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Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands

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Abstract

Comparisons of nutrient concentrations (N, P, K^+, Ca^{++}, Mg^{++}) found in canopy throughfall and litterfall were made on the H. J. Andrews Experimental Forest. Six old-growth Douglas-fir (Pseudotsuga menziesii) *stands were studied which represented six forest communities common to the western Cascades of Oregon. These community types span a large portion of the temperature and moisture gradients present in the area. The preliminary data indicate that nutrient concentration in throughfall was highest during the summer and fall, and lowest during the winter. Nutrient input through throughfall generally followed the same trends. Nutrient return through litterfall was greatest in the needles. More amounts of N, P, and Ca^{++} were transferred to the soil through litterfall than through throughfall, while more K^+ and Mg^{++} were added to the soil through throughfall. Litterfall was maximum during the winter. Future studies will correlate the results from the nutrient analysis to the moisture and temperature gradients.*

Introduction

The worldwide interest of scientists in litterfall production during the past century, has been shown by Bray and Gorham (1964) in their review of litter production in the forests of the world. Methodology reports ranged from utilization of randomly located collection devices of varied design, separation, ovendrying, and chemical analysis of several litter components, to merely raking up and air drying the litter on a unit area basis. In spite of the large number of papers cited in the above review, data of litter production from natural, old-growth ecosystems are meager. Even less is known about litterfall in old-growth Douglas-fir *(Pseudotsuga menziesii)* forest types. The examination of seasonal fluctuations, nutrient concentration changes associated with defoliation, and nutrient composition of various litterfall categories are scarce (Kira and Shidei 1967).

The first published report of an investigation of litterfall in coniferous forests of the Pacific Northwest is that of Tarrant, Isaac, and Chandler (1951). These workers collected the litter of several species for 1 year and estimated nutrient movement by multiplying litter weight by the percent elemental content of foliage collected from trees, an inexact procedure. More detailed measurements of the nutrient cycle in Douglas-fir forests have been published for stands in New Zealand (Will 1959) and the United States (Dimock 1958). In addition, workers at both the University of Washington (Rahman 1964) and Oregon State University[1] have collected substantial data describing litterfall in both managed and natural Douglas-fir stands. Riekerk and Gessel (1965) and Cole and Gessel (1968) summarize

[1] D. P. Lavender, unpublished data.

a number of very sophisticated studies of nutrient movement through Douglas-fir ecosystems in Washington.

All of the above studies, save that of Tarrant et al., however, were concerned with litterfall and nutrient movement through relatively young stands.

Several studies (LeClerc and Breazeale 1908, Mes 1954, Tukey and Amling 1958, and Tukey et al. 1958) have demonstrated that rainfall may remove substantial quantities of nutrient elements from the foliage of horticultural plants. Similarly, studies of the elemental content of precipitation under forest stands (Tamm 1951, Madgwick and Ovington 1959, Will 1959, and Voigt 1960) have demonstrated that rainwater which has passed through tree crowns ("throughfall") contains significantly higher quantities of many nutrient elements than rainfall collected in adjacent openings.

In the Pacific Northwest, studies reported by Rahman (1964), Tarrant et al. (1968) and Cole and Gessel (1968) have yielded data which describe the movement of nutrients from the atmosphere and tree crowns to the forest floor by precipitation. Finally, unpublished data by Lavender describe the movement of nutrients from the crowns of both fertilized and control second-growth Douglas-fir stands to the forest floor by precipitation.

The purpose of the present study was to measure the movement of nutrients in canopy throughfall and litterfall in several association types of old-growth Douglas-fir stands. These community types were selected to represent the range of environments occurring on the H. J. Andrews Experimental Forest and are also indigenous to the Pacific Northwest. This paper will report on the results of our efforts to date.

Study Area

The H. J. Andrews Experimental Forest encompasses 15,000 acres and is characterized by steep topography with approximately one-fifth of its land area in gentle slopes or benches. Elevations within the forest vary from 457 m to more than 1,523 m. Precipitation is heavy, varying from 226 cm per year at lower elevations to as much as 356 cm per year along the highest ridges. A considerable snowpack develops on the higher slopes while rain predominates at the lower elevations. Mean temperatures within the forest range from 35°F in January to 65°F in midsummer (Berntsen and Rothacher 1959).

Methods

Within the Experimental Forest, six communities were chosen (table 1), each named for characteristic plants in both the overstory and understory. The six old-growth communities are presented in order of increasing elevation. Each of the six plots are 0.2024 hectare in size and are equipped with eight litter traps; each is 2,601 cm^2 in area, located on a random basis in each plot. Litter was collected every 4 to 6 weeks during the snow-free months of 1970-71. Heavy snow pack prevented litter collection during much of the winter of 1970. Therefore, data describing nutrient movement in the litter for this period are weak because: (1) the necessarily infrequent collections do not permit accurate assessment of the rate of litterfall, and (2) litter which remained in the traps for long periods was subjected to leaching. The following fall, three litter traps on each plot were equipped with a 113-liter reservoir to collect the precipitation which passed over the litter. Analysis of this water will provide a measure of the nutrients leached from the litter. Crown and stem maps were made for each plot to aid in evaluating the variation of litterfall between traps.

After collection the litter for each trap was dried at 70°C, separated into classes (needles, cones, twigs, branches, hardwoods, bark, lichens and mosses), and weighed. Prior to chemical analyses, litter from the eight litter traps per plot was composited into two samples, each representing four traps. In addition, some consolidation of litter collected on different dates was necessary. Each sample was analyzed to determine the levels of nitrogen, phosphorus, potassium, calcium and

Table 1.—Characteristics of study plots

Plot	Elevation	PPT/ year	Percent species composition[1]		Diameter range	Average d.b.h.	Basal area[2]	Stems/ hectare
	meters	*centimeters*			*- - - centimeters - - - -*			
1. *Pseudotsuga-Holodiscus*	457	211.8	Psme	89.3	11 – 163	46.7	83.06	277
			Tsme	5.4				
			Tabr	3.6				
			Acci	1.7				
2. *Tsuga-Rhododendron-Berberis*	488	228.3	Psme	17.0	8 – 139	37.8	97.55	494
			Tsme	69.0				
			Tabr	8.0				
			Thpl	5.0				
			Conu	1.0				
3. *Tsuga-Polystichum*	762	230.6	Psme	26.5	10 – 213	68.1	120.87	168
			Tsme	61.8				
			Tabr	8.8				
			Thpl	2.9				
4. *Tsuga-Rhododendron-Gaultheria*	610	229.6	Psme	52.8	8 – 157	34.0	69.77	450
			Tsme	23.1				
			Tabr	1.1				
			Thpl	19.8				
			Cach	2.2				
			Conu	1.1				
5. *Tsuga-Abies-Linneae*	975	—	Psme	16.1	8 – 173	66.3	129.60	277
			Tsme	46.4				
			Thpl	33.9				
			Tabr	3.6				
6. *Abies-Tiarella*	1,311	—	Psme	46.3	8 – 117	55.4	109.63	331
			Tsme	16.4				
			Abam Abpr	37.3				

[1] Psme *Pseudotsuga menziesii*
Tsme *Tsuga mertensiana*
Tabr *Taxus brevifolia*
Acci *Acer circinatum*
Thpl *Thuja plicata*
Conu *Cornus nutallii*
Cach *Castanopsis chrysophylla*
Abam *Abies amabilis*
Abpr *Abies procera*

[2] Square meters/hectare.

magnesium.

In addition to the litter traps, each plot was equipped with four 20-inch-high rain gages. Each gage was assigned to one of 20 random locations within the plot after each collection, in accordance with a method described by Wilm (1943). Higher elevation plots also contain a rain gage on a platform 10 feet from ground level to provide a water sample during months of heavy snow cover. Water was collected and the volume measured at approximately 2-week intervals. The samples were returned to the laboratory on the day of collection, filtered, and stored at -12°C until thawed for analysis. For analysis, the four samples per plot were combined into two samples and analyzed for total potassium, calcium, magnesium, orthophosphate, and total phosphorus. Nitrogen in the form of ammonium, nitrate, nitrite, and organic nitrogen was also determined.

Precautions were taken to keep contamination of water samples to a minimum. Funnels with glass wool stoppers were provided for each rain gage to keep organic matter from contaminating water samples. Mercuric chloride was added to the rain gages in the summer and fall to keep microorganism activity to a minimum. The cold temperature helped to reduce microorganism and insect activity during the winter.

Several techniques were investigated in an effort to arrive at a measure of crown density. Basal area and volume poorly describe intercepting crown cover in old-growth defective stands as canopy development tends to remain constant after trees reach maturity; hence, direct estimates were used. Photographs which were taken above each sampling point with a 35-mm camera were shown over a spherical dot grid to give a means of comparing crown densities.

Results and Discussion

Throughfall Results

Nutrient concentration in throughfall samples for plots 1 through 4 for all elements appeared to be the same during each season (fig. 1). Water sample concentrations were highest during the summer when precipitation was minimal (table 2). Concentrations were lowest during the winter when precipitation was highest. As precipitation decreased from winter to spring, concentration of throughfall samples for each element increased. Throughfall concentrations were also high during the fall when precipitation first starts.

Unlike N, the average total input of P, Mg^{++}, Ca^{++}, and K^{+} generally follows the same trend as did the concentration curves (fig. 2). The greatest amount of each element was leached out during the fall when precipitation first washes the canopy. Decreasing amounts were leached out with increasing precipitation. Potassium input reached a low point during the winter, at which time 68 percent of the total precipitation had fallen, and

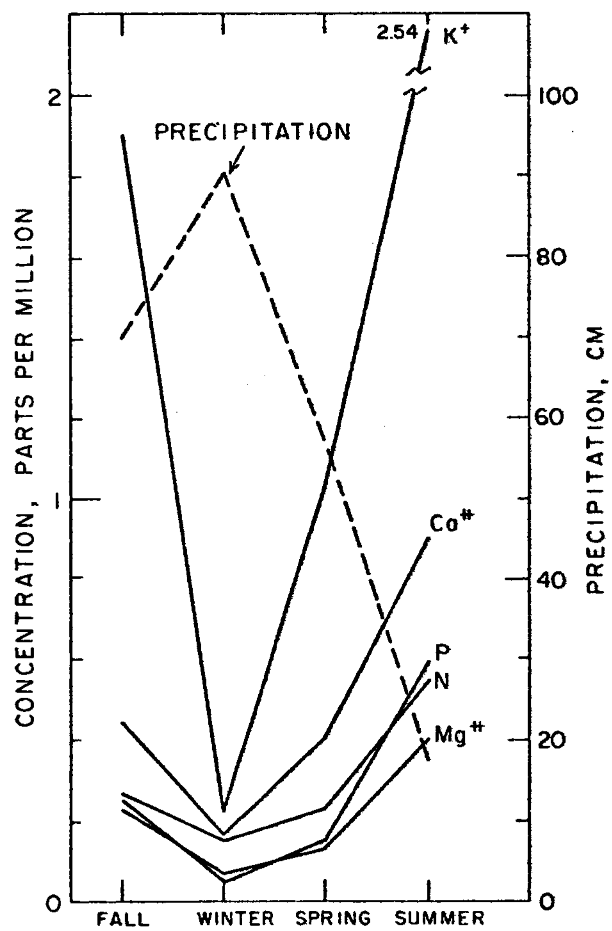

Figure 1. Average concentration of plots 1 through 4 for each element by season.

Table 2.—Average total precipitation across all plots by season

Season	Precipitation
	centimeters
Fall	70.89
Winter	92.05
Spring	57.96
Summer	18.08
Total	238.98

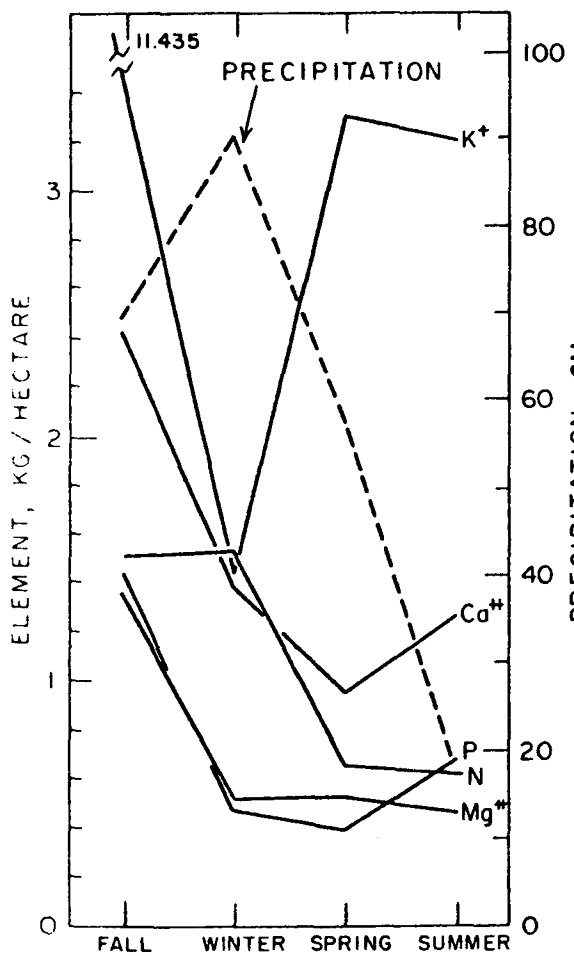

Figure 2. Total average kg per hectare of plots 1 through 4 for each element by season.

increased sharply from winter to spring, slightly decreasing from spring to summer. Calcium and P reached low points during the spring, at which time 92 percent of the total precipitation had fallen, and increased from spring to summer. Magnesium input was greatest from fall to winter and remained approximately the same from winter to summer. Nitrogen input slightly increased from fall to winter, decreasing from winter to spring reaching a low point during the summer.

There appears to be no difference in terms of net kg per hectare per year between plots 1 to 4 for each element with the exception of plot 3 (table 3). Plot 3 had more K^+ and less Ca^{++} than plots 1, 2, and 4.

Throughfall Discussion

In general, the total nutrient input and throughfall concentrations were highest in the summer and fall and lowest during the winter and spring months. This seems to indicate that each tree or canopy has a constant fraction of elements which can be removed from the foliage through leaching elements. Once the rains start in the fall, the majority of each nutrient is leached out. As the rains increase in quantity and duration during the winter and spring months, the available fraction of nutrients is further depleted. Decreasing precipitation from spring to the end of summer allows the nutrient fraction to increase again until the total fraction of leachable nutrients is reached.

Variations found between plot 3 and plots 1, 2, and 4 with respect to K^+ and Ca^{++} could be due to differences in soil types (data not available yet). If soil types are different with respect to nutrient availability, the differences between plots could be explained by luxury consumption.

Another possible source of the nitrogen found in the throughfall samples is nitrogen-fixing bacteria. Jones (1970) in his study of nitrogen fixation by bacteria in the phyllosphere of Douglas-fir *(Pseudotsuga douglasii)* in England isolated bacteria from the leaf surfaces of Douglas-fir. He found that the bacteria could fix atmospheric nitrogen when provided with a carbohydrate source. The fate

Table 3.—Net kg per hectare per year of nutrients collected in throughfall gages

Item	N	P	K^+	Ca^{++}	Mg^{++}
Input from atmosphere[1]	1.298	0.232	0.106	2.085	1.273
Throughfall input:					
Plot 1	3.999	2.308	17.416	5.983	2.608
2	2.979	2.398	15.749	4.438	2.086
3	3.729	2.970	30.350	2.134	1.456
4	2.710	3.283	23.379	5.104	2.343
Average	3.354	2.740	21.724	4.416	2.123

[1] Fredriksen unpublished data—data collected from open area on the H. J. Andrews Experimental Forest at 610 meters.

Table 4.—Distribution of metric tons/hectare between litter components by plot

Plot	1	2	3	4	5a	5b[1]	6	Average[2]
Needles	2.002	2.246	2.950	3.200	2.533	2.533	3.741	2.777
Percent of total	32.84	35.56	46.44	62.30	15.17	55.91	54.10	47.15
Reproductive structures	.834	1.141	1.284	.742	.536	.536	.518	.743
Percent of total	13.68	18.06	20.22	14.46	3.20	11.83	7.49	14.31
Wood material	2.280	2.760	1.876	1.009	13.479	1.267	2.524	1.953
Percent of total	37.40	43.68	29.53	19.66	80.74	27.96	36.50	33.14
Hardwoods and mosses	1.022	.175	.401	.197	.195	.195	.206	.365
Percent of total	16.77	2.77	6.32	3.84	1.17	4.30	2.98	6.20
Total	6.138	6.317	6.512	5.131	16.694	4.530	6.916	5.891

Note: In plot 5, an extremely large slab of bark from a nearby snag fell into a trap causing high values for total tons/hectare. Over a longer period of time, this type of variation between litter components can be expected to occur randomly throughout each plot. However, due to the limited sampling time thus far recorded, the one extreme value will be temporarily ignored.

[1] Excluding extreme bark sample.

[2] Excluding 5a.

of the nitrogen was not determined. However, Jones suggested that it could be washed to the ground.

Litterfall Data

Despite the differences in stand characteristics shown in table 1, little variation in total litter production was found among stands for the year 1970-71 (table 4). Average yearly litterfall production for all plots was 5.89 metric tons/hectare. This is approximately 1½ times the average 3.5 metric tons per hectare reported by Bray and Gorham (1964) for cool, temperate forests, but closer to the yield they reported for a latitude comparable to their study area (fig. 1). From worldwide data, these authors reported that nonleaf litter averaged from 27 percent to 31 percent of total litter production. The stands reported here averaged 47 percent nonleaf (woody) litter for the 1-year period.

In terms of total kg/hectare of litter, the vast majority fell during the winter (fig. 3). This is the period when snowfall is greatest, consequently much litter breaks under the weight of the snow. Needle cast was greatest in the fall, decreasing during the winter, and gradually increasing during spring. Hardwood and moss litter was greatest in the fall, decreasing throughout the rest of the year. Woody material and cone litterfall was greatest during the winter.

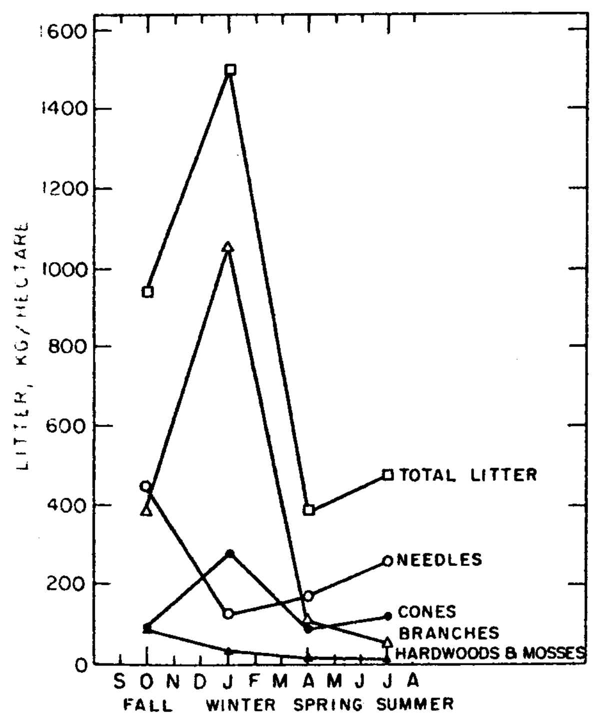

Figure 3. Average kg per hectare by season and litter component.

Nutrient concentration of litterfall components varied considerably among plots and seasons (table 5). Plots 1 and 3 were chosen to represent the range of values that can be found in nutrient return through litterfall. There appears to be no consistent trend by season or plot for the litter component concentrations. However, average yearly concentrations of each nutrient for each litter class are comparable between plots 1 and 3. There is a substantial difference between total kg/hectare for N, P, K^+, and Ca^{++} between plots (table 6). Plot 1 had more kg of Ca^{++} per hectare than did plot 3. Plot 3 had greater amounts of N, P, and K^+ than did plot 1. Little difference occurred among plots for Mg^{++}.

The greatest portion of nutrient input through litterfall came in the needles (table 7). Needle litterfall contributed about 54 percent of the total nutrient input. Cone litterfall accounted for 13 percent while twig litterfall accounted for 11 percent of the total. Together, the needle, cone, and twig litterfall account for 78 percent of the total nutrient input through litterfall.

Litterfall Discussion

Variations in nutrient concentration found between litterfall components among plots and season can be expected if foliage characteristics such as age and species are not constant. We also observed that the age of the tissue, and when it falls, varies throughout the year for each plot. This is primarily due to environmental parameters such as wind action, rainstorms, and snowfall. Differences in soil types could also have affected concentrations.

Differences between total nutrient input through litterfall (table 6) are affected by the distribution of litter components within the total. Where two plots seem to produce com-

Table 5.—Average percent of N, P, K^+, Ca^{++}, and Mg^{++} by season, plot, and litter component

Litter component and season	Plot 1					Plot 3				
	N	P	K^+	Ca^{++}	Mg^{++}	N	P	K^+	Ca^{++}	Mg^{++}
Needles:										
Fall	0.368	0.087	0.109	1.901	0.017	0.434	0.120	0.161	1.815	0.020
Winter	.691	.108	.210	1.305	.018	.763	.124	.280	1.103	.081
Spring	.462	.124	.159	1.241	.028	.717	.119	.103	1.112	.017
Summer	.467	.143	.200	1.740	.034	.474	.105	.145	1.286	.025
Average	.497	.115	.169	1.546	.024	.597	.117	.172	1.329	.020
Cones:										
Fall	.530	.084	.122	.397	.045	.518	.063	.099	.149	.015
Winter	.294	.029	.046	.146	.016	.387	.033	.051	.148	.011
Spring	.488	.049	.133	.214	.041	.544	.064	.102	.178	.011
Summer	.487	.068	.151	.369	.027	.561	.063	.159	.206	.016
Average	.449	.057	.105	.281	.032	.502	.055	.103	.170	.013
Twigs:										
Fall	.340	.033	.051	.852	.009	.434	.051	.124	1.107	.016
Winter	.375	.040	.057	1.261	.011	.398	.032	.075	1.110	.012
Spring	.424	.072	.076	.999	.081	.358	.047	.046	.823	.008
Summer	.408	.043	.105	1.034	.013	.363	.055	.102	1.054	.015
Average	.386	.047	.072	1.036	.013	.388	.046	.086	1.023	.013
Branches:										
Fall	.218	.017	.030	.713	.008	.207	.013	.025	.522	.006
Winter	.028	.017	.080	.598	.006	.296	.039	.082	.843	.010
Spring	—	—	—	—	—	—	—	—	—	—
Summer	—	—	—	—	—	.102	.008	.030	.338	.005
Average	.213	.017	.055	.655	.007	.201	.020	.046	.567	.007
Bark:										
Fall	.332	.047	.076	.566	.014	.417	.038	.074	.517	.010
Winter	.404	.033	.050	.963	.010	.431	.035	.057	.413	.009
Spring	—	—	—	—	—	.476	.080	.055	.300	.009
Summer	.320	.030	.051	.637	.011	.541	.056	.163	.474	.012
Average	.352	.036	.059	.722	.011	.466	.052	.087	.426	.010
Hardwoods:										
Fall	.630	.095	.167	2.395	.037	.591	.124	.475	2.428	.061
Winter	—	—	—	—	—	—	—	—	—	—
Spring	—	—	—	—	—	—	—	—	—	—
Summer	.546	.092	.302	2.127	.070	—	—	—	—	—
Average	.588	.094	.234	2.261	.053	.591	.124	.475	2.428	.061
Mosses and lichens:										
Fall	.417	.053	.117	.408	.016	.659	.126	.229	.413	.019
Winter	1.264	.100	.132	.567	.015	1.234	.122	.350	.329	.017
Spring	—	—	—	—	—	—	—	—	—	—
Summer	1.313	.100	.246	.376	.020	1.427	.130	.284	.364	.018
Average	.998	.084	.165	.450	.017	1.106	.126	.287	.368	.018

Table 6.—Total kg per hectare per year for plots 1 and 3 for each element by litter class

Litter class	Plot 1					Plot 3				
	N	P	K^+	Ca^{++}	Mg^{++}	N	P	K^+	Ca^{++}	Mg^{++}
Needles	7.93	2.27	3.16	35.89	0.47	15.61	3.82	5.89	44.08	0.65
Percent of total	36.12	58.85	49.54	50.22	44.61	47.76	68.20	60.25	69.90	59.79
Cones	3.46	.45	.83	2.06	2.13	6.60	.69	1.33	2.05	.17
Percent of total	15.74	11.59	13.03	2.89	20.31	20.23	12.40	13.63	3.24	15.46
Branches	1.97	.16	.74	5.09	.06	.82	.12	.29	2.15	.02
Percent of total	8.98	4.06	11.56	7.13	5.28	2.50	2.00	2.97	3.40	2.06
Twigs	3.52	.38	.66	12.01	.10	3.54	.34	.75	9.56	.10
Percent of total	16.07	9.86	10.33	16.79	9.50	10.82	6.20	7.67	15.15	9.27
Bark	1.62	.11	.07	3.56	.30	3.00	.28	.49	3.18	.06
Percent of total	7.39	3.17	3.08	4.97	2.92	9.18	5.00	5.04	5.03	5.15
Hardwoods	2.33	.39	.67	12.48	.17	.38	.06	.11	1.51	.05
Percent of total	10.60	9.17	10.49	17.46	16.06	1.16	1.00	1.14	2.39	4.12
Moss and lichens	1.12	.08	.12	.39	.01	2.73	.28	.90	.54	.03
Percent of total	5.10	2.11	1.98	.54	1.32	8.35	5.00	9.16	.85	3.09
Total	21.95	3.86	6.39	71.49	1.07	32.68	5.59	9.77	63.06	1.09

Table 7.—Average percent of litterfall totals for plots 1 and 3 for each element by litter class

Litter class	N	P	K^+	Ca^{++}	Mg^{++}	Average
Needles	41.9	63.5	54.9	60.1	52.2	51.52
Cones	18.0	12.0	13.3	3.1	17.9	12.86
Branches	5.7	3.0	7.3	5.3	3.7	5.00
Twigs	13.4	8.0	9.0	16.0	9.4	11.16
Bark	8.3	4.1	4.1	5.0	4.0	5.10
Hardwoods	5.9	5.1	5.8	9.9	10.1	7.36
Moss and lichens	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

parable total quantities of litter on a yearly basis, amounts of the various litter components are important. The amounts of each litter component are important because concentrations of nutrient elements vary for each litter component (see table 5). Table 4 shows that the greatest differences between plots 1 and 3 in terms of kg/hectare of litterfall occur between needles and woody material. Plot 3 produced 947 kg/hectare more of needles than plot 1, while plot 1 produced 403 kg/hectare more of woody material than plot 3. However, table 5 shows that the average concentration of nitrogen, for example, is much higher in needles than it is in woody material; consequently, variations such as found in table 6 are brought about.

Nutrient input in both throughfall and litterfall appears to have the same trend for K^+, P, and Ca^{++} when comparing plots 1 and 3. The litterfall analysis shows plot 3 having more K^+, P, and less Ca^{++} than plot 1. The throughfall data for plots 1 and 3 show the same results (table 3). However, differences between N and Mg^{++} input through throughfall and litterfall for each plot do not agree. Table 3 shows little difference in N input for each plot, while table 6 shows N being higher in plot 3. A possible explanation for this has been given in the preceding paragraph. Table 3 shows that plot 1 had more Mg^{++} input than plot 3. Litterfall input for Mg^{++} was about the same between plot 1 and 3. A possible explanation for the difference between plots 1 and 3 for Mg^{++} in throughfall might be that the hardwood litterfall accounted for 10.1 percent of the total Mg^{++} input (table 7). Table 1 shows that 1.7 percent of the species composition in plot 1 was hardwoods, while plot 3 shows no hardwoods.

More amounts of N, P, and Ca^{++} were transferred to the soil through litterfall than through throughfall; while more K^+ and Mg^{++} were added to the soil through throughfall (table 8).

There appeared to be no relationship between nutrient concentration and elevation. Rather, concentration on each plot seemed to be correlated with crown density. Basal area and crown density in old-growth Douglas-fir stands seem to be distributed randomly over the sites on the H. J. Andrews Experimental Forest. Consequently, no real correlation could be seen between basal area and crown density with moisture and elevation. This could also be due to the fact that the range of environments sampled on the H. J. Andrews Experimental Forest was not great enough, indicated by total precipitation. Table 1 shows that there was no real difference in total precipitation between plots 1 through 4.

Summary

The preliminary data indicate that nutrient concentration in throughfall varied with season. Highest concentrations were found in the summer and lowest concentrations during the winter. Nutrient input through throughfall generally followed the same trends as did nutrient concentrations. Nutrient return through litterfall was greatest in the needles. Together, the needles, twigs, and cones accounted for 78 percent of the nutrient input

Table 8.—Total nutrient input in kg per hectare per year

Input	N	P	K^+	Ca^{++}	Mg^{++}
Average throughfall input	3.3544	2.740	21.7230	4.416	2.123
Average litterfall input	27.3235	4.725	8.0784	67.2738	1.080
Total	30.6779	7.465	29.8014	71.6888	3.203

through litterfall. More amounts of N, P, and Ca^{++} were transferred to the soil through litterfall than through throughfall, while more K^{+} and Mg^{++} were added to the soil through throughfall. Litterfall was maximum during the winter.

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