevation 1817 m.

Rock outcrops and boulders: garnet-biotite-gneiss, feldspar muscovite, and quartz.

Collected: August 12, 1969.

01  5-0.5 cm; litter of fir needles.

02  0.5-0 cm; many small roots.

A1  0-6 cm; black (5YR 2/1, moist) to dark reddish brown (5YR 3/2, dry) sandy loam; granular; very friable; stones absent; roots, many up to 1.7 cm; pH 3.8 (water), 3.2 (KCl).

B21ir  6-13 cm; dark reddish brown (2.5YR 2/4, moist) to dark brown (7.5YR 4/2, dry) sandy loam; subangular blocky; firm; stones 10%; roots, many; pH 4.0 (water), 3.6 (KCl).

B22ir  13-28 cm; dark reddish brown (5YR 3/3, moist) to dark gray brown (10YR 4/2, dry) sandy loam; subangular blocky; firm; stones 25%; many roots up to 0.5 cm diameter; pH 4.2 (water), 3.9 (KCl).

B31  28-38 cm; dark yellowish brown (10YR 3/4, moist) to yellowish brown (10YR 5/4, dry) coarse sandy loam with gravel; weak subangular blocky; friable; stones 50%; roots occasional; pH 5.2 (water), 4.2 (KCl).
B32 38-71 cm; yellowish brown (10YR 5/6, moist) to yellow (10YR 7/6, dry) coarse sandy loam with gravel; friable; stones 50%; no roots; pH 4.8 (water), 4.4 (KCl).

R 71+ cm.

Pedon 43-1

Location: plot 43 on Lone Bald in a stand dominated by red spruce and with Fraser fir and birch; uniform microtopography.

Slope 54%; Azimuth 30°; elevation 1768 m.

Rock outcrops and boulders: meta graywache.

Collected: August 12, 1969.

01 1.9-0.6 cm; spruce litter.

02 0.6-0 cm; many fine roots.

A1 0-10 cm; black (10YR 2/1, moist) to dark reddish brown (5YR 3/2, dry) sandy loam; fine granular; very friable, clear wavy boundary; stones 10%; many roots 0.6 cm and smaller in diameter; pH 3.8 (water), 3.3 (KCl).

B2 10-43 cm; very dark brown (10YR 2/2, moist) to dark brown (10YR 4/3, dry) sandy loam; coarse granular; very friable, clear smooth boundary; stones 5%; many roots but fewer than in A1.

B31 43-56 cm; dark brown (10YR 3/3, moist) to dark yellowish brown (10YR 4/4, dry) sandy loam; coarse granular; friable; clear smooth boundary; stones 5%; occasional roots; pH 4.8 (water), 4.3 (KCl).

B32 56-86 cm; dark yellowish brown (10YR 4/4, moist) to yellowish brown (10YR 5/4, dry) sandy loam; granular; friable; clear smooth; rocks 20%, roots occasional; pH 4.8 (water), 4.3 (KCl).

R 86+ cm
Pedon 49-1

Location: plot 49 at summit of Richland Balsam in Fraser fir stand with some red spruce and Rhododendron. Uniform microtopography.

Slope 52%; Azimuth 52°; elevation 1951 m.

Rock outcrops and boulders: quartzite; garnet mica schist.


01 26-14 cm; litter predominantly of fir needles.
02 14-0 cm; black (N2/, moist) to black (5YR 2/1, dry) muck; roots, many up to 1.9 cm diameter nearly forming a mat; pH 3.9 (water), 3.2 (KCl).

A1 0-28 cm; black (10YR 2/1, moist) to dark reddish brown (5YR 3/2, dry) sandy loam; subangular blocky; friable; many roots but of smaller diameter than 02 horizon; stones absent; pH 4.4 (water), 3.8 (KCl).

B 28-47 cm; dark brown (7.5YR 4/4, moist) to yellowish brown (10YR 5/6, dry) loamy sand; subangular blocky; firm; rocks, 80%; roots absent; pH 4.5 (water), 4.2 (KCl).

Pedon 49-2

Location: plot 49, at summit of Richland Balsam in Fraser fir stand; uniform microtopography.

Slope 52%; Azimuth 52°; elevation 1951 m.

Rock outcrops and boulders: quartzite.


01 12-2.5 cm; 01 litter a thick mat of fir needles.
02 2.5-0 cm.

A1 0-10 cm; black (5YR 2/1, moist) to dark brown (7.5YR 4/2, dry) sandy loam; granular; very friable; stones 10%; many roots up to 1.7 cm diameter; pH 4.4 (water), 4.1 (KCl).
A3 10-25 cm; dark reddish brown (5YR 2/2, moist; 5YR 3/2, dry) sandy loam; weak subangular blocky; friable; stones 10%; roots numerous; pH 4.5 (water), 4.1 (KCl).

B1 25-43 cm; black (5YR 2/1, moist) to dark reddish brown (5YR 3/3, dry) sandy loam; weak subangular blocky; very friable; stones 30%; numerous roots up to 1.7 cm diameter.

B2 43-58 cm; dark reddish brown (2.5YR 2/4, moist; 5YR 3/3, dry) sandy loam; weak subangular blocky; friable; gradual boundary; stones 40%; small roots numerous; pH 4.7 (water), 4.3 (KCl).

R 58+ cm.

Pedon 57-1

Location: plot 57, slope of Richland Balsam, ca 50 m west of Blue Ridge Parkway; in a dense Fraser fir stand; soil pit located in mound of an old windthrow.

Slope 20%; Azimuth 159°; elevation 1832 m.

Rock outcrops and boulders: garnet-muscovite gneiss.

Collected: August 12, 1969.

01 1.7-0.3 cm; litter composed of fir needles.

02 0.3-0 cm; poorly developed.

A1 0-5 cm; black (N2/, moist) to dark reddish brown (5YR 2/2, dry) sandy loam; granular; very friable; abrupt boundary; stones 5%; many fine roots; pH 3.6 (water), 3.1 (KCl).

A3 5-7 cm; black (10YR 2/1, moist) to reddish brown (5YR 5/4, dry) sandy loam; weak subangular blocky; friable; abrupt boundary stones absent; many small roots; pH 3.6 (water), 3.3 (KCl).

B1 7-33 cm; reddish brown (2.5YR 4/4, moist) to very pale brown (10YR 7/4, dry) sandy loam; granular, friable, clear boundary; stones 5%; roots occasional; pH 4.6 (water), 4.2 (KCl).
B2 33-46 cm; dark brown (10YR 3/3, moist) to brown (10YR 5/3, dry) sandy loam; weak subangular blocky friable; pH 4.6 (water), 4.2 (KCl) mixed with red (2.5YR 5/6, moist) to very pale brown (10YR 7/4, dry) sandy loam; granular, very friable; clear wavy boundary; stones 5%, roots occasional.

B3 46-83+ cm; red (2.5YR 5/6, moist) to very pale brown (10YR 7/4, dry) coarse sandy loam; coarse granular; friable, stones 15%; roots very rare; pH 4.7 (water), 4.3 (KCl).

Pedon 57-2

Location: plot 57 on slopes of Richland Balsam ca 50 m west of Blue Ridge Parkway on uniform microtopography in a dense Fraser fir stand.

Slope 20%; Azimuth 159°; elevation 1832 m.

Rock outcrops and boulders: garnet-muscovite gneiss.


01 7-2.5 cm; litter well developed consisting of needles and branches of Fraser fir.

02 2.5-0 cm; some small roots present.

A1 0-8 cm; black (10YR 2/1, moist) to dark reddish brown (5YR 3/2, dry) loam; massive; friable, gradual boundary, stones 10%; many roots from small up to 1.7 cm diameter; pH 3.5 (water), 3.1 (KCl).

B1 8-22 cm; dark brown (10YR 3/3, moist) to dark brown (7.5YR 4/2, dry) sandy loam; subangular blocky, friable; gradual boundary; stones 10%; many roots from small up to 1.7 cm diameter; pH 4.2 (water), 3.8 (KCl).

B2 22-30 cm; dark yellowish brown (10YR 4/4, moist) to yellowish brown (10YR 5/4, dry) sandy loam; subangular blocky; friable, clear boundary; stones 10%; many roots up to 0.3 cm diameter; pH 4.6 (water), 4.1 (KCl).
B3  30-56 cm; yellowish brown (10YR 5/8, moist) to yellow (10YR 7/6, dry) sandy loam; weak subangular blocky; friable; clear boundary; stones 5%; roots rare; pH 4.2 (water), 3.8 (KCl).

C  56 to 79+ cm; olive (5YR 5/4, moist) to very pale brown (10YR 8/3, dry) fine sand; single grained; friable; stones and roots absent; pH 4.8 (water), 4.1 (KCl).
## APPENDIX C

### TABLE LXIII

SOIL TEMPERATURES AT SELECTED LOCATIONS WITHIN THE STUDY AREA

<table>
<thead>
<tr>
<th>Station</th>
<th>Elevation m</th>
<th>Azimuth</th>
<th>Date</th>
<th>Soil Temperature °C Depth, Cm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Plot 38</td>
<td>1585</td>
<td>259°</td>
<td>10/2/69</td>
<td>-b</td>
</tr>
<tr>
<td>(Yellow birch)</td>
<td></td>
<td></td>
<td>1/21/70</td>
<td>c</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3/23/70</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>6/28/70</td>
<td>13.3</td>
</tr>
<tr>
<td>Plot 2</td>
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<td>328°</td>
<td>10/2/69</td>
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<tr>
<td>(Spruce)</td>
<td></td>
<td></td>
<td>1/21/70</td>
<td>d</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3/23/70</td>
<td>e</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>6/28/70</td>
<td>13.3</td>
</tr>
<tr>
<td>Plot 54</td>
<td>1920</td>
<td>71°</td>
<td>10/2/69</td>
<td>10.6</td>
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<tr>
<td>(Fraser fir)</td>
<td></td>
<td></td>
<td>1/21/70</td>
<td>f</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3/23/70</td>
<td>f</td>
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<tr>
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<td></td>
<td></td>
<td>6/28/70</td>
<td>11.7</td>
</tr>
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<td>Station</td>
<td>Elevation m</td>
<td>Azimuth</td>
<td>Date</td>
<td>Soil Temperature °C</td>
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</tr>
<tr>
<td>Plot 26</td>
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<tr>
<td>(Fraser fir)</td>
<td>1829</td>
<td>284°</td>
<td>10/2/69</td>
<td>f</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1/21/70</td>
<td>e</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>6/28/70</td>
<td>10.6</td>
</tr>
</tbody>
</table>

aPredominant canopy tree.
bMeasurement not made.
cIce from 0 - 8.0 cm depth.
dIce from 0 - 10 cm depth.
eIce from 0 - 23 cm depth.
fIce from 0 - 16 cm depth.
VITA

The author was born and reared on the family farm in Union County, Illinois. Early elementary education was in a nearby rural school and later elementary and secondary education was in the schools of Jonesboro and Anna, Illinois. The Bachelor of Arts degree with a major in Zoology and minor in Botany and Master of Science in Education were earned in 1960 and 1963, respectively, from Southern Illinois University. Between 1960 and 1967 the author taught science courses in the secondary schools of Dongola and Anna, Illinois. Study toward the Ph.D. was begun in 1967 at The University of Tennessee. In 1970 the author joined the faculty of the Botany Department, Southern Illinois University and transferred to the Department of Forestry of that University in the fall of 1971. In 1960 he and Marita A. Hogue were married; they have three sons: Bradley A., 1961; Douglas S., 1964; and Eric W., 1967.