

Utah State University

DigitalCommons@USU

Aspen Bibliography

Aspen Research

1990

Nutrient cycling in aspen ecosystems

John Pastor

Follow this and additional works at: https://digitalcommons.usu.edu/aspen_bib



Part of the [Forest Sciences Commons](#)

Recommended Citation

Pastor, John. 1990. Nutrient cycling in aspen ecosystems. Aspen Symposium '89 : Proceedings. General Technical Report NC-140. North Central Forest Experiment Station Forest Service, U.S. Department of Agriculture St. Paul, Minnesota. 21-38.

This Contribution to Book is brought to you for free and open access by the Aspen Research at DigitalCommons@USU. It has been accepted for inclusion in Aspen Bibliography by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



NUTRIENT CYCLING IN ASPEN ECOSYSTEMS

John Pastor¹

ABSTRACT.-- The cycles of nutrients in aspen ecosystems from the Great Lakes region to Alaska have been intensively studied by researchers since the early 1970s. These studies have revealed several patterns common to most aspen stands. In general, aspen rapidly takes up large quantities of nutrients and stores them in woody tissues, particularly bole bark and bole wood. The small amounts of nutrients that are returned in leaf litter are released relatively rapidly during decay. The net result is that aspen retains nutrients effectively within the ecosystem, leaching losses are minimal and decrease quickly after fire or clearcutting, and soil fertility is improved. However, nutrient removals in harvested biomass can be quite high, particularly when whole tree harvests are combined with short rotations.

INTRODUCTION

Aspen stands became established over much of the northern Lake States following forest fires and logging of the white pines around the turn of the century. Aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.) constitutes more than half of the Lake States' total pulpwood cut (Keays 1972). National domestic consumption plus exports of pulpwood rose steadily from 8.6 million cords in 1920 to 88.8 million cords in 1972, and are expected to rise to 178 million cords by the year 2000 (USDA 1974). Besides this increased demand for the more traditional forest products, the demand of forests for recreation use is also rising (Clausen 1978).

In order to meet these increased demands on decreased amounts of forest land, many timber companies and public foresters are considering managing current forest lands more intensively. Intensive management may include species conversion, stand improvement, and fertilization, but more often refers to the harvest of greater amounts of the aboveground biomass.

Intensive harvesting is expected to drain considerable amounts of nutrients from stands (Kimmins 1977). Rising energy costs make it unlikely that these losses can be offset economically by fertilization. It appears that forest managers will need to rely on the existing nutrient capital of the forest to "maintain continuous production" (Jorgensen et al. 1975). Proper use and conservation of this capital will rely on knowledge of the distribution and cycling of nutrients within the forest-soil ecosystem.

The major objective of this paper is to describe the nutrient cycles in aspen stands in comparison with associated upland forest types. Specific purposes of this review will be: (1) To acquaint the reader with the major findings of nutrient cycling research in aspen ecosystems. Particular emphasis will be placed on the biologic pattern of the cycle, especially the uptake and retention of nutrients by trees, and their return and incorporation into the soil by processes operating in the forest floor. (2) To compare the cycling of nutrients by aspen stands to cycling by other forest types collectively known

¹John Pastor, Research Associate, Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota 55811

as cool temperate forests. (3) To point out areas in the literature not yet fully addressed, or which have been recognized only recently. (4) To point out some ecological, silvicultural and pedological implications of nutrient cycling.

The cycling of nutrients in an ecosystem has both static and dynamic aspects. The static aspects are the distribution of organic matter and nutrients in the plant-forest floor-mineral soil system. The dynamic aspects are: (1) the inputs of nutrients by precipitation and weathering, (2) fluxes of nutrients between trees, forest floor, and mineral soil, and (3) outputs of nutrients by runoff or leaching.

DISTRIBUTION OF BIOMASS, ORGANIC MATTER, AND NUTRIENTS WITHIN THE ECOSYSTEM

Organic matter, or more generally biomass, of a forest ecosystem is generally greatest in vegetation, followed by the mineral soil and the forest floor (Curlin 1968). The relative amounts in the forest floor and mineral soil depend on whether the stand is coniferous or deciduous (MacLean and Wein 1977).

The biomass (i.e., weight of living vegetation) of cool temperate forests is generally between 100 and 200 t/ha (Whittaker and Marks 1975). Biomass of mature aspen stands in the Lake States is between 205 and 230 t/ha (Bray and Dudkiewicz 1963, Alban et al. 1978). A pole-size aspen stand in the Lake States has a biomass of approximately 100 t/ha (Crow 1978) while aspen stands on poor sites could have biomasses as low as 5 to 60 t/ha (Bray and Dudkiewicz 1963, James and Smith 1977) and mature aspen stands on productive sites could have biomasses approaching 250 t/ha (Pastor and Bockheim 1981, 1984).

The weight of the forest floor of cool temperate forests is generally less than 60 t/ha (Foster and Morrison 1976, Gosz et al. 1976, MacLean and Wein 1977) and is somewhat greater in conifer stands than hardwood stands (MacLean and Wein 1977). An Alaskan aspen stand had a mor floor which weighed 42 t/ha (Van Cleve and Noonan 1975). Mors beneath aspen stands in the Lake States weigh between 20 and 55 t/ha (Alway and Kittredge 1933, Stoekeler 1961, Alban et al. 1978). In contrast, mulls beneath oak stands have been reported to weigh between 1.4 and 11 t/ha (Nielsen and Hole 1963, Lang and Formann 1978).

Within trees, the distribution of nutrients depends on both tissue concentration and tissue biomass. Concentrations of nutrients in most trees is greatest in leaves, followed by bark, branches, bole wood, and roots (Curlin 1968). In aspen, concentrations are highest in leaves, followed by current twigs, bark, branches, roots, dead branches, and finally bole wood (Young and Gunn 1966, Johnston and Bartos 1977). Biomass of most tree tissues is generally distributed in the order bole wood, roots, branches, bark, and leaves (Curlin 1968). Biomass of aspen trees is also distributed in this order, except that the weight of bark is generally greater than the weight of branches (Johnston and Bartos 1977, Alban et al. 1978, Crow 1978). Aspen bark contains the greatest amount of nutrients within the tree because of its relatively high biomass and nutrient concentrations, followed by roots, bole wood, branches, and leaves (Alban et al. 1978, Pastor and Bockheim 1984).

Total amounts of nutrients within trees is distributed in the order $Ca, N > K > Mg > P$ (Curlin 1968). In deciduous trees, including aspen, the amount of Ca is greater than the amount of N, while in conifers N is greater than Ca (Foster and Morrison 1976, MacLean and Wein 1977, Alban et al. 1978).

The relative amounts of nutrients within the forest floor and amounts of available nutrients within the mineral soil follows the same distribution as in trees (Cole et al. 1967, Alban et al. 1978). However, the distribution of nutrients in a total elemental analysis of soil reflects that of the initial material, generally $K \gg Ca > Mg \gg P > N$ (Barth 1961, Johnson et al. 1968, Foster and Morrison 1976). Amounts of organic matter and nutrients within aspen forest floors are greater in the H layer, if present,

followed by the F and L layers (Stoeckeler 1961, Van Cleve and Noonan 1976, Lang and Forman 1978). Concentrations of nutrients within the mineral soil are usually highest within the A1, if present, but the bulk density and thickness of the B horizon result in its having the greatest amount of nutrients in aspen as well as other stands (Cole et al. 1967, Foster and Morrison 1976, Alban et al. 1978).

INPUTS OF NUTRIENTS TO A FOREST ECOSYSTEM

Inputs of nutrients to a forest ecosystem are by weathering of the soil, precipitation, and atmospheric fixation. The latter, while important as a source of nitrogen and sulfur (Likens et al. 1977), is difficult to measure and represents an unknown quantity in most nutrient cycling studies. For most nutrients, precipitation and weathering are the main sources.

PRECIPITATION

For most nutrients, the input by precipitation is less than the input by weathering. Yet, precipitation may annually contribute nutrient amounts equal to those tied up annually in the bole (Ovington 1962). Concentrations of nutrients in precipitation in the Northeast are generally less than 1 mg/l, except for sulfate, which can be as high as 3 mg/l (Eaton et al. 1973). In the Lake States concentrations are slightly higher (Comerford and White 1977, Verry and Timmons 1977). These higher concentrations may be the result of agricultural activity (Fisher 1968). Vitousek (1977) and Cronan and others (1978) found precipitation chemistry to control the concentrations of chloride and sulfate within the ecosystem.

WEATHERING

Weathering is especially important in the supply of cations in forms available for plant uptake. Weathering in a nutrient cycling context has been studied most successfully by using an equation of Barth (1961):

$$W = \frac{D}{C - S}$$

Where W is the amount of rock weathered per unit time over unit land surface; D is cation output in the same units; C is percent of element in unweathered material, and S is percent of element in weathered material. Johnson et al. (1968), using streamwater fluxes for D, A2 concentrations for S, and bedrock concentrations for C, calculate that approximately 800 kg/ha of initial material are weathered per year in New England. This equation assumes that there are no sinks within the ecosystem, such as vegetation or the exchange complex of the soil, where nutrients can accumulate. Ignoring such sinks underestimates weathering rates by a factor of two or more (Likens et al. 1977). By taking the vegetation sink into account in a mass balance estimate of weathering, Likens and others (1977) calculate annual supply of cations by weathering of a spodosol to be 21.1 kg/ha Ca, 7.1 kg/ha K, 5.8 kg/ha Na, and 3.5 kg/ha Mg.

This approach does not work for aspen ecosystems because the large uptake and retention rates, to be discussed further below, distort the calculations and lead to unrealistically high estimates (Pastor and Bockheim 1984). By leaching columns of soil with aspen leaf litter extracts, Adams and Boyle (1979) estimated weathering rates of less than 1 kg/ha per year apiece for calcium and magnesium and 4 kg/ha per year for potassium. However, this begs the question of what are the sources of these nutrients for annual uptake if not weathering. The most likely explanation is that suggested by data of Alban (1982), namely that nutrients are accumulating in vegetation at the expense of their exchangeable pools in the soil. In addition, an unknown but potentially large portion of calcium in aspen may be as calcium oxalate, particularly in bark. Calcium oxalate, also produced by soil fungi, is easily weathered

and speeds weathering of other soil minerals and increases nutrient availability to vegetation (Graustein et al. 1977). Further research on weathering rates in aspen stands should focus on the formation and dissolution of calcium oxalate and its interactions with calcium and other nutrients.

NUTRIENT FLUXES WITHIN THE ECOSYSTEM

PLANT UPTAKE AND RETENTION OF NUTRIENTS, AND PRODUCTION OF DRY MATTER

Production of dry matter is usually considered along with biomass in the literature. In this review, production is not considered along with biomass, but with nutrient uptake by trees because the dynamics of nutrient uptake is directly related to the dynamics of tree growth (Curlin 1968). Whittaker and Marks (1975) give a range of 4.5 to 24 t/ha annual dry matter production in cool temperate forests, with a mean of around 10 t/ha. Annual production of dry matter by aspen stands in the Lake States ranges from 4 t/ha on a poor site to 12.5 t/ha on good sites (Bray and Dudkiewicz 1963, Crow 1978, Pastor and Bockheim 1984).

The rate of dry matter production changes during the life of a stand, the greatest rate of production being in pole-size stands (Ovington 1962, Lieth 1974) or even in younger stands (Marks 1974). As a tree grows, production is increasingly concentrated in leaves and branches (Whittaker et al. 1974). In most trees, including aspen, production of dry matter by leaves is greatest, followed by wood, branches, roots, bark, and fruits (Whittaker and Marks 1972, Crow 1978).

Most of the nutrient uptake of a tree is directed into metabolically active tissues, such as leaves and branches (Woodwell et al. 1975). In contrast to many other species, aspen bark is also metabolically active because of its photosynthetic capability (Pearson and Lawrence 1958). Uptake of nutrients in northern hardwoods, and in trees in general, follows the order: N,Ca > K > Na > S > Mg > P (Likens et al. 1977). Uptake by European aspen (*P. tremula*) and quaking aspen follow this pattern except that the uptake of Ca is greater than N (Rodin and Bazilevich 1965, Pastor and Bockheim 1984). In addition, aspen in Wisconsin accumulates zinc in amounts seven times higher than the minimum required by most plants (Gerloff et al. 1966). Much research remains to be done on nutrient uptake by aspen, especially in relation to soil fertility.

In most forests, approximately 50 to 80 percent of annual uptake is returned to the soil by litterfall, throughfall, and stemflow (Curlin 1968, Duvigneaud and Denaeyer-De Smet 1970). In contrast, aspen returns less than half the annual uptake of each nutrient and is particularly efficient at retaining calcium, sulfur and zinc, especially in bark (Alban et al. 1978, Pastor and Bockheim 1984). Mean annual nutrient retention by aspen in Minnesota was found to be 21.4 kg Ca/ha, 9.2 kg N/ha, 7.2 kg K/ha, 1.4 kg Mg/ha, and 1.2 kg P/ha (Alban et al. 1978). Even greater retention rates have been reported for an aspen-maple forest in Wisconsin (Pastor and Bockheim 1984).

THROUGHFALL

Throughfall returns less nutrients to the soil than litter but more than stemflow (Curlin 1968, Duvigneaud and Denaeyer-De Smet 1970). The only exception is K, for which throughfall is the principal return mechanism (Cole et al. 1967, Cromack and Monk 1975, Foster and Morrison 1976). In general, nutrients are leached from the leaves in the order S > K > Ca,N,Mg > P (Curlin 1968, Eaton et al. 1973, Gosz et al. 1975). Aspen (Verry and Timmons 1977) and birch (Comerford and White 1977) throughfall is especially high in calcium, reflecting the high concentrations of Ca in the leaves (Young and Gunn 1966). Aspen leaves may take up ammonium and nitrate directly from rain, decreasing their concentrations in throughfall compared to precipitation (Timmons et al. 1977, Pastor and Bockheim 1984).

STEMFLOW

The amount of water flowing down the boles of trees is generally less than 5 percent of the total rainfall, and the amount of nutrients returned by stemflow is less than 10 percent of that returned by throughfall and stemflow combined (Eaton et al. 1973, Foster and Morrison 1976). Stemflow concentrations, however, are generally two to three times higher than throughfall concentrations (Voigt 1960). Stemflow from aspen is especially rich in Ca, Mg, and K, and returns substantial amounts of these nutrients to the soil (Mahendrappa 1974, Verry and Timmons 1977). The concentrations of nutrients in stemflow are influenced by species, bark roughness, rainfall intensity, and mosses and lichens growing on the bole (Eaton et al. 1973, Patterson 1975). Stemflow may cause high concentrations of nutrients in the soil near the bole of the tree (Gersper and Holowaychuk 1971, Patterson 1975), although it is difficult to separate these effects of stemflow from similar effects of bark litter (Zinke 1962).

LITTER

Except for potassium, litterfall is the major pathway by which nutrients are returned to the soil (Curlin 1968). The pronounced autumn litterfall in cool temperate forests is the most dramatic aspect of nutrient cycling. Annual litter production ranges from 1 t/ha for Arctic-Alpine environments to 11 t/ha for Equatorial forests, with cool temperate forests having a mean of 3.5 t/ha (Bray and Gorham 1964). Leaves constitute up to 70 percent of total litterfall, branches 12 to 22 percent, bark 1 to 14 percent, and miscellaneous plant parts up to 10 percent (Bray and Gorham 1964, Gosz et al. 1972). Branch litterfall can constitute a higher proportion of the total litter in old-growth oak stands (Lang and Forman 1978) or in aspen stands in advanced stages of deterioration (Graham et al. 1963). Leaf litterfall in a mature Alaskan aspen stand is approximately 1.9 t/ha per year (Van Cleve and Noonan 1975), while in the Lake States aspen leaf litterfall ranges between 1.4 and 4.5 t/ha per year (Stoekeler 1961).

Nitrogen, calcium and potassium made up 81 percent of the total amount of nutrients returned in litterfall in a northern hardwoods stand (Gosz et al. 1972). Other nutrients are returned in the order Mg > S > P > Zn. Aspen litterfall is especially high in Ca (Stoekeler 1961, Van Cleve and Noonan 1975) and zinc (Van Cleve and Noonan 1975).

DECOMPOSITION AND INCORPORATION OF NUTRIENTS INTO SOIL

The forest floor and decomposition therein play an active role in the nutrient cycle because the processes of incorporation of litter into the soil take place in the floor and because the floor has a high permeability, permitting precipitation to infiltrate the soil. The soil organic matter, of which the forest floor is a major part, is a large pool through which nutrients cycle slowly, and as such regulates the flow of nutrients in a forest ecosystem (O'Neill et al. 1975, Gosz et al. 1976).

Decomposition of aspen leaf litter is more rapid than spruce in boreal forests but less rapid than maple in northern hardwood forests (Flanagan and Van Cleve 1983, McClaugherty et al. 1985). This appears to be because of the moderate amounts of lignin in aspen leaf litter, compared with low amounts in maple and much greater amounts in spruce (Flanagan and Van Cleve 1983, McClaugherty et al. 1985, Pastor and Post 1986).

Aber and Melillo (1980) have proposed a three-stage theory of decomposition which unifies previous theories: (1) an initial period in which nutrients are leached from litter; (2) a period of active decomposition of tissues; and (3) a final period in which nutrients involved in microbial respiration are flushed from the system.

The initial leaching stage is probably very rapid (Aber and Melillo, 1978). Evidence is provided by Melin (1930), Nykvist (1959) and Gosz and others (1975). The removal of water soluble substances may be especially important in the decomposition of bigtooth aspen (P. grandidentata) leaves (Melin 1930).

The behavior of various elements varies during the second stage, depending on mobility, availability to microorganisms, and place in leaf tissue. Nitrogen and phosphorus, being in short supply to microbes, are immobilized during the first half of this stage as the microbes decompose organic compounds (Lutz and Chandler 1946, Gosz et al. 1973, Aber and Melillo 1978). Aspen leaves have unusually high nitrogen immobilization rates, exceeding 9.5 mg nitrogen per g total mass loss during decay (McClaugherty et al. 1985). Of species that normally grow with aspen, this is exceeded only by spruce (Pastor and Post 1986). Therefore, immobilization of nitrogen by microbes decomposing aspen leaf litter represent a secondary retention mechanism within the aspen ecosystem.

Once mineralization begins during decomposition, Curlin (1968) gives the rate of release of nutrients from decomposing tissue as $K > P > Ca = N$. Gosz and others (1973) found Mg to be released most rapidly from sugar maple litter, followed by K, S, Ca, N, and P. Nutrients are released from aspen leaves in Alaska in the order K, Ca, Mg, Zn, P, N, and Fe (Van Cleve and Noonan 1975).

Animals, especially earthworms (Lumbricus terrestris), can greatly increase decomposition of litter by disintegration of tissues, increasing tissue surface area, chemical digestion, mixing organic matter with mineral soil, and dispersing microorganisms (Nielsen and Hole 1963, Witkamp and Crossley 1966, Edwards et al. 1970, Jensen 1974). Animals important in aspen floors include mites, spring tails, flies, and beetles (Wagner et al. 1977, Mitchell 1978) and possibly earthworms (Bleak 1970).

Decomposition of wood is much slower than that of leaves. In the first year after sugar maple, yellow birch, and beech branches were deposited on the soil surface, Gosz and others (1973) found little or no weight loss except that caused by bark sloughing. The slow decomposition of wood is ascribed to its high C:N ratio (Lutz and Chandler 1946) which results in immobilization of N during wood decomposition (Allison and Murphy 1962, Allison et al. 1963). Wood can be important sites of nitrogen-fixation (Cornaby and Waide 1963). Lang and Forman (1978) say that, because of its slow decomposition and high C:N ratio, woody detritus can be an important buffer in the cycling of nutrients. Despite the recognized importance of woody detritus to nutrient cycling, there have been no studies to date on natural decay of aspen wood and bark.

MOVEMENT OF NUTRIENTS DOWNWARD INTO THE SOIL PROFILE

Once nutrients are released from decomposed tissue, they can be taken up by plants, and enter the biologic cycle again, or they can move downward into the profile in solution. Except for stemflow, the maximum concentrations of nutrients in solution occur as water passes through the forest floor (Cole et al. 1967, Best and Monk 1975, Feller 1977).

In a series of papers, McColl studied the aqueous transfer of nutrients from the floor to the mineral soil (McColl 1972, 1973a,b). Using electrical conductivity of the solution as an index of total nutrient content, McColl found that nutrient movement from the floor depends on total water flow, the length of the dry period preceding flushing, and the temperature of the dry period. The last two factors relate to the rate of decomposition of the organic matter. McColl (1973b) proposed that the concentration of nutrients in soil solution is determined by the forest floor where biologic activity is the greatest and that "concomitant changes occur as the solution passes through the solum." Also, the solution characteristics of a given horizon are largely determined by the horizon above it (McColl 1973b).

Seasonal variation in microbial and plant uptake cause seasonal variations in nutrient content of soil water. McColl (1972) and Feller (1977) found electrical conductivity and nutrient concentrations of

water draining from the forest floor of Douglas fir stands to be highest in late summer. On the other hand, Remezov (1958) found concentrations of nutrients in both soil water and mineral soil to be highest in the spring and lowest in late summer beneath an aspen (P. tremula) stand. In all three cases, this was ascribed to seasonal patterns of litter decomposition.

Remezov (1958) found annual leaching losses from an aspen (P. tremula) forest floor to be 85.3 kg Ca/ha, 42.7 kg K/ha, 31.7 kg N/ha, 21.0 kg Si/ha, 9.9 kg P/ha, and 6.0 kg Al/ha. Remezov (1958) and Timmons and others (1977) suggest that the forest floor and mineral soil beneath aspen stands are important sinks for nutrients as they move downward in solution.

NUTRIENT OUTPUTS

To one degree or another, outputs of nutrients from a forest are dependent on the inputs and cycling of nutrients within the forest. Outputs are small in relation to annual uptake by plants (Cole et al. 1967, Likens et al. 1977) indicating that forests possess efficient cycling and storage mechanisms (Likens et al. 1977). Outputs of nutrients in runoff is generally small because of the high permeability of the forest floor (Likens et al. 1969) and most nutrient output is by leaching beyond the rooting zone.

Likens and others (1969) stress the role of the hydrologic cycle in controlling leaching losses. Johnson and others (1969) propose a model in which concentration of nutrients in solution is inversely related to water flux but directly related to residence time of water in the ecosystem, and the concentrations of nutrients in soil water and rainwater. Johnson and Swank (1973) found concentrations of nutrients in leachate fluctuate independently of flow rate, and propose biologic control rather than hydrologic control. Remezov (1958) observed "no direct relation between the volume of drainage and the total amount of Ca ... and K lost from soil [in an oak stand]." Vitousek and Reiners (1975) and Vitousek (1977) showed that nutrient losses are inversely related to the rate at which each nutrient is accumulated in growing biomass.

Concentrations of nutrients in leachate from a northern hardwood forest decrease in the order SO₄, Ca, NO₃, Na, Cl, Mg, K, NH₄. Concentrations in leachate from a Douglas fir stand decrease in the order Ca, K, N, P (Cole et al. 1967). In contrast, concentrations of calcium in leachate from aspen stands are higher than in leachate from other stands, while nitrogen is much lower (Verry 1972, Richardson and Lund 1975, Timmons et al. 1977, Pastor and Bockheim 1984). On the other hand, Remezov (1958) observed N concentrations in water draining from aspen (P. tremula) stands to be similar to those in water draining from oak stands. Concentrations of nutrients in leachate from soils beneath aspen stands are in the order Ca > Mg > Na, K > NO₃ > NH₄ (Remezov 1958, Verry 1972, Richardson and Lund 1975, Timmons et al. 1977, Pastor and Bockheim 1984). In contrast, larger amounts of nutrients can be lost during snowmelt in aspen stands, mainly because the trees are not actively taking up nutrients in late winter (Timmons et al. 1977).

SOME ECOLOGICAL AND SILVICULTURAL IMPLICATIONS OF NUTRIENT CYCLING

ECOLOGICAL IMPLICATIONS

Odum (1969) considered nutrient cycling to be related to the successional status of a stand. He proposed that climax forests are stable in part because they cycle nutrients efficiently, while successional stands are unstable because they "leak" nutrients. However, a number of recent studies indicate that early successional stands of pin cherry (Prunus pensylvanica Ehr.) and aspen tie up nutrients in rapidly growing biomass and thereby lose less through leaching than climax stands (Marks and Bormann 1972, Marks 1974, Vitousek and Reiners 1975, Richardson and Lund 1975).

In recent years, the cycling of nutrients by plants has come to be regarded as part of the species niche, that is, the "multi-dimensional space representative of the environment in which a species exhibits positive fitness" (Garten 1978). Woodwell and others (1975) and Gerloff and others (1966) allude to niche differentiation as a process leading to species differences in nutrient concentrations in tissues. Using multivariate analytical techniques, Garten (1978) found floodplain species to be dispersed in a "tissue concentration space" and interpreted this as one aspect of the species' niches. In particular, species were most different with regard to their ability to take up and store K, which was in low supply in these soils. Monk (1966) and Day and McGinty (1975) proposed that species differences in nutrient cycling allows species to maximize utilization of soil nutrient reserves. They also suggested that the different ways in which species cycle nutrients underlie ecosystem structure. The ability of aspen to accumulate large amounts of zinc and other trace elements (Gerloff et al. 1966) may be one reason why aspen can survive on mine spoil banks where few other species can (Leisman 1957). Pastor and Bockheim (1984) found that productive aspen-maple ecosystems in Wisconsin retain large amounts of nutrients because of aspen's ability to take up large quantities of nutrients and maple's ability to cycle nutrients in the shade of aspen.

The role of nutrient cycling in soil genesis has received much attention in Europe as a result of the biogeocoenose concept (Remezov and Pogrebnyak 1965). Until recently in America, soil genesis has had a strong mineralogical flavor. A notable exception is the Soil Survey of Menominee County (Milfred et al. 1967), in which soil differences between hemlock and maple stands are related to differences in nutrient content of throughfall and litter, among other factors. Mention has been made above of the ability of aspen to extract nutrients from subsoil and redistribute them to the top of the soil, but this is another area in which fruitful research could be done.

SILVICULTURAL IMPLICATIONS

It has been shown repeatedly that aspen cycles large amounts of Ca, Mg, N, and Zn in litterfall, throughfall and stemflow, and uptake (Van Cleve and Noonan 1975, Verry and Timmons 1977, Alban et al. 1978). Not surprisingly, growth and site index (height at a reference age) of aspen have been correlated with the nutrient content of the soil, especially Ca, but also Mg and N (Kittredge 1938, Voigt et al. 1957, Stoeckeler 1960, Fralish and Loucks 1975). Growth has also been correlated with physical properties of the soil, especially those leading to greater moisture retention such as water holding capacity, silt + clay content, and presence of pans (Kittredge 1938, Stoeckeler 1960, Graham et al. 1963, Fralish and Loucks 1975). While this has been interpreted as indicating the demand of aspen for water, it should also be noted that these properties also decrease loss of nutrients by leaching.

The life history of aspen has been reviewed by Graham and others (1963), Fowells (1965) and Brinkman and Roe (1975). Aspen reproduces most commonly by root sprouting of suckers after fire, logging, or other disturbance and the establishment of these sucker stands is the silvicultural basis for clearcutting aspen (Graham et al. 1963). From the standpoint of nutrient cycling, the rapid and dense growth of aspen sucker stands may ameliorate leaching loss (Richardson and Lund 1975).

Mortality is high in the first few years, and stands go through several periods of natural thinning. After 50 to 60 years, the aspen stand deteriorates because of disease. Stand break-up is very rapid, often less than five years (Graham et al. 1963, Fralish and Loucks 1975). Break-up may be delayed on sites high in nutrients (Graham et al. 1963). On good sites in the Lake States, aspen is succeeded by northern hardwoods, especially sugar maple, while on poor sites a second sucker stand may sprout, or aspen may be replaced by brush species (Kittredge 1938, Fralish 1975). A key unresolved question in aspen nutrient cycling research is how the different nutrient cycles are reorganized after the return of two thirds of aboveground biomass to the soil within the five years it takes for a stand to break up, and how the reorganization of the nutrient cycles by the succeeding species affect subsequent stand productivity. To date, there have been no studies that have followed a single stand through the breakup phase into the succeeding generation.

Theoretically, to the extent that the succeeding species cycle nutrients differently than aspen, soil properties and productivity will be altered as succession proceeds (Pastor and Post 1986). Thus, as we consider the effect of different species on nutrient cycles, especially the cycles of the more limiting nutrients such as nitrogen, the concept of site index as a fixed estimate of site quality becomes less tenable. For example, aspen has been called a "soil improver" (Stoekeler 1961) in that it replenishes nutrients to the soil surface, allowing more demanding species, such as sugar maple (Farnsworth and Leaf 1963, Post 1968) to succeed it. As with aspen growth, sugar maple growth is influenced by physical properties of the soil (Westveld 1933), but growth has also been correlated with total soil nitrogen and exchangeable magnesium (Post 1968). In contrast, the succession of aspen to spruce in boreal forests may cause soil nitrogen availability to decline because of the slower decay and greater immobilization of nitrogen by spruce litter; model simulations show that spruce dieback may result (Pastor et al. 1987). Thus the growth of species that succeed aspen depends to a great extent on what aspen did to the soil during its previous occupancy and how these properties are subsequently modified by the succeeding species.

Concern for water quality and maintenance of forest productivity has led to increased research in the effects of harvesting on nutrient cycling (Cole and Gessel 1965, Likens et al. 1970, Johnson and Swank 1973). The two major effects of harvesting on nutrient cycling are increased loss of nutrients by leaching and removal of nutrients in harvested biomass.

Following deforestation of a northern hardwoods stand in New Hampshire, Likens and others (1970) observed up to sixty-fold increases in NO_3^- concentrations in streamwater draining the stand. This was accompanied by increased nitrification and decomposition of the forest floor (Smith et al. 1968, Likens et al. 1969). Increased nitrification and decomposition produced more H^+ which replaced cations on exchange sites, thereby causing increased leaching losses of other ions (Likens et al. 1969, McColl 1972). Sulfate losses, however, decreased after deforestation (Likens et al. 1969, 1970). This may be due to the toxic effects of nitrate on *Thiobacillus thiooxidans*, a sulfur oxidizing bacterium (Likens et al. 1969) or to decreased fixation of atmospheric SO_2 by plants (Hoeft et al. 1972). Reduced evapotranspiration by plants after cutting led to increased water losses through runoff and leaching, as well as increased nutrient losses (Likens et al. 1970). Vitousek (1977) showed that reduced plant uptake, as well as nitrification, can also lead to increased nutrient loss.

Less drastic changes may occur with more conventional management practices (Ovington 1960, Patric and Smith, 1975). Losses from conventional clearcuts in New England followed the same pattern as losses from the deforested area, but were not as high (Pierce et al. 1972). In other areas, clearcutting, including clearcutting of aspen, did not appreciably affect water quality or nutrient losses by leaching (Cole and Gessel 1965, Verry 1972, Fredricksen et al. 1975, Richardson and Lund 1975). This is most likely due to plant uptake by regrowth (Marks 1974, Richardson and Lund 1975). Species conversion, thinning, and selective cutting may decrease nutrient losses by causing transfer of nutrients to more vigorous trees (Ovington 1960, Johnson and Swank 1973).

The recovery of an ecosystem from harvesting may depend on plant growth and on the type of harvesting. Leaching losses can return to control levels after two years or less (Likens et al. 1978), primarily because of increased plant uptake (Marks and Bormann 1972, Marks 1974, Bormann et al. 1974, Vitousek and Reiners 1975, Henderson and Harris 1975, Richardson and Lund 1975).

Aber and others (1978) suggest that the pattern of recovery is different following removal of the entire aboveground biomass ("whole-tree harvesting") than following conventional clearcutting, in which only the bole is removed. This is due to the presence or absence of slash:

...dead wood acts as an important buffer, minimizing nitrogen losses immediately after cutting by providing a carbon-rich substrate for immobilization of nitrogen by microbes and then gradually giving this nitrogen back through its slow rate of decomposition.

Their model showed decreasing amounts of available N in the floor following successive whole-tree harvests at short rotation. A model by Waide and Swank (1975) predicts reduced yields following whole-tree harvesting, primarily for the same reason. Williams and Mace (1975) investigated a whole-tree harvest and conventional clearcut and found nitrogen immobilization in the floor of the clearcut and high nitrate losses by leaching from the floor of the whole-tree harvested area. However, they also found greater nitrification and N losses at depth in the soil of the clearcut compared to the whole-tree harvest. They attributed this to greater soil compaction in the clearcut which increased soil temperature and water retention, resulting in turn in increased microbial growth at depth in the soil.

Nutrient removals in harvested biomass are drains on the nutrient reserves of managed forests. These removals are not thought to be significant in relation to soil nutrient reserves for selection, thinning, or even harvesting of all tree boles (Ovington 1960, Patric and Smith 1975). However, whole-tree harvesting and short rotations (30 years or less) remove substantially more nutrients because a great deal of nutrients are stored in tree crowns (Boyle and Ek 1972, Weetman and Webber 1972, White 1974). These losses can be as much as five times as great for whole-tree harvesting as compared to conventional bole harvesting (Mälkönen 1973). Boyle and Ek (1972) suggested that calcium would limit aspen growth only after nine, 30-year whole-tree harvests. However, Alban and others (1978) suggested that one whole-tree harvest of a mature aspen stand might severely deplete the site of K and P. In the Lake States, nitrogen is the most limiting nutrient to aspen productivity. Pastor and Bockheim (1984) found 350 kg of N per ha in aboveground biomass of a mature aspen stand at culmination of mean annual increment, and inputs in precipitation of approximately 5 kg per ha per year. If all 350 kg were removed in a complete whole tree harvest, then 60 years would be required to replenish this amount in the soil nitrogen pool. Thus, 60 years, or the amount removed in harvested biomass divided by input rates, could be thought of as the sustainable rotation age; rotations shorter than this would presumably lead eventually to nutrient depletion and losses of productivity.

Kimmins (1977) proposes several questions which must be answered before the effects of whole-tree harvesting can be fully evaluated, including: (1) What proportion of site nutrient reserves are removed in biomass? (2) What are the size of reserves in the soil? (3) How rapidly do nutrients cycle after harvesting? (4) How rapid are nutrients removed in harvesting replenished by weathering and other inputs? (5) What are the nutrient requirements of succeeding crops? (6) How great are other harvest-induced losses, such as erosion or leaching?

Except for the study of Williams and Mace (1975) and the models proposed by Aber and others (1978) and Waide and Swank (1975), little work has been done on the actual cycling of nutrients in intensively-harvested stands. Not surprisingly, this has led to considerable disagreement on the possible effects of whole-tree harvesting and short rotation on future stand productivity. However, it is clear that the intensification of aspen stand management cannot be sustained without due consideration given to the distinct manner that aspen cycles nutrients in contrast to associated and succeeding species, and the effects of different harvesting regimes on nutrient distributions and flows.

LITERATURE CITED

- Aber, J.D., D.B. Botkin, and J.M. Melillo, 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* 8:306-315.
- Aber, J.D., and J.M. Melillo. 1980. Litter decomposition: Measuring relative contributions of organic matter and nitrogen to forest soils. *Can. J. of Botany* 58:416-421.
- Adams, P.W., and J.R. Boyle. 1979. Cation release from Michigan Spodosols leached with aspen leaf litter extracts. *Soil. Sci. Soc. Am. J.* 43:593-596.
- Alban, D.H. 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. *Soil Sci. Soc. Am. J.* 46:853-861.

- Alban, D.H., D.A. Perala, and B.E. Schlaegel. 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. *Can. J. For. Res.* 8:290-299.
- Allison, F.E., and R.M. Murphy. 1962. Comparative rates of decomposition in soil of wood and bark particles of several hardwood species. *Soil Sci. Soc. Am. Proc.* 26:463-466.
- Allison, F.E., R.M. Murphy, and C.J. Klein. 1963. Nitrogen requirements for the decomposition of various kinds of finely ground woods in soil. *Soil Sci.* 96:187-190.
- Alway, F.J., and J. Kittredge, Jr. 1933. The forest floor under stands of aspen and paper birch. *Soil Sci.* 35:307-312.
- Barth, T.F.W. 1961. Abundance of the elements, areal averages and geochemical cycles. *Geochim. Cosmochim. Acta* 23:1-8.
- Best, G.R., and C.D. Monk. 1975. Cation flux in hardwood and white pine watersheds. P. 847-861 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry, and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Bleak, A.T. 1970. Disappearance of plant material under a winter snow cover. *Ecology* 51: 915-917.
- Bormann, F.H., G.E. Likens, T.G. Siccama, R.S. Pierce, and J.S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. *Ecol. Monogr.* 44:255-277.
- Boyle, J.R., and A.R. Ek. 1972. An evaluation of some effects of bole and branch pulpwood harvesting on site macronutrients. *Can. J. For. Res.* 2:407-412.
- Bray, J.R., and L.A. Dudkiewicz. 1963. The composition, biomass and productivity of two Populus forests. *Bull. Torrey Bot. Club* 90:298-308.
- Bray, J.R., and E. Gorham. 1964. Litter production in forests of the world. *Adv. Ecol. Res.* 2:101-157.
- Brinkman, K.A., and E.I. Roe. 1975. Quaking aspen: Silvics and management in the Lake States. USDA Agric. Handbook 486. 52 p.
- Clausen, J. 1978. Wisconsin goes wild. *Wis. Nat. Resour.* 2(2):12-17.
- Cole, D.W., and S.P. Gessel. 1965. Movement of elements through a forest soil as influenced by tree removal and fertilizer additions. P. 95-104 *in* Forest-soil relationships in North America. C.T. Youngberg, ed. Oregon State Univ. Press, Corvallis.
- Cole, D.W., S.P. Gessel, and S.F. Dice. 1967. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir ecosystem. P. 197-232 *in* H.E. Young, ed. Primary production and mineral cycling in natural ecosystems. Univ. Maine Press, Orono.
- Comerford, N.B., and E.H. White. 1977. Nutrient content of throughfall in paper birch and red pine stands in northern Minnesota. *Can. J. For. Res.* 7:556-561.
- Cornaby, B.W., and J.B. Waide. 1973. Nitrogen fixation in decaying chestnut logs. *Plant Soil* 39:445-448.

- Cromack, K., Jr., and C.D. Monk. 1975. Litter production, decomposition and nutrient cycling in a mixed hardwood watershed and a white pine watershed. P. 609-624 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Cronan, C.S., W.A. Reiners, R.C. Reynolds, Jr., and G.E. Lang. 1978. Forest floor leaching: Contributions from mineral, organic, and carbonic acids in New Hampshire subalpine forests. *Science* 200:309-311.
- Crow, T.R. 1978. Biomass and production in three contiguous forests in northern Wisconsin. *Ecology* 59:265-273.
- Curlin, J.W. 1968. Nutrient cycling as a factor in site productivity and forest fertilization. P. 313-325 *in* Tree growth and forest soils. C.T. Youngberg and C.B. Davey, eds. Proc. Third North American Forest Soils Conf., Oregon State Univ. Press, Corvallis.
- Day, F.P., Jr., and D.T. McGinty. 1975. Mineral cycling strategies of two deciduous and two evergreen tree species on a southern Appalachian watershed. P. 736-743 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Duvigneaud, P., and S. Denaeyer-De Smet. 1970. Biological cycling of minerals in temperate deciduous forests. P. 199-225 *in* Analysis of temperate forest ecosystems. D.E. Reichle, ed. Springer-Verlag, New York.
- Eaton, J.S., G.E. Likens, and F.H. Bormann. 1973. Throughfall and stemflow chemistry in a northern hardwood forest. *J. Ecol.* 61:495-508.
- Edwards, C.A., D.E. Reichle, and D.A. Crossley, Jr. 1970. The role of soil invertebrates in turnover of organic matter and nutrients. P. 147-172 *in* Analysis of temperate forest ecosystems. D.E. Reichle, ed. Springer-Verlag, New York.
- Farnsworth, C.E., and A.L. Leaf. 1963. An approach to soil-site problems: Sugar maple-soil relations in New York. P. 279-298 *in* Forest-soil relationships in North America. C.T. Youngberg, ed. Oregon State Univ. Press, Corvallis.
- Feller, M.C. 1977. Nutrient movement through western hemlock-western redcedar ecosystems in southwestern British Columbia. *Ecology* 58:1269-1283.
- Fisher, D.W. 1968. Annual variations in chemical composition of atmospheric precipitation. Eastern North Carolina and Southeastern Virginia, Water Supply Pap. 1535-M, USGS.
- Flanagan, P.W., and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Can. J. For. Res.* 13:795-817.
- Foster, N.W., and I.K. Morrison. 1976. Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosystem. *Ecology* 57:110-120.
- Fowells, H.A. 1965. Silvics of forest trees of the United States. USDA, For. Serv., Agric. Handbook No. 271. 762 p.
- Fralish, J.S. 1975. Ecological and historical aspects of aspen succession in northern Wisconsin. *Trans. Wis. Acad. Sci., Arts, Letters* 63:54-65.

- Fralish, J.S., and O.L. Loucks. 1975. Site quality evaluation models for aspen (Populus tremuloides Michx.). *Can. J. For. Res.* 5:523-528.
- Fredricksen, R.L., D.G. Moore, and L.A. Norris. 1975. The impact of timber harvest, fertilization, and herbicide treatment on streamwater quality in western Oregon and Washington. P. 283-313 *in* Forest soils and forest land management. B. Bernier and C.H. Winget, eds. Laval Univ. Press, Quebec.
- Garten, C.T., Jr. 1978. Multivariate perspectives on the ecology of plant mineral element composition. *Am. Nat.* 112:533-544.
- Gerloff, G.C., D.G. Moore, and J.T. Curtis. 1966. Selective absorption of mineral elements by native plants of Wisconsin. *Plant Soil* 25:393-405.
- Gersper, P.L., and N. Holowaychuk. 1971. Some effects of stem flow from forest canopy trees on chemical properties of soils. *Ecology* 52:691-702.
- Gosz, J.R., G.E. Likens, and F.H. Bormann. 1972. Nutrient content of litter fall on the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* 53:769-784.
- Gosz, J.R., G.E. Likens, and F.H. Bormann. 1973. Nutrient release from decomposing branch litter in the Hubbard Brook Forest, New Hampshire. *Ecol. Monogr.* 43:173-191.
- Gosz, J.R., G.E. Likens, and F.H. Bormann. 1976. Organic matter and nutrient dynamics of the forest and forest floor in the Hubbard Brook Forest. *Oecologia* 22:305-320.
- Gosz, J.R., G.E. Likens, J.S. Eaton, and F.H. Bormann. 1975. Leaching of nutrients from leaves of selected tree species in New Hampshire. P. 630-641 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Graham, S.A., R.P. Harrison, and C.E. Westell. 1963. Aspen, phoenix trees of the Lake States. Univ. Michigan Press, Ann Arbor. 272 p.
- Graustein, W.C., K. Cromack, and P. Sollins. 1977. Calcium oxalate: occurrence in soils and effect on nutrient and geochemical cycles. *Science* 198:1252-1254.
- Henderson, G.S., and W.F. Harris. 1975. An ecosystem approach to characterization of the nitrogen cycle in a deciduous forest watershed. P. 179-193 *in* Forest soils and land management. B. Bernier and C.H. Winget, eds. Les Presses de l'Universite Laval.
- Hoelt, R.G., D.R. Keeney, and L.M. Walsh. 1972. Nitrogen and sulfur in precipitation and sulfur dioxide in the atmosphere in Wisconsin. *J. Environ. Qual.* 1:203-208.
- James, T.D.W., and D.W. Smith. 1977. Short-term effects of surface fire on the biomass and nutrient standing crop of Populus tremuloides in southern Ontario. *Can. J. For. Res.* 7:666-679.
- Jensen, V. 1974. Decomposition of angiosperm tree leaf litter. P. 69-104 *in* Biology of plant litter decomposition, Vol. 1. C.H. Dickinson and G.J.F. Pugh, eds. Academic Press, New York.
- Johnson, P.L., and W.T. Swank. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. *Ecology* 54:70-80.
- Johnson, N.M., G.E. Likens, F.H. Bormann, and R.S. Pierce. 1968. Rate of chemical weathering of silicate minerals in New Hampshire. *Geochim. Cosmochim. Acta* 32:531-545.

- Johnston, R.S., and D.L. Bartos. 1977. Summary of nutrient and biomass data from two aspen sites in Western United States. USDA, For. Serv. Res. Note 9NT-227. 15 p.
- Jorgensen, J.R., C.G. Wells, and L.J. Metz. 1975. The nutrient cycle: Key to continuous forest production. *J. Forestry* 73:400-403.
- Keays, J.L. 1972. The resource and its potential in North America. P. 4-9 in *Aspen Symposium Proceedings*, USDA, For. Serv. Gen. Tech. Rep. NC-1.
- Kimmins, J.P. 1977. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. *Forest Ecol. Manage.* 1:169-183.
- Kittredge, J., Jr. 1938. The interrelations of habitat, growth rate, and associated vegetation in the aspen community of Minnesota and Wisconsin. *Ecol. Monogr.* 8:152-245.
- Lang, G.E., and R.T.T. Forman. 1978. Detrital dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. *Ecology* 59:580-595.
- Leisman, G.A. 1957. A vegetation and soil chronosequence on the Mesabi Iron Range spoil banks, Minnesota. *Ecol. Monogr.* 27:221-245.
- Lieth, H. 1974. Primary productivity of successional stages. P. 187-193 in *Handbook of vegetative science*, Pt. VIII. R. Tilxén, ed. Dr. W. Junk, Publ., The Hague.
- Likens, G.E., F.H. Bormann, and N.M. Johnson. 1969. Nitrification: Importance to nutrient losses in a cutover forested ecosystem. *Science* 163:1205-1206.
- Likens, G.E., F.H. Bormann, N.M. Johnson, and R.S. Pierce. 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. *Ecology* 48:772-785.
- Likens, G.E., F.H. Bormann, R.S. Pierce, and D.W. Fisher. 1969. Nutrient-hydrologic cycle interaction in small forested watershed-ecosystems. P. 553-563 in *UNESCO, Productivity of forest ecosystems. Proc. Brussels Symp.*
- Likens, G.E., F.H. Bormann, R.S. Pierce, and W.A. Reiners. 1978. Recovery of a deforested ecosystem. *Science* 199:492-496.
- Likens, G.E., F.H. Bormann, N.M. Johnson, D.W. Fisher, and R.S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol. Monogr.* 40:23-47.
- Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton, and N.M. Johnson. 1977. *Biogeochemistry of a forested ecosystem.* Springer-Verlag, New York. 146 p.
- Lutz, H.J., and R.F. Chandler. 1946. *Forest soils.* John Wiley & Sons, Inc., New York. 514 p.
- MacLean, D.A., and R.W. Wein. 1977. Nutrient accumulation for post-fire jack pine and hardwood succession patterns in New Brunswick. *Can. J. For. Res.* 7:562-578.
- Mahendrappa, M.K. 1974. Chemical composition of stemflow from some eastern Canadian tree species. *Can. J. For. Res.* 4:1-7.
- Mälkönen, E. 1973. Effect of complete tree utilization on the nutrient reserves of forest soils. P. 377-386 in *IUFRO Biomass Studies*, June 25-29, 1973, Nancy, France. H.E. Young, ed. Univ. Maine Press, Orono.

- Marks, P.L. 1974. The role of pin cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* 44:73-88.
- Marks, P.L., and F.H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady state nutrient cycling. *Science* 176:914-915.
- McClaugherty, C.A., J. Pastor, J.D. Aber, and J.M. Melillo. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66:266-275.
- McCull, J.G. 1972. Dynamics of ion transport during moisture flow from a Douglas-fir forest floor. *Soil Sci. Soc. Am. Proc.* 36:668-674.
- McCull, J.G. 1973a. A model of ion transport during moisture flow from a Douglas-fir forest floor. *Ecology* 54:181-187.
- McCull, J.G. 1973b. Environmental factors influencing ion transport in a Douglas-fir forest floor soil in Western Washington. *J. Ecol.* 61:71-83.
- Melin, E. 1930. Biological decomposition of some types of litter from North American forests. *Ecology* 11:72-101.
- Milfred, C.J., G.W. Olson, and F.D. Hole. 1967. Soil resources and forest ecology of Menominee County, Wisconsin. *Univ. Wisconsin, Geol. Nat. Hist. Surv., Madison.* 203 p.
- Mitchell, M.J. 1978. Vertical and horizontal distributions of oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. *Ecology* 59:516-526.
- Monk, C.D. 1966. An ecological significance of evergreenness. *Ecology* 47:504-505.
- Nielsen, G.A., and F.D. Hole. 1963. A study of the natural processes of incorporation of organic matter into soil in the University of Wisconsin Arboretum. *Trans. Wis. Acad. Sci., Arts, Letters* 52:213-227.
- Nykvist, N. 1959. Leaching and decomposition of litter. I. Experiments on leaf litter of Fraxinus excelsior. *Oikos* 10:190-211.
- O'Neill, R.V., W.F. Harris, B.S. Ausmus, and D.E. Reichle. 1975. A theoretical basis for ecosystem analysis with particular reference to nutrient cycling. P. 28-40 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164:262-270.
- Ovington, J.D. 1960. The nutrient cycle and its modification through silvicultural practice. *Proc. Fifth World Forestry Congr.* 1:533-538.
- Ovington, J.D. 1962. Quantitative ecology and the woodland ecosystem concept. *Adv. Ecol. Res.* 1:103-192.
- Pastor, J., and J.G. Bockheim. 1981. Biomass and production of an aspen-mixed hardwood-spodosol ecosystem in northern Wisconsin. *Can. J. For. Res.* 11:132-138.
- Pastor, J., and J.G. Bockheim. 1984. Distribution and cycling of nutrients in an aspen-mixed hardwood-spodosol in northern Wisconsin. *Ecology* 65:339-353.

- Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2:3-27.
- Pastor, J., R.H. Gardner, V.H. Dale, and W.M. Post. 1987. Successional changes in nitrogen availability contributing to spruce declines in boreal North America. *Can. J. For. Res.* 17:1394-1400.
- Patric, J.H., and D.W. Smith. 1975. Forest management and nutrient cycling in eastern hardwoods. USDA, For. Serv., Northeast Forest Exp. Sta. Res. Pap. NE-324. 12 p.
- Patterson, D.T. 1975. Nutrient return in the stemflow and throughfall of individual trees in the Piedmont deciduous forest. P. 800-812 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Pearson, L.C., and D.B. Lawrence. 1958. Photosynthesis in aspen bark. *Am. J. Bot.* 45:383-387.
- Pierce, R.S., C.W. Martin, C.C. Reeves, G.E. Likens, and F.H. Bormann. 1972. Nutrient loss from clearcuttings in New Hampshire. P. 285-295 *in* Symposium on watersheds in transition, Am. Water Res. Assoc., Ft. Collins, CO.
- Post, B.W. 1968. Soil-site relations. P. 15-19 *in* Proceedings Sugar Maple Conference, August 20-22, 1968, Houghton, MI. E.A. Bourdo, Jr., ed.
- Remezov, N.P. 1958. Relation between biological accumulation and eluvial process under forest cover. *Soviet Soil Sci.* 6:589-598.
- Remezov, N.P., and P.S. Pogrebnyak. 1965. Forest soil science. Nat. Tech. Infor. Serv., Arlington. Israel Program for Scientific Translations. 261 p.
- Richardson, C.J., and J.A. Lund. 1975. Effects of clearcutting on nutrient losses in aspen forests on three soil types in Michigan. P. 673-686 *in* Mineral cycling in southeastern ecosystems. F.G. Howell, J.B. Gentry and M.H. Smith, eds. ERDA Symposium Series, Technical Information Ctr., VA.
- Rodin, L.E., and N.I. Bazilevich. 1965. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, London. 288 p.
- Smith, W., F.H. Bormann, and G.E. Likens. 1968. Response of chemoautotrophic nitrifiers to forest cutting. *Soil Sci.* 106:471-473.
- Stoekeler, J.H. 1960. Soil factors affecting the growth of quaking aspen forests in the Lake States. Univ. Minnesota Agric. Sta. Tech. Bull. 233:1-48.
- Stoekeler, J.H. 1961. Organic layers in Minnesota aspen stands and their role in soil improvement. *For. Sci.* 1:66-71.
- Timmons, D.R., E.S. Verry, R.E. Burwell, and R.F. Holt. 1977. Nutrient transport in surface runoff and interflow from an aspen-birch forest. *J. Environ. Qual.* 6:188-192.
- USDA, Forest Service. 1974. The outlook for timber in the United States. U.S. For. Serv., For. Resour. Rep. No. 20. 374. p.
- Van Cleve, K., and L.L. Noonan. 1975. Litter fall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. *Can. J. For. Res.* 5:626-639.

- Van Cleve, K., and L.L. Noonan. 1976. Physical and chemical properties of the forest floor in birch and aspen stands in interior Alaska. *Soil Sci. Soc. Am. Proc.* 35:356-360.
- Verry, E.S. 1972. Effect of an aspen clearcutting on water yield and quality in northern Minnesota. P. 276-284 *in* National Symposium on Watersheds in Transition. S.C. Csallany, T.G. McLaughlin and W.D. Striffler, eds. *Am. Water Res. Assoc.*
- Verry, E.S., and D.R. Timmons. 1977. Precipitation nutrients in the open and under two forests in Minnesota. *Can. J. For. Res.* 7:112-119.
- Vitousek, P.M. 1977. The regulation of element concentrations in mountain streams in the northeastern United States. *Ecol. Monogr.* 47:65-87.
- Vitousek, P.M., and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* 25:376-380.
- Voigt, G.K. 1960. Alteration of the composition of rainwater by trees. *Am. Midl. Natur.* 63:321-326.
- Voigt, G.K., M.L. Heinselman, and Z.A. Zasada. 1957. The effect of soil characteristics on the growth of quaking aspen in northern Minnesota. *Soil Sci. Soc. Am. Proc.* 21:649-652.
- Wagner, T.L., W.J. Mattson, and J.A. Witter. 1977. A survey of soil invertebrates in two aspen forests in Minnesota. USDA, For. Serv., North Central Forest Exp. Sta. GTR NC-40. 23 p.
- Waide, J.B., and W.T. Swank. 1975. Nutrient recycling and the stability of ecosystems: implications for forest management in the southeastern U.S. P. 404-424 *in* Proc. 1975 Nat. Conv., Soc. Am. For., Washington, D.C.
- Weetman, G.F., and B. Webber. 1972. The influence of wood harvesting on the nutrient status of two spruce stands. *Can. J. For. Res.* 2:351-369.
- Westveld, R.H. 1933. The relation of certain soil characteristics to forest growth and composition in the northern hardwood forest of northern Michigan. *Mich. Agr. Exp. Sta. Tech. Bull.* 135. 52 p.
- White, E.H. 1974. Whole-tree harvesting depletes soil nutrients. *Can. J. For. Res.* 4:530-535.
- Whittaker, R.H., and P.L. Marks. 1975. Methods of assessing terrestrial productivity. P. 55-118 *in* Primary productivity of the biosphere. H. Lieth and R.H. Whittaker, eds. Springer-Verlag, New York.
- Whittaker, R.H., F.H. Bormann, G.E. Likens, and T.G. Siccama. 1974. The Hubbard Brook ecosystem study: Forest biomass and production. *Ecol. Monogr.* 44:233-252.
- Williams, T.M., and A.C. Mace, Jr. 1975. Effect of alternative harvesting systems on cycling of major nutrients in a forest soil. P. 220-234 *in* Forestry issues in urban America. Proc. 1974 Nat. Conv., Soc. Am. For., New York.
- Witkamp, M., and D.A. Crossley, Jr. 1966. The role of arthropods and microflora in breakdown of white oak litter. *Pedobiologia* 6:293-303.
- Woodwell, G.M., R.H. Whittaker, and R.A. Houghton. 1975. Nutrient concentrations in plants in the Brookhaven oak-pine forest. *Ecology* 56:318-332.

Young, H.E., and V.P. Gunn. 1966. Chemical elements in complete mature trees of seven species in Maine. TAPPI 49:190-197.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. *Ecology* 43:130-133.