

Ecosystem Succession and Nutrient Retention: A Hypothesis

Peter M. Vitousek and William A. Reiners

Twenty-four broad hypotheses for trends associated with successional development of ecosystems were presented in Odum's very important paper, "The Strategy of Ecosystem Development" (1969). This series of hypotheses has helped to organize thinking on ecosystem dynamics and to focus further research. In this paper, we wish to examine one of these hypotheses, which suggests that as ecosystems mature their ability to conserve nutrients increases. Our objective is to show through logical examination of characteristics of succession, and through presentation of critical field data, that this hypothesis cannot be stated quite so simply. We also intend to show that uncritical utilization of this hypothesis, especially when combined with an unclear understanding of steady state conditions in the field, can lead to erroneous interpretations of biogeochemical behavior of ecosystems. Although our argument is developed in a forest ecosystem context, it should apply, with various modifications, to all terrestrial ecosystems.

Ecosystems are open systems in which biogeochemical functions consist of inputs from various sources, outputs to various sinks, and a variable degree of internal recycling. At the onset of succession in such a system, as in an unoccupied sand dune, for example, elemental inputs through precipitation will be more or less equaled by elemental loss through hydrologic outputs. Such a system does not have any means of conserving nutrients; any element supplied to the sand from precipitation

will be leached out and lost. The development of biomass through succession provides a mechanism for elemental uptake and, more importantly, establishes compartments, or pools, for elemental storage in biomass (Fig. 1A). As plants become established on the sand dune, elements essential to plants will accumulate in the organic matter of this simple ecosystem. As long as biomass continues to increase, uptake and storage will occur, and elemental inputs will exceed outputs (Fig. 1B). In this phase of succession, the ecosystem will demonstrate a greater capability of retaining inputs than did the unoccupied sand dune. Furthermore, since at first the growth in storage capacity of biomass and detritus pools accelerates with increasing maturity, the difference between inputs and outputs will grow, fulfilling the prediction of Odum's hypothesis.

Growth in biomass (including detritus, in this paper) cannot continue indefinitely, however. In fact, other of Odum's hypotheses describe the pattern of deceleration and cessation of growth in ecosystems (Fig. 1A). Odum suggests that ecosystems eventually reach a point where production is equal to respiration—thus net ecosystem production is equal to zero (see also Woodwell and Sparrow 1965). If this is the true pattern of biomass change and stabilization, then as storage capacity approaches a steady state, elemental outputs must again equal elemental inputs. In other words, according to this idealized view, an ecosystem will show an excess of inputs of a particular element over outputs roughly in proportion to the rate at which that particular element is bound into net ecosystem production, or the net increment of biomass (*sensu* Rodin and Bazilevich 1967). After peak net increment has been passed, this difference will decline toward zero as net growth approaches zero. Thus, a

steady state in terms of mass must show the same balance of inputs to outputs as the original unoccupied site. The presence or kind of organic matter may affect rock-weathering rates, but will not alter the essential relationships between inputs and outputs. The ability of the most mature stage of succession to conserve nutrients can be no greater than that of the original unoccupied site. Furthermore, the differences in nutrient retention between any two stages of unequal maturity will depend on their relative positions on the net increment curve as graphed in Fig. 1A. The net increment curve is skewed with a peak toward early stages of succession to be consistent with what appears to be the general pattern of net growth rate for forests (Rodin and Bazilevich 1967).

The complement of input retention—nutrient loss—is given as a family of curves in Fig. 1B. For any given element, outputs will be controlled by the amount of the element supplied through precipitation, rock weathering, and other processes, and storage changes within biomass. Both the amount of new biomass and its elemental composition would be expected to vary through succession. In forest ecosystems, for example, the elemental composition of the net biomass increment will change as the ratio of leaves to wood decreases during succession. Consequently, for forests in general the biomass composition probably becomes relatively dilute in some elements such as nitrogen.

We have used primary succession as an example in describing this model for the relationship of nutrient retention to ecosystem maturity. In primary succession, soil profile development in general represents an increase in nutrient storage capacity, contributing to input retention as ecosystems mature (Crocker and Major 1955, Olson 1958). For a whole ecosystem to be in a steady state, this process of nutrient accumulation in

Peter M. Vitousek is with the Department of Zoology, Indiana University, Bloomington, IN 47041. William A. Reiners is with the Department of Biological Sciences, Dartmouth College, Hanover, NH 03755.

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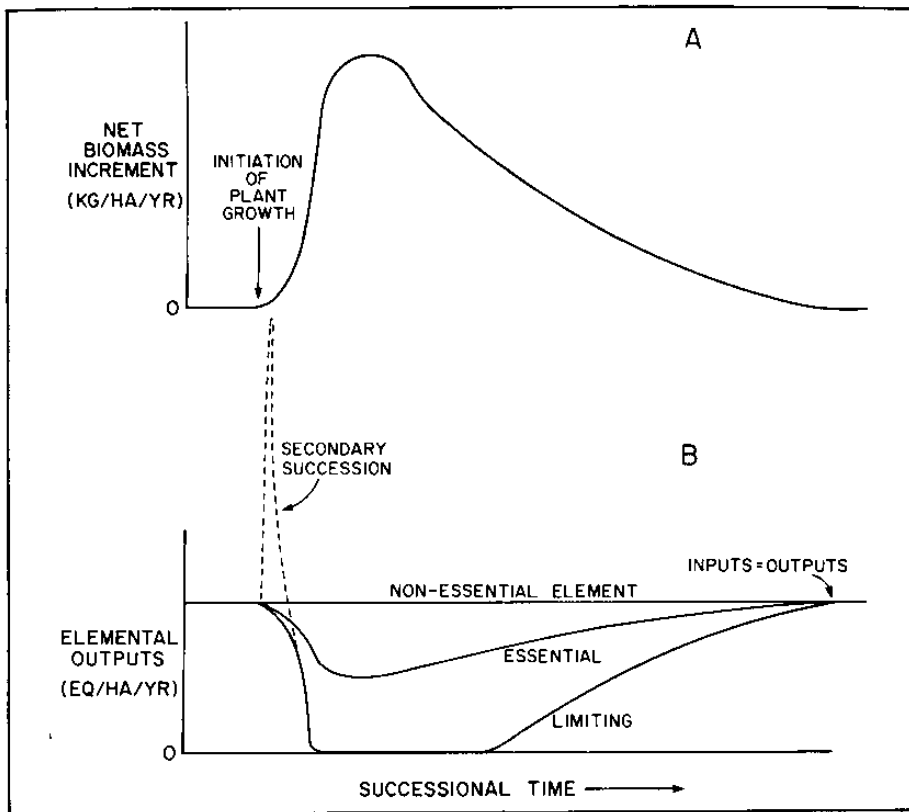


Fig. 1. A. Variation in net biomass increment with time in a primary successional sequence. Biomass accumulates rapidly at first, then the rate of biomass accretion declines gradually to zero. (From Rodin and Bazilevich 1967 and Odum 1969.) B. Variation in nutrient losses with time in a primary successional sequence. Nutrients are retained within an ecosystem as storage pools of nutrients in biomass and soil grow, but when storage pools reach steady state, nutrient outputs must equal inputs. Elements limiting to plant growth are retained most strongly; losses of these elements may decline to near zero. Elements essential but not limiting to plant growth will be significantly retained within ecosystems, but outputs will not approach zero. Outputs of elements which are nonessential to plants and which are not accumulated within ecosystems will vary little over the course of succession. The dotted line represents very high rates of nutrient loss immediately after disturbance in a secondary successional sequence. Total biomass in the ecosystem would decrease during this period of high losses.

soil must eventually approach zero so that the effect of profile development is additive to the general pattern we have hypothesized. Furthermore, in many soils, nutrient retention is to a large degree related to soil organic matter accumulation, which is included in our broad definition of biomass. The pattern of soil influences will be different for secondary succession, where increase in soil nutrient storage is far less important since the soil has already been modified by previous ecosystem processes (e.g., Mellinger¹). Of far more im-

portance in secondary succession is the potential for temporary, rapid losses of nutrients stored in detritus and soils, particularly in organic matter which may decompose rapidly under the conditions of devegetation. Rather sensational rates of nutrient loss can be found for instances in which clear-cutting or other disturbances can permit rapid nutrient losses from detritus and soils before the rate of biomass uptake increases to where nutrients are utilized at the rate supplied by mineralization of detritus plus normal atmospheric inputs (Likens et al. 1970).

Our hypothesis for the relationship between the degree of maturity of an ecosystem and its nutrient retention properties is summarized in Figs. 1A

and 1B. We suggest that the difference between net input and output of a particular element will be proportional to the rate at which that element is incorporated into the net biomass increment for the system. Net biomass increment may be negative at the onset of secondary succession, and thus outputs of elements may be higher than inputs. In general, nutrient incorporation into biomass will increase rapidly in early succession, will reach a maximum, and will slowly decline to zero as a steady state is approached. Conversely, nutrient loss rate will be the complement of the rate of incorporation into biomass for that element.

This hypothesis can also be explained in terms of the balance between biological uptake and recycling for a given element. Recycling, the sum of all the processes that return an element from organisms to the soil, will be less than biological uptake of an element as long as that element is incorporated into net biomass increment. The difference between uptake and recycling will be greatest when net biomass increment is largest (Fig. 1A), and will decline gradually thereafter. In steady state ecosystems, recycling will equal biological uptake.

The first portion of the nutrient loss curve (Fig. 1B) describing a decrease in nutrient losses as succession proceeds has been extensively documented in a number of ecosystem studies (Johnson and Swank 1973, Pierce et al. 1972, Woodwell 1974). The inhibition of nitrification has been proposed as a mechanism controlling this decline in nutrient losses (Likens et al. 1969, Rice and Pancholy 1972, Woodwell 1974). Although there may be differences in nitrification in some of the successional sequences examined, we believe that variation in the net biomass increment is sufficient to explain most of the results reported to date.

The remainder of this paper is devoted to a test of this hypothesis through examination of our data and reexamination of other published data.

METHODS

We tested this hypothesis in watershed ecosystems in the White Mountains of New Hampshire. The plant communities in the area range from northern hardwoods forests at lower elevations through spruce-fir and fir forests at intermediate elevations to alpine tundra on the higher mountain peaks (Bliss

¹Mellinger, M. V. 1972. Dynamics of plant succession on abandoned hay fields in central New York State. Ph.D. dissertation, Syracuse University, New York.

1963, Bormann et al. 1970). Almost all of the northern hardwoods forests and many of the spruce-fir forests have been extensively logged within the last 100 years; the high elevation fir forests and the alpine tundra, on the other hand, have been little affected by human disturbance.

We examined watersheds along the entire elevational gradient from northern hardwoods forest to alpine tundra. In this paper, we will describe results from the watersheds in the spruce-fir zone (750-1,200 meters). The spruce-fir zone is the only area where many but not all watersheds have never been subject to logging. It thus provides an area suitable for testing our hypothesis.

All of the watersheds reported on in this study were located on Mt. Moosilauke, a 1,462 m mountain only 13 km from the Hubbard Brook Experimental Forest. Watersheds on two major west-facing ridges with similar bedrock were sampled. One of the ridges has no record of logging above 750 meters, and if this ridge was ever logged, cutting must have occurred over 100 years ago (conversation, September 1974, J. W. Brown, Society for the Protection of New Hampshire Forests). The other ridge was partially logged in 1946-1948 following severe damage in a 1938 hurricane (Brown 1958). Seven watersheds were studied on each ridge between 750 and 1,200 meters. Two of the watersheds on the recently logged ridge escaped logging, whereas the other five were in intermediate stages of succession following logging. None of the watersheds was subjected to any kind of human use at any time during this study.

Streams in all of the watersheds were sampled every two weeks during the growing season and every three to four weeks during the winter. Samples were collected in polypropylene bottles. Dissolved organic carbon concentrations were comparable with low levels found by Hobbie and Likens (1973), indicating that dissolved organic nitrogen was also low. Ammonium and nitrate were measured with an Orion ammonia electrode (Anonymous 1972). Metallic cations were analyzed by atomic absorption spectroscopy, and chloride was analyzed potentiometrically using a silver ion specific electrode.

RESULTS

Ideally, hydrologic nutrient losses from watersheds are compared in terms

of loss rate per unit area (i.e., equivalents/hectare/year). This can be done by multiplying streamwater concentrations by flow volume over time and dividing by area. If several assumptions are satisfied, however, streamwater concentrations alone can suffice for comparisons of outputs between watersheds. These assumptions are that the watersheds being compared have similar hydrologic regimes and precipitation chemistry and similar amounts of deep seepage drainage, preferably none. Hydrologic regimes include precipitation quantity and distribution in time, evapotranspiration rate, soil water retention, and storm flow characteristics. Precipitation chemistry includes the distribution of elemental concentrations by storm volume and through time. Differences in deep seepage are important if seepage alters discharge characteristics or if the chemical composition of seepage is different from that of surface runoff.

In this case, all the watersheds are located within 4 km of one another on one mountain. They are also at the same elevation, on west-facing slopes, and on the same bedrock. Their close proximity in similar physical settings minimizes the possibility of significant differences in precipitation regimes or chemistry, or in evapotranspiration. The bedrock common to all the watersheds is the massive, metamorphic Littleton Formation which is considered to be relatively free of deep seepage (Likens et al. 1967). We believe that the assumptions listed above are satisfied and that it is

therefore reasonable to use elemental concentrations as accurate indexes of outputs in comparing these watersheds.

We will emphasize nitrogen losses from these watersheds in this report because (a) nitrogen is an important, frequently limiting plant nutrient; (b) nitrification may, at times, control cation losses from some ecosystems (Likens et al. 1969); and (c) nitrogen losses changed dramatically in this region with disturbance and subsequent recovery (Likens et al. 1970, Pierce et al. 1972). Fixed nitrogen could enter these ecosystems either in precipitation or by nitrogen fixation; it could leave through denitrification or streamflow. Nitrogen fixation has been estimated by acetylene reduction in soil, litter, logs, and moss mats and found to be minimal in these highly acid coniferous forest sites (conversation, September 1974, M. Cepuran and R. L. Lambert, Department of Biological Sciences, Dartmouth College). No nitrogen-fixing lichens are present in the tree crowns. Denitrification should also be minimal in these steep, well-drained soils. Thus precipitation represents the only major input of fixed nitrogen to these ecosystems, and streamflow the only major output.

As demonstrated in Table 1, there is a substantial difference between ionic concentrations of discharge waters from the two sets of watersheds. Nitrate concentrations in particular are considerably higher in streams draining the more mature ecosystems. Although ammonium was detectable in precipitation

TABLE 1. Mean growing season (1 June-30 September 1973, 1974) streamwater concentrations from five intermediate-aged successional logged vs. nine old-aged ecosystems. Watersheds were located on west-facing slopes on Mt. Moosilauke, New Hampshire. Values are in microequivalents/liter, with standard errors of the means in parentheses.

Elements	Streamwater concentrations ($\mu\text{eq/l}$)		Ratio of concentrations	Precipitation concentrations*
	Unlogged watersheds	Logged watersheds		
NO_3^-	53(5)	8(1.3) [†]	6.62	40 [‡]
K^+	13(1)	7(0.5) [†]	1.81	
Mg^{++}	40(4.9)	24(1.6) [†]	1.66	
Ca^{++}	56(4.5)	36(2.5) [†]	1.56	
Cl^-	15(0.3)	13(0.3) [†]	1.16	10
Na^+	29(2.6)	28(0.9)	1.03	

*Precipitation concentrations are derived from Likens (1970) and our own data. Concentrations are presented only when this represents the only significant input for the element.

[†]Difference between watershed types significant at $P < 0.01$ level.

[‡]Calculated assuming all fixed N in precipitation is converted to nitrate.

throughout this study, no ammonium was detectable at any time in any of these streams. Based on these concentrations, nitrate outputs from old-age ecosystems are approximately equal to precipitation inputs of fixed nitrogen when a correction for the concentrating effect of evapotranspiration is applied. This suggests that the ammonium in precipitation is quantitatively converted to nitrate within these ecosystems.

Potassium, magnesium, and calcium—all essential plant nutrients—are also retained more effectively in the successional ecosystems than in the more mature ecosystems. Concentrations of chloride, a micronutrient, are slightly higher in the streams draining the more mature ecosystems, though we doubt if this has any ecological significance. Finally, concentrations of sodium, an element not accumulated above trace levels in plant biomass in humid regions, are virtually identical in the streams draining these two ecosystem types. The similarity of concentrations of biologically less significant ions (chloride and sodium) supports our assumption that comparison of stream-water concentrations as an index of output is meaningful.

These data support the hypothesis illustrated in Fig. 1B. The variation in nitrate loss is similar to that proposed for a "limiting" nutrient. Potassium, magnesium, and calcium follow our expectations for essential but nonlimiting nutrients, and chloride and sodium (particularly sodium) follow the pattern we expected for nonessential elements.

Another line of evidence supporting the importance of biotic factors in controlling nutrient losses is seasonal variation in nutrient outputs. We would expect that elements that are retained in ecosystems by being bound up in growing biomass would have pronounced seasonal cycles with lowest losses during the growing season. Fig. 2 shows seasonal variation in nitrate concentrations of drainage waters from the watersheds described previously. The undisturbed watersheds have high, relatively constant nitrate outputs, whereas the successional ecosystems have a pronounced seasonal cycle with a growing season minimum. This seasonal cycle is consistent with our hypothesis that plant uptake regulates nitrogen losses in these ecosystems, a mechanism that would, of course, be effective only during the season of root uptake. Root uptake is particularly seasonal at the elevations studied because the soil is frozen from

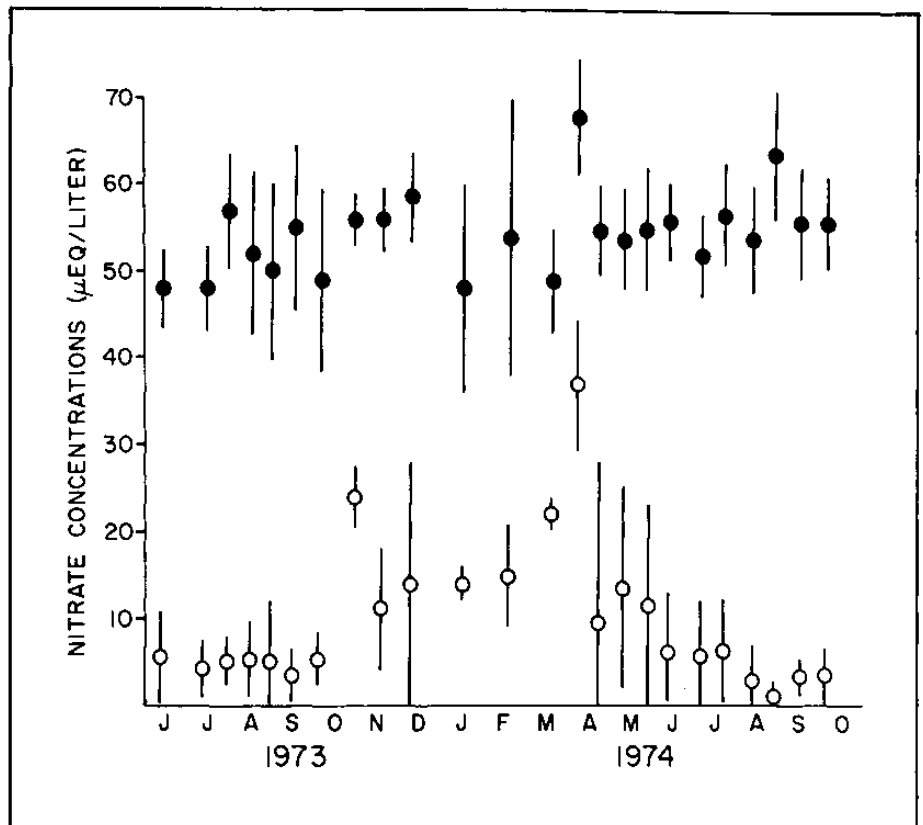


Fig. 2. Seasonal variation in nitrate concentrations in streams draining intermediate-aged successional (hollow dots) and old-aged (solid dots) forest ecosystems. Each point represents the mean of five streams for the successional forests and nine streams for the old-aged forests; the bars represent plus or minus one standard error of the mean. Nitrate concentrations are relatively constant and high in streams draining old-aged watershed ecosystems; they are low and distinctly seasonal in streams draining successional watershed ecosystems.

November to May (conversation, September 1974, T. Fahey and G. E. Lang, Department of Biological Sciences, Dartmouth College). In milder environments, the cycle may be less marked or even absent, although such a cycle is obvious at lower elevations in our region (Likens et al. 1970).

DISCUSSION

According to our hypothesis, the differences in nutrient loss rates between ecosystems of differing maturity will depend on their relative positions on the net increment curve in Fig. 1A. In the case of the data just described, the old-aged watersheds are represented somewhere near zero on the right limb of the curve, whereas the successional watersheds probably fall between the maximum on the left and the zero level on the right limb.

A similar situation is suggested by a comparison between one of the few uncut northern hardwood watersheds in New Hampshire and the younger Hubbard Brook forests (Leak 1974). Again, nitrate levels were higher in the growing

season for the old-aged forest than for the younger forests of Hubbard Brook.

A third case has been reported by Johnson and Swank (1973) for southern Appalachian forests at Coweeta Hydrologic Laboratory. They found that a 14-year-old pine watershed lost less calcium and magnesium than did a 50- to 60-year-old hardwoods watershed. They ascribed this difference to higher net productivity in younger pines. We agree, and would restate this difference as probably being caused by a higher net biomass increment in the younger vegetation, perhaps near the maximum in the curve of Fig. 1A, compared with the older hardwood forest, which is probably past the maximum for net increment. Species-specific requirements of pine relative to hardwoods may also be involved, and in this case we are probably not dealing with a single successional sequence because the white pines were planted and hardwood sprouts eliminated.

A reverse relationship between loss rates and maturity, which is consistent with this hypothesis, is expressed by

data from the Hubbard Brook watershed study. In this case, loss rates from an initial, extended disturbance condition are compared with loss rates from a 60-year-old forest (Likens et al. 1970). The revegetated watershed has a negative net biomass increment, whereas the older forest is represented to the right of the maximum rate of accretion.

We would expect that the nutrients most strongly accumulated in developing ecosystems might well be the ones most rapidly lost when net biomass increment is negative. This pattern was in fact observed at Hubbard Brook: nitrate concentrations increased 57-fold after clearcutting; potassium, calcium, and magnesium concentrations increased 15.6-, 4.2-, and 4.1-fold, respectively; and sodium and chloride concentrations increased only 1.8- and 1.3-fold. The high losses of limiting and essential elements represent the inverse of the accumulation of these elements in biomass in developing ecosystems.

Based on productivity data for early stages from Marks (1974) and for the 60-year-old forest from Whittaker et al. (1974), we would predict that these very rapid loss rates will decline drastically to a minimum within 10 years after revegetation commences.

Woodwell (1974) has presented data for loss rates from two fields of abandoned agricultural land in comparison with older pine and oak forests. Nitrate losses were much greater from the two young stages than from the forest stands. The higher losses are probably caused by the imbalance of plant uptake with meteoric inputs and mineralization of stored nitrogen. Leaching of residual fertilizer may also be involved as has been demonstrated for abandoned fields in So. Carolina (Odum 1960). The abandoned fields would be represented to the left of the maximum of the net increment curve of Fig. 1A, and the forest stands to the right of the maximum point but having a higher rate of accrual than the young stages. The data presented do not permit further distinction between the two abandoned fields or between the two forest stands.

A recent noncomparative study of nitrogen losses from a 450-year-old Douglas fir-dominated watershed would seem to be a severe test of our hypothesis. Fredriksen (1972) reported that losses were low for what might seem to be a steady state system. There is no evidence, however, that total biomass has ceased to accumulate even at this old age. Old-age vegetation of this type

may still be accumulating biomass, albeit at a much lower rate than at a younger age. Indeed, this might well be the general case in the absence of natural disturbance factors. We will return to this point later.

There is another line of evidence supporting an increase in nutrient losses from steady state ecosystems as compared with intermediate-age systems. Olson (1958) examined soil and vegetation development through primary succession on Lake Michigan sand dunes. Soil nitrogen initially increased rapidly, then asymptotically approached a steady state value. Because living biomass, as indicated by basal areas, was constant over the late successional stages, it can reasonably be assumed that total ecosystem nitrogen content approached a steady state. As Olson pointed out, if the nitrogen content of the dune ecosystem is not changing, then nitrogen inputs must equal outputs. A similar, but less complete example was presented by Crocker and Major (1955) for primary succession following deglaciation in southeastern Alaska.

Evaluation of our general hypothesis requires a consideration of the nature of steady state in terrestrial, especially forest, ecosystems. One view of forest dynamics consistent with concepts of steady states in terms of mass is that forests maintain their species composition, basal area, leaf area index, and biomass in small-scale processes of individual tree death and replacement.

We suggest that the bulk of the evidence supports a contrary view: that most forests turn over in patches of various sizes controlled by intrinsic characteristics of the ecosystem or by extrinsic factors of the environment. Watt (1947) has reviewed a number of cyclic, upgrade-downgrade processes generated largely by intrinsic properties of specific plant communities. The literature is replete with evidence for sudden terminations of forest growth by natural catastrophes. Only a few may be mentioned here: Cooper (1913) for periodic blowdowns of boreal forests; Raup (1967) and Stephens² for hurricanes; Henry and Swan (1974) for local windstorms; Heinselman (1973), Rowe and Scotter (1974), Viereck (1973), and Kilgore (1973) for effects of fires; Morris (1963) for insect epidemics; and

Flaccus (1959) for periodic debris avalanches.

Admittedly, all of these references describe temperate forests; however, little literature is available for tropical forests to permit more widespread analysis. These examples suggest that the history of forest vegetation is one of long periods of biomass accumulation punctuated by short periods of destruction. The areas, or patches, having common origins from the most recent destructive event may vary in size from small areas resulting from the turnover of single trees to vast areas resulting from very large fires. With the present state of understanding of forest maintenance, we believe that processes generating a small patch size characteristic of tree-for-tree replacement may prevail for a few forest types all of the time, and may occur for all forest types for small periods of time, but that the prevailing processes for most forests, most of the time, generate larger scale cyclic patterns of growth and destruction.

The implications of this view of forest dynamics are obvious for the "climax" concept of community ecology (Sprugel³, Wright 1974). Its immediate relevance to this paper, however, is in identifying situations in which watersheds may be in steady states. If the patch size of vegetation turnover is small relative to the size of a watershed, then the watershed can integrate all of the patches within it into a steady state whole. This was also the case in the old-aged spruce-fir communities that we studied, where wind-throws, a few wave-type disturbances (Sprugel⁴), and other incompletely understood natural disturbance patterns combine to generate a mosaic of small patches.

If the patch size of turnover is larger than a single watershed ecosystem, however, then it will be impossible to measure steady state conditions in a single watershed. The vegetation of such a watershed will either be growing, or it will be being rapidly destroyed. This may explain why even very old watershed ecosystems in fire-dominated regions such as the Pacific Northwest are losing less nitrogen through streamflow than they gain in precipitation (Fredriksen 1972).

³Sprugel, D. G. 1974. Natural disturbance and ecosystem responses in wave-generated *Abies balsamea* forests. Ph.D. dissertation, Yale School of Forestry, Connecticut.

⁴See footnote 3.

²Stephens, E. P. 1955. The historical-developmental method of determining forest trends. Ph.D. dissertation, Harvard University, Massachusetts.

It may be convenient to designate control watersheds in experimental studies as "mature" or "climax" in terms of a vegetational cycle, but there should be no confusion between mature or climax in the phytosociological sense and steady state in the ecosystem sense. Misuse of this terminology can lead to conceptual difficulties. For example, statements to the effect that mature systems are "tight" whereas disturbance can lead to "leakage" of nutrients are misleading. Such statements can only apply to very recently disturbed systems and should not be used to characterize immature ecosystems relative to mature ones. Furthermore, such statements only apply to certain kinds of disturbances such as those involving destruction of biomass. Steady states by definition must include elemental losses distributed in some pattern over sufficient space or time. We maintain that intermediate-aged successional ecosystems will have lower nutrient losses than either very young or very old (mature) ecosystems. We wish to emphasize that proper analysis of ecosystems, whether for elemental losses or other functions, requires a consideration of the developmental position of the ecosystem and a clear understanding of changes in net increment with time.

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