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Gail A. Baker[1], Mark E. Harmon[1], Sarah E. Greene[2]

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Natural variation of ecosystem processes must be documented in order to assess the impact of airborne pollutants. The Hoh Rain Forest in Olympic National Park offers an opportunity to study ecosystem processes in a relatively pollutant free environment. The processes we selected for study are sensitive to airborne pollutants and important contributors to long-term ecosystem productivity. They included lichen and moss productivity, litter fall and decay rates and conifer needle population structure and retention times. Current seasonal patterns and characteristics of these processes were quantified. Each process is evaluated with regard to its utility as an index for the effects of pollutant stress.

1. Forest Science Dept., Oregon State University, Corvallis, OR 97331; 2. Forestry Sciences Lab., Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, OR 97331

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BACKGROUND

In response to concerns about the spread of air borne pollution and its potential effects on the environment, baseline data collection has been initiated in many areas of the western United States. Documenting current ecosystem conditions provides data against which future comparisons can be made. In many areas now subjected to pollution these data are lacking. Without historical comparison determining the response of ecosystems to increasing pollutant input is hampered.

Complex ecosystem interactions and the variability associated with biological systems add other confounding factors to determining ecosystem response to pollutants. The range of natural variability is an important aspect of an ecosystem parameter because it represents the limits of utility of the parameter is a pollution index. During extreme environmental conditions, short time periods or early stages of pollutant input it may be difficult to distinguish between natural variation and pollutant induced change. In this case parameters with predictable fluctuations would aid in making that distinction.

OBJECTIVE

The objective of this study was to document the current state of five ecosystem processes in a relatively pollutant free area. In a pollutant free site the variability associated with the processes should reflect natural patterns. The range of natural variation determines if parameters can be sensitive enough indices of pollutant stress.

Olympic National Park, Washington was chosen as a study site because it has the cleanest air on the North American continent (Herrmann 1986). Despite this distinction the Park will not remain entirely free from future atmospheric pollutant deposition. The kinds of pollutant threatening this area, and other remote regions, are those capable of long range transport. There is increasing evidence that long range transport of trace elements, gases and manmade organics is a valid phenomenon (Henderson et al. 1985). Sources of these pollutants are the industrial centers of the eastern U.S., Europe, Japan, China and the U.S.S.R. (Rahn 1981).

The five processes chosen were lichen and moss productivity, canopy litter fall and decay rates and conifer needle retention times. These processes have all responded to increased pollution in other ecosystems or in the laboratory, and are important to longterm ecosystem productivity.

SITE DESCRIPTION

The study plot is a 1 ha area located at 176 m elevation near East Twin Creek in the Hoh River Valley, Olympic National Park, WA. The site is a temperate rain forest representative of the Picea sitchensis-Tsuga heterophylla plant community (Franklin and Dyrness 1973). There are 221 trees over 5 cm diameter at breast height and a total basal area of 74.4 m^2 ha^{-1} in the plot. Tree diameter class distribution show an abundance of small and large P. sitchensis (Sitka spruce), intermediate sized T. heterophylla (western hemlock) and 2 large Pseudotsuga menziesii (Douglas fir). Understory trees and shrubs include Acer circinatum, Vaccinium alaskaense and V. parvifolium. Ferns and herbaceous perennials are seasonally abundant. The forest floor is almost completely covered by a luxuriant layer of moss.

The maritime climate of the Hoh Valley is temperate with mean rainfall of 355 cm yr^{-1}. The rainfall has a distinctly seasonal pattern with 75 % of the precipitation falling between November and April. The coolest temperatures coincide with the wettest months (Fig. 1). Daily temperatures and rainfall are monitored at the NADP weather station 5 km from the study plot. Concentrations of NO_3, SO_4 are considerably lower than other regions of the USA and mean rainfall pH from 1980 to 1984 was 5.42 (NAPD 1985).

METHODS

Needle Population Structure: Needle Retention and Loss Rates

Needle population structure was studied on the two dominant conifer species, Tsuga heterophylla and Picea sitchensis. The main objective was to estimate how long needles were retained on twigs. Branches were collected from recently windblown trees at three canopy levels: lower, middle and upper. Needle loss rates were determined by counting needles and/or measuring branch length for each year of growth up to

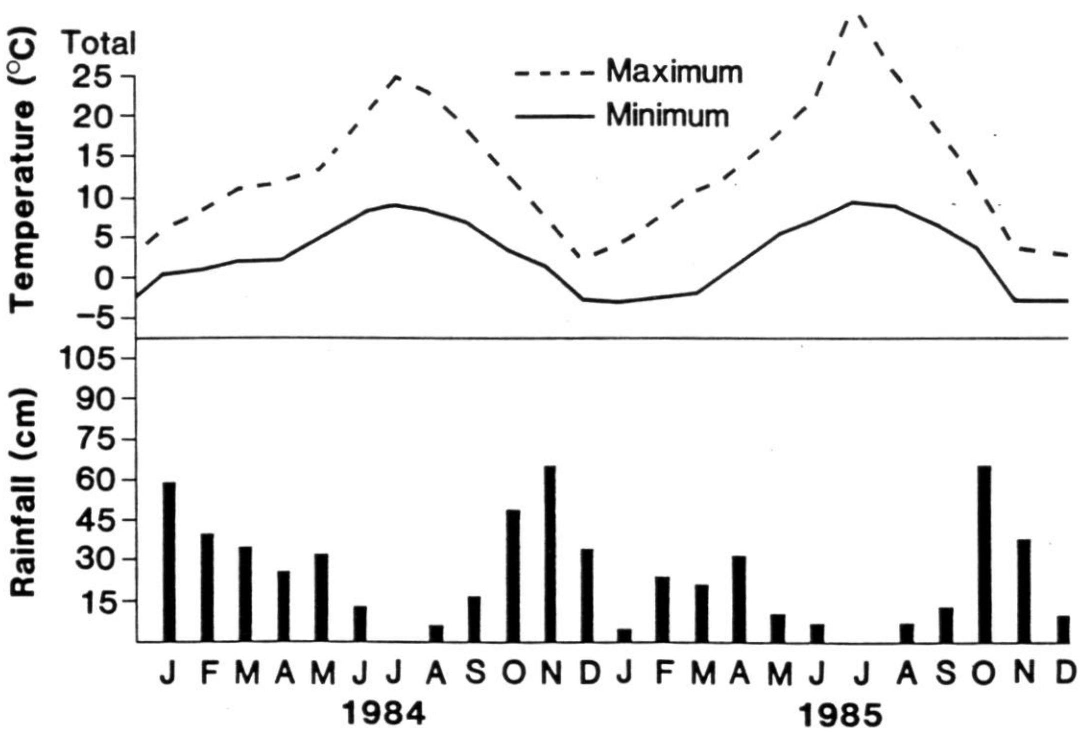

Fig 1. Total monthly rain fall and mean minium and maximum air temperatures recorded at the NADP station 5 km from the sudy plot.

9 yr. Twigs <3 years old retain most of their needles and had visible needle scars which facilitated counting the original number of needles. On older twigs needle scars were not readily apparent; therefore a regression that predicted the number of needles initially present from twig length was developed using 1-3 year old twigs. This regression was used to estimate the original number of needles retained on twigs ≥3 years old. The end product was a survivorship table of needles.

Moss Biomass and Productivity

Moss species composition and biomass were measured by harvesting mosses in 50 randomly placed 8.2 cm diameter cores. Ten cores were randomly distributed over each of five 35 m transects within the 1 ha plot. Total moss biomass was sampled from the forest floor but not from fallen logs which covered approximately 10% of the forest floor. The harvested mosses were separated from litter and vascular plants and then sorted into the following species: Hylocomium splendens, Eurhynchium oreganum, Rhytidiadelphus loreus, Sphagnum girgensohnii and miscellaneous moss species. Samples were oven dried at 50 °C for 41 hours and weighed immediately after removal from the oven.

Seasonal growth patterns and estimates of annual productivity can be made for H. splendens because it posseses clearly recognizable annual growth increments (Tamm 1953, Binkley and Graham 1981). Each month 25 individual H. splendens stems were harvested from the study plot. The length of the current growth (< 1yr) was measured on each individual. They were then sectioned into 6 growth classes; current, 1, 2, 3, 4, and $\geq$5 yrs. The growth class sections were pooled, oven dried for 48h at 50°C and weighed. The proportion of biomass in each growth class was then calculated and an age structure-biomass relationship was determined.

A second method to estimate moss production is currently being employed. This method will allow us to test our original H. splendens measurements and to estimate the production of the three other moss species. Production was measured by placing a known mass of living moss in the field and weighing it after growth. Air dried samples of moss were weighed and placed in 11 cm diameter x 7 cm deep plastic cups. Ten replicates were made for each species and placed at the study plot in a randomized block design. The cups were sunk in the moss turf. The experiment began in June 1985 and cups will be collected in November 1986 in order to encompass one complete season of uninterrupted growth.

Lichen Productivity

Lichen productivity experiments followed a methodology developed by Dr. W. Denison of the Oregon State University Botany Department (manuscript in progress). Twenty thalli of Lobaria oregana were strung on each of 30 monofilament lines to make a lichen string. The strings were air dried, weighed, and hung in the field on a PVC frame. Lichen strings were collected at 3 mo intervals, air dried and weighed to determine biomass increases. All thalli were returned to the field except for two strings at each weighing. These thalli were removed and their air dry and oven dried weights were determined. New thalli replaced the harvested ones and were returned to the field.

Occassionally thalli died. If greater than 50% of a single thallus had turned brown it was removed from the string but not replaced. If over 50% of the thalli on the string were dead all were replaced with healthy thalli.

Litter Production and Decomposition

Rates of fine litter production from the forest canopy were determined using 25 buckets randomly placed throughout the study site in June 1984. Material falling into the buckets was caught in nylon liners and collected at monthly intervals. The area of a single bucket is .066 m^{-2}, combined area of 25 buckets was 1.65 m^{-2}. The samples were oven dried, sorted into ten major components and weighed. Seasonal patterns of absolute litter fall and component proportions were then calculated. The needle component was pooled for every 2 month period beginning with Nov-Dec 1984 continuing through 1985. These seven sample groups were analyzed for lignin and nitrogen composition.

Annual decay rates of leaf litter for Abies procera, Acer circinatum, A. macrophyllum, Alnus rubra, Cornus nutallii, Picea sitchensis, Thuja plicata, Populus trichocarpa, Pseudotsuga menziesii and Tsuga heterophylla were estimated using standard litter bag methodology (Singh and Gupta 1977). Leaves were gathered just prior to abscission in the fall and air dried. Subsamples of the leaves were analyzed for initial lignin and nitrogen content. In addition the proportion of readily leachable matter was estimated by soaking the leaves in distilled water at room temperature for 48 hours.

Approximately 10 g of leaves were inserted into each of the numbered, 20 X 20 cm polyester bags with a 1 mm mesh size (Crossley and Hoglund 1962). Litter bags were placed on the forest floor in November 1984 for 12 months to determine the annual decay rate. Bags were randomly located through the plot in 5 blocks consisting of 20 bags, 2 bags for each species.

To determine if decay rates change through time, 48 bags of Acer macrophyllum and Pseudotsuga menziesii were set out. Each month two bags of each species were collected. Monthly collections will continue through November 1986, providing 24 months of data.

After the litter bags were removed from the field, the remaining tissue was oven-dried at 50 °C for 48 hr. The sample was weighed and the loss of litter was expressed as a percentage and as the decay rate constant, k (Jenny et al. 1949, Olson 1963).

RESULTS AND DISCUSSION

Needle Population Structure

Our preliminary work indicated the original number of needles on twigs was well correlated with twig length for *T. heterophylla* (r^2 = 0.93, Fig. 2). *Picea sitchensis* had an identical r^2 value. Given the fact the number of needles and internodes is fixed during bud development, these results indicated internodal distance on many twigs is relatively constant. Severe stress induced by pathogens, drought, pollution or mechanical injury may lead to shorter internode elongation than observed in our preliminary sample; therefore these equations are only appropriate to predict needle numbers for healthy trees. Needle retention patterns

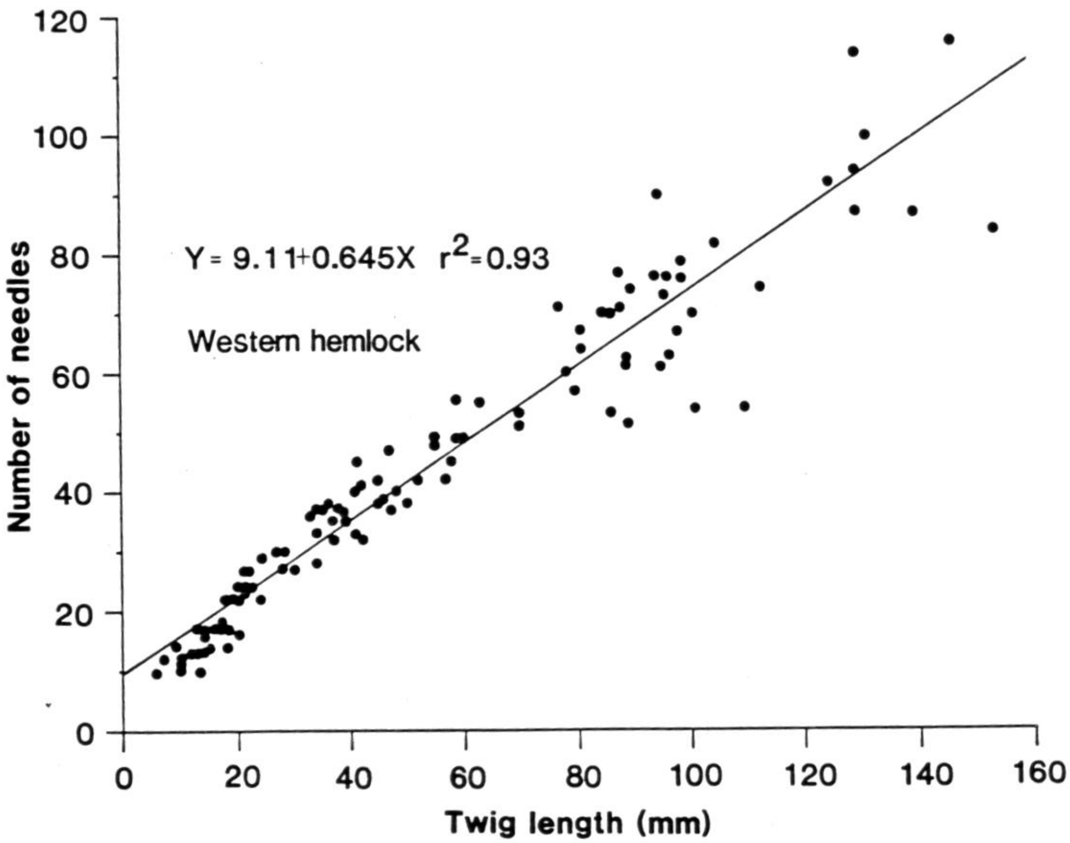

Fig. 2. Relatioship between twig length and the number of needles for one year old twigs of *Tsuga heterophylla*.

in *P. sitchensis* and *T. heterophylla* varied slightly. Both species lost needles in significant number after 3 years and approximately 60% of their needles were missing from 6 yr old branches (Fig. 3). However, the total length of needle retention in *P. sitchensis* appeared to be a year or two longer than for *T. heterophylla*.

The length of time needles are retained by twigs directly influences the quality of the litter that falls to the forest floor and determines the amount of leaf area in a forest canopy. If needle survivorship decreases stand primary productivity would be affected (Waring 1985). The importance of needle population structure to primary productivity and its predictability suggest that this parameter is a useful indicator of ecosystem stress.

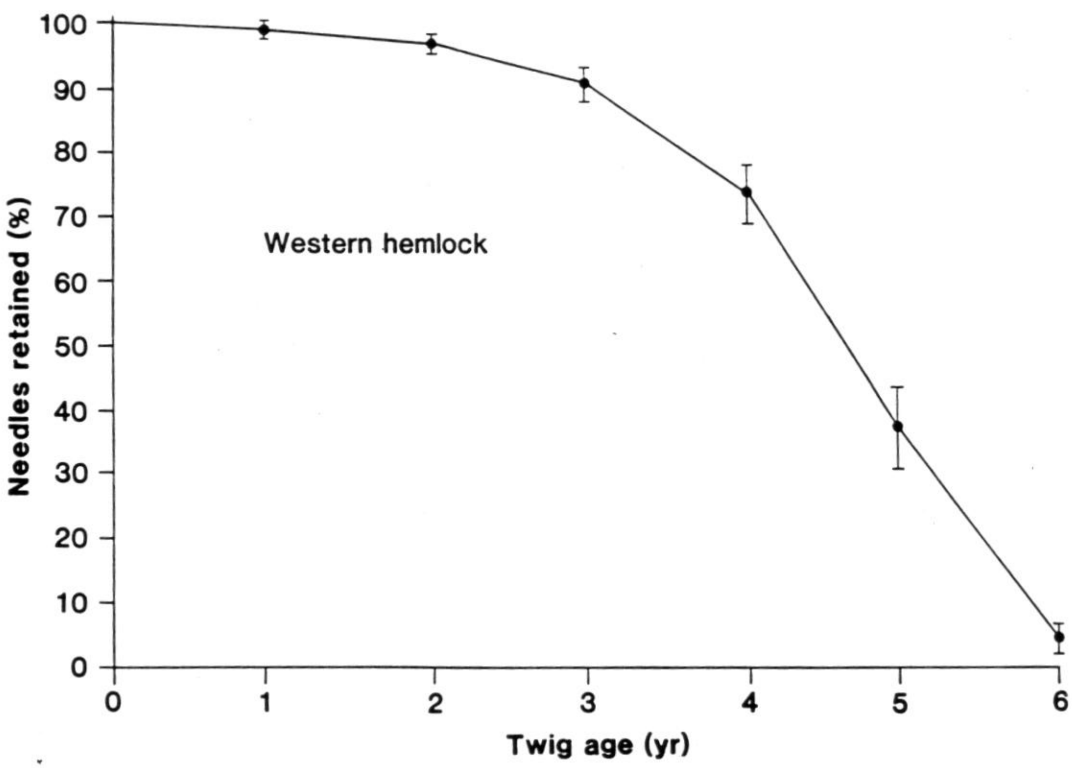

Fig 3. *Tsuga heterophylla* needle retention as a function of time.

Moss Inventory and Productivity

The four dominant forest floor moss species in the study plot were *Hylocomium splendens*, *Eurhynchium oreganum*, *Rhytidiadelphus loreus* and *Sphagnum* girgensohnii with a combined mean biomass of 186.23 gm^{-2}. Hylocomium splendens and S. girgensohnii had the greatest mean biomass values, 76.11 and 77.02 $g\ m^{-2}$ respectively, and represented 82% of the forest floor moss biomass. A marked difference between H. splendens and S. girgensohnii was their distribution on the forest floor. The latter forms distinct monospecific patches, growing in thick, tightly packed mats. Hylocomium splendens is a feathery moss carpeting the forest floor, intermingling with the less abundant species. This may reflect different moisture requirements and/or growth patterns of the two species. Eurhynchium oreganum and R. loreus were almost as widespread as H. splendens but were much less abundant, 9.51 gm^{-2} and 12.68 gm^{-2} respectively. The remainder of the moss cover was made up of a variety of species that include Plagiomnium spp. and Isothecium stoloniferum.

There were two distinct growth periods associated with phenological development of H. splendens; January to June and September thru November (Fig. 4). New stems were visible at the apex of the previous years growth by November. The stem lengthens 30 to 40 mm during the wet spring months.

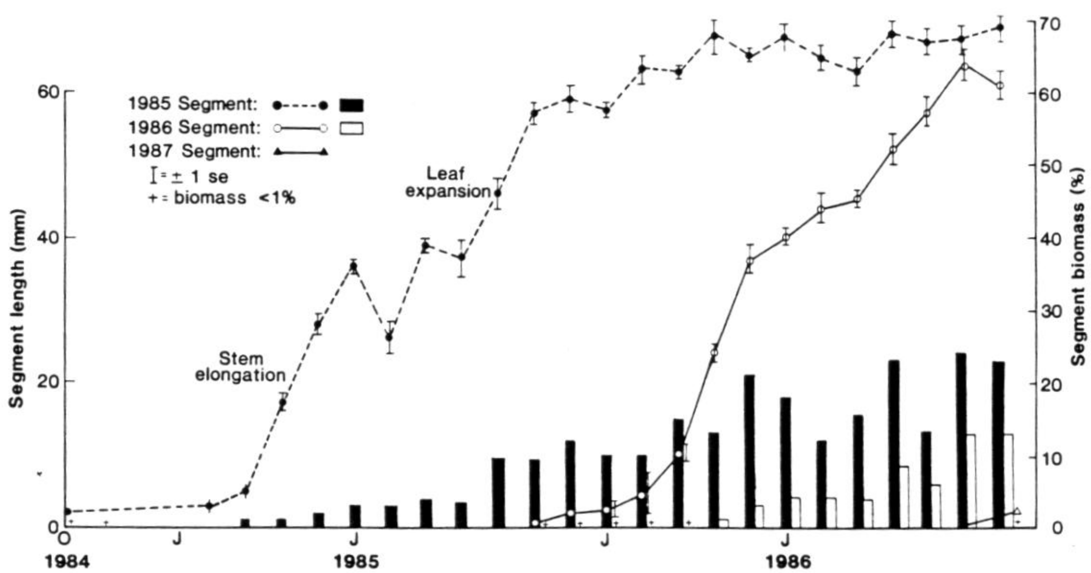

Fig 4. Seasonal growth patterns and biomass increase in the 1985 and 1986 segments of Hylocomium splendens.

During the dry summer period biomass remained constant with some shrinking of the desiccated stem. Growth resumes and leaf expansion begins in the autumn. Biomass increase of the youngest segments progresses slowly at first with the greatest increase coming at the time of leaf expansion. The new growth accounts for up to 20% of the biomass after 19 months of growth. Tamm (1953) observed that this segment continues increasing in biomass through its second year. Annual productivity must then include new growth on both current and year old segments.

An age structure- biomass relationship constructed each month showed segments ≤3 yr old make up 75% of the H. splendens standing crop. The proportion of biomass allocated to each of those segments is approximately equal except for the current segment which is a small proportion initially and increases over the year. Segments ≥4 yr old were over-topped by the younger segments and lost biomass due to decay.

The biomass and length variations seen in the 1985 segment as it entered its second year of growth (Fig. 4) may be due to natural variation. However, they are more likely due to the influence of the 1986 segment and the difficulties in measuring a feathery leaf as opposed to a lengthening stem. The answer to this question is being pursued during the 1986 measurement.

A mechanism explaining pollutant toxicity to lichens has been suggested by Fields and St. Clair (1984). The physiological aspects of pollutant toxicity are not as well known for mosses. Hylocomium splendens shows consistent seasonal growth and productivity patterns. This species and others similar to it are also found in industrial countries (Barclay-Estrup and Rinne 1978, Rühling and Tyler 1970, Rieley et al. 1979, Nakamura 1984). Monitoring moss growth rates in addition to accumulation of heavy metals and other pollutants in tissue may be an indication of atmospheric quality.

Lichen Productivity

Lobaria oregana thalli gained at least 20% of their dry weight biomass during a 3 month period (Table 1). However large portions of biomass were lost due to thallus mortality. During early winter, 17% of the thalli on the strings died. Temperatures during that time were typical for the season, but there was a more persistent snow cover than usual. We do not know if snow collected and remained on the lichen strings. Denison (unpublished) found this lichen species stored in a lab over 100 days loses viability. The thalli used in this experiment were strung and set in the field within 48 hr of collection. The cause of mortality remains uncertain.

Table 1. Biomass measurements of Lobaria oregana thalli over a 12 month period.

Interval	Mean Biomass Change (%)
Mar-Jun 1985	22
Jul-Sep	20
Oct-Dec	-15*
Jan-Mar 1986	26

*17% of the thalli had died by this date.

The growth of healthy thalli was highly variable. Lichen strings gained from 1% to 75% of their dry weight during any three month interval, dead thalli excluded. Keeping this variability in mind we estimate the mean annual productivity to be 50%. Using the same methodology and species Denison (unpublished) found annual growth rates between 13% and 30% in the drier climate of central Oregon, with less variability between strings.

Typical habitat for L. oregana is in the canopy of conifer trees in Pacific Northwest forests. On the east side of the Cascade Mountains in central Oregon, Rhoades (1977) found that L. oregana populations in the crowns of old-growth Douglas fir are in a state of dynamic equilibrim. Often dry weight gained by thallus growth is off-set by loss of whole thalli and fragments to decomposition, consumption and litter fall. The thalli that do survive however are estimated to have a net annual production of 31.1% of the standing biomass (Rhoades 1983).

Mosses and lichens have been widely used as indicators of air borne pollutants (Barkman 1969, Brodo 1966, LeBlanc and DeSloover 1970). The majority of studies quantified species diversity declines and/or accumulation of pollutants in tissue (Tuominen and Jaakkola 1973, Rühling and Tyler 1970). Estimates of lichen productivity are highly variable and may not be adequate indicators of pollutant stress, especially over time spans less than 5 years.

Litter Production

Annual canopy litter fall during 1985 was 2790 kg ha. This value is within the range of litter fall for similar forest communities in Oregon and Washington (McShane et al. 1983). Monthly amounts of litter fall were variable and showed no distinct seasonal pattern (Fig. 5). However when monthly inputs of separate components were considered on a proportional basis, seasonal fluctuations were suggested. Three dominant components of litter fall were conifer needles, cones and fine branches (Fig. 6). Minor components include deciduous leaves and "Other" comprised of reproductive tissue, moss, lichens, and miscellaneous indistinct organic matter. Needles, cones and deciduous leaves show seasonal fluctuations.

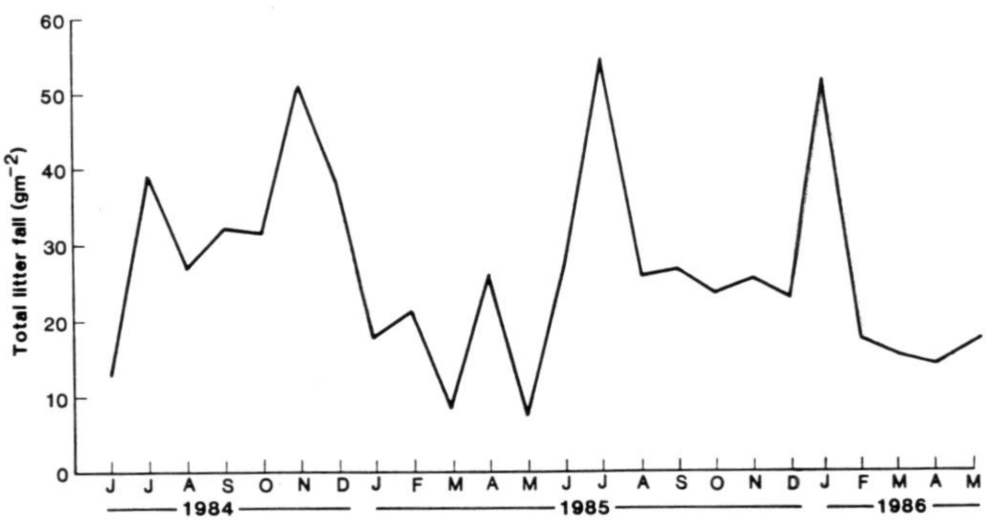

Fig 5. Total monthly canopy litter fall.

Needles from all three conifer species made up the most important litter component. The period of greatest needle fall was during the dry summer season when needles comprised from 65% to 85% of the litter fall. There was also a seasonal fluctuation in the lignin and nitrogen composition of the needle litter (Table 2). Both lignin and nitrogen decreased during the months of July and August. However, the lignin:nitrogen ratio remained fairly constant through the year with a mean value of 31.9. The predicted decay rate, k, for this value is 0.3 yr^{-1}.

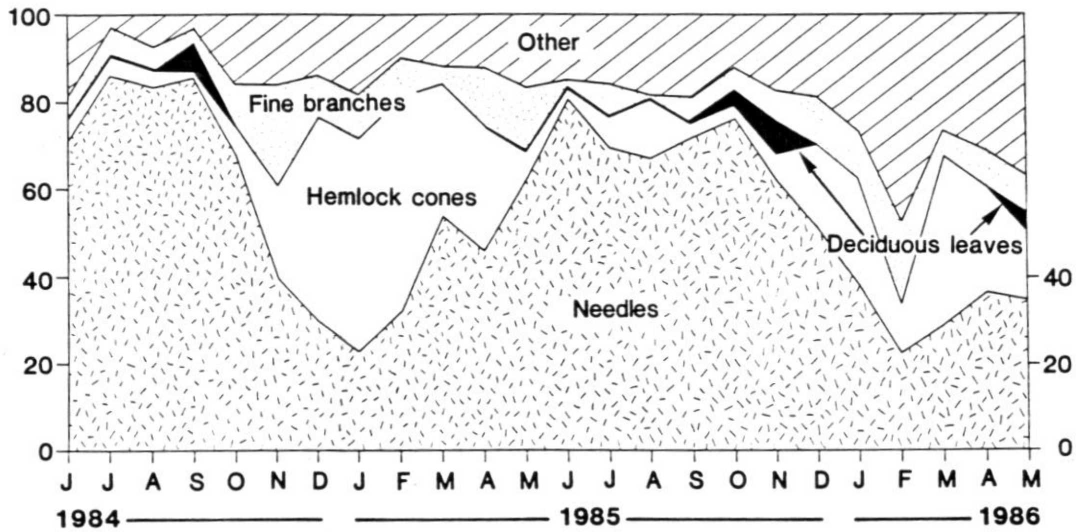

Fig 6. Monthly proportions of four litter fall components. Dark portion represents deciduous leaves. See text for description of the "Other" category.

Table 2. Initial lignin and nitrogen content of the confier needle component of canopy litter fall. Samples pooled over 2 month periods through 1985.

MONTHS	MEAN* % LIGNIN	MEAN % N	LIGNIN:NITROGEN
Nov-Dec 1984	26.2	.81	32
Jan-Feb 1985	29.1	.88	33
Mar-Apr	26.3	.95	28
May-June	22.6	.70	31
Jul-Aug	18.6	.57	33
Sept-Oct	21.3	.72	30
Nov-Dec	26.6	.73	36

*N=3

Ninety-nine percent of the cone component was from T. heterophylla trees with only occassional P. sitchensis cones and none from P. menziesii. The cone component peaked in the winter of 1985 and showed another increase 13 months later.

Acer circinatum and the two species of Vaccinium made up the deciduous component. Their input may have been underestimated because the buckets were 1 to 1.5 m above the ground which exceeds the height of some of the Vaccinium shrubs. They showed the expected seasonal peak in autumn. This is a good reference point for determining the variable timing of autumn leaf abscission in relation to climatic patterns.

Fine branches had a constant input through the year and never fluctuated much below or above the range of 5 to 10%. The "Other" component represented a small percentage of the litter input and had a constant low input.

Bark and wood fragments comprised less than 5% of the annual litter fall and fell irregularly. They are both dense and when present their weight obscures the proportions of the remaining components. For these reasons they were excluded when component percentages were calculated.

The annual amount of litter input is an indication of the biomass added to the detrital pool on the forest floor. The proportions of individual litter components are a measure of litter quality. Conifer needles are the major component of litter at our study site and alteration in their input and/or decay rates may affect the forest nutrient cycles.

Litter Decomposition

Decomposition of leaf and needle litter is related to the initial concentrations of lignin and nitrogen in the tissue (Melillo et al. 1982). The 10 species used in our experiment represented a gradient of lignin:nitrogen ratios ranging from 5 for Cornus nuttalii to 53 for Thuja plicata. Decay rate constant, k, was well correlated ($r^2 = .83$) with initial lignin:nitrogen ratios (Fig. 7). The deciduous leaves of Alnus rubra did not conform to the model. Alnus rubra, a nitrogen-fixer, decays slower than predicted, indicating factors other than nitrogen limit decay in this species.

Data from monthly collection of litter bags suggested decay rates were not constant through time; Decompositon during the first 3 months was faster than subsequent months; decay of Acer macrophyllum leaves and Pseudotsuga menziesii needles

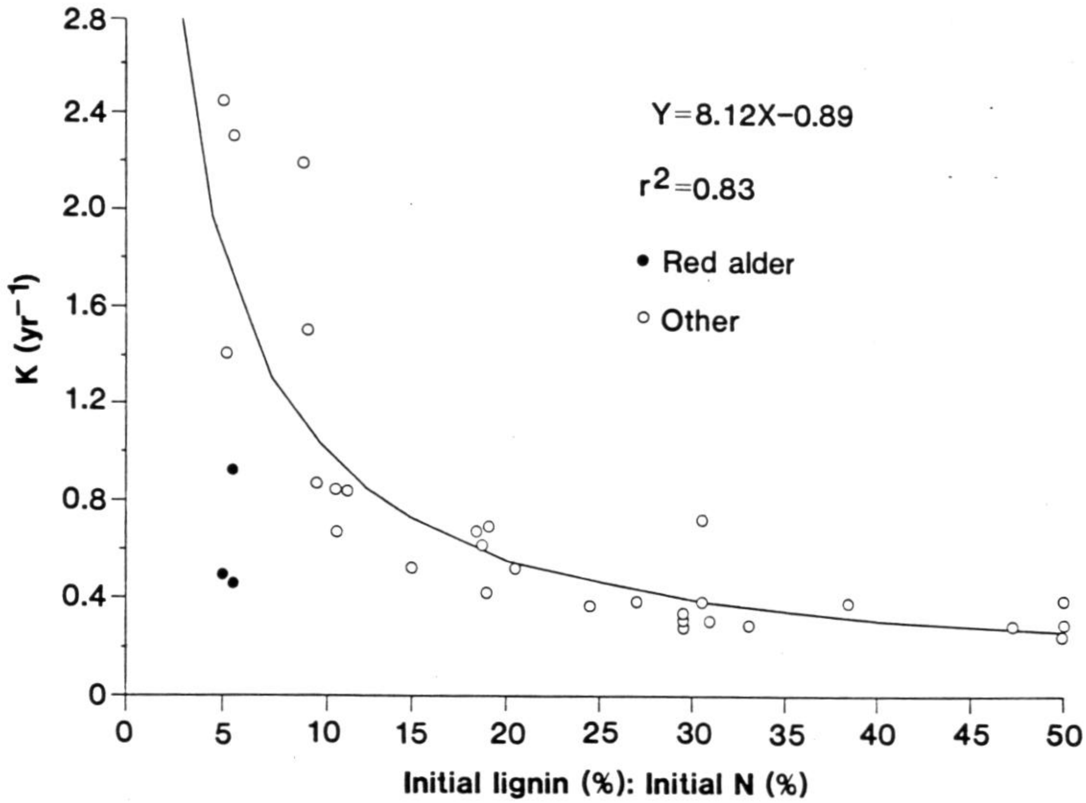

Fig 7. Relationship between the annual decay rate constant, k, and the ratio of initial lignin and nitrogen content of leaf litter.

was modelled with a double-exponential curve (Fig. 8). The main distinction between species was the proportion of fast and slow decay components. In contrast, the rates of each component were quite similar between the two species.

The initial content of readily leachable fraction in fresh litter differed significantly between species (Table 3). We felt that there might also be significant year to year variation within a species because phenological and nutrient status at the time of collection may differ from year to year. It was surprising to find similar readily leachable fraction values in both 1983 and 1984 in all but one species.

Litter decay includes both physical and biological removal of materials. The physical process of leaching by rain increases the proportion of lignin in the remaining tissue. Biological decay of remaining tissue is slower. Incubation time must be standardized (ie. 1 yr) to encompass biological

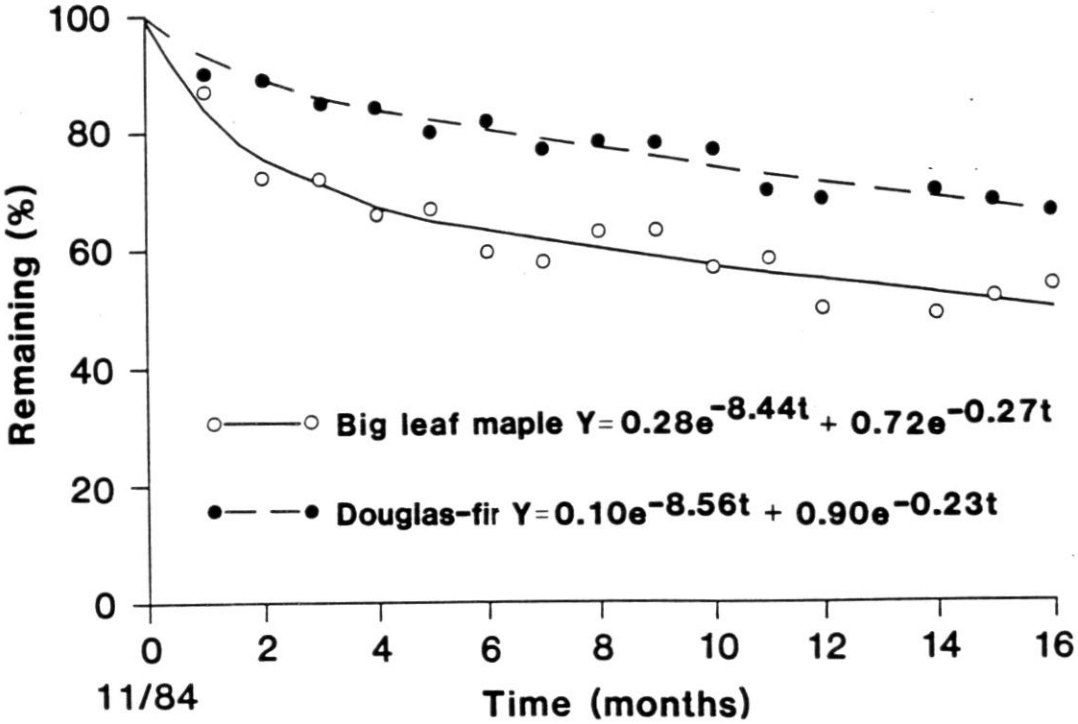

Fig 8. Decay of *Acer macrophyllum* and *Pseudotsuga menziesii* leaves modelled with a double-exponential curve.

Table 3. Variation in readily leachable fraction of fresh leaf litter.

Species	Readily Leachable Fraction (%)	
	1983	1984
Acer circinatum	31.4	20.9
Acer macrophyllum	14.3	12.4
Cornus nutalii	28.9	26.5
Populus trichocarpa	25.4	24.6
Pseudotsuga menziesii	7.3	8.1
Thuja plicata	5.3	4.0

decomposition processes. The physical process of leaching by rain proceeds quickly, and is probably not as sensitive to pollution effects as biological processes. The separation of the readily leachable and unleachable compounds in the leaf tissue may aid in distinguishing the decay rates associated with the physical and biological decay processes.

SUMMARY

A framework for monitoring ecosystem conditions has been suggested by McShane et al. (1986). They believe that parameters used to measure environmental conditions should reflect an ecosystem process which is measureable through time. In addition, the natural variability of the process should be established and be predictable enough to allow detection of deviation from the norm. Rapport et al. (1985) have stated that the parameters should represent several general categories including nutrient cycling, primary productivity, species characteristics (diversity, composition and size distribution), and the frequency of certain factors like disease incidence and fluctuations of component populations. Ideally one process or parameter from each category would be chosen to establish an ecosystem profile (Odum and Cooley 1980). In this way more perspectives are considered. For example, in a grassland ecosystem primary productivity may remain constant over the years while species composition fluctuates (Rapport et al. 1985). Monitoring only one of these parameters could lead to different conclusions.

The processes we have studied fulfill most of the criteria suggested for ecosystem monitoring. However we lack a long-term data base. Two to three years of documentation is not enough time to sample the range of variability that undoubtably exists. Nevertheless, it is enough time to begin to establish the factors controlling ecosystem processes.

Litter fall, needle retention times and litter decay are a related group of ecosystem processes which stand out because of their predictable seasonal patterns and application to the majority of forest ecosystems. Variability within and between seasonal fluctuations can be associated with climatic patterns and/or species characteristics which are readily distinguished. More precise indications of the sensitivity of these processes will come from data sets which extend over longer periods of time and a broader geographic range.

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