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Abstract approved:

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To investigate the movement of elements (N, P, K, Ca, and Mg) from the tree crowns by natural litterfall and leave wash, plots were established on six 450 year-old growth stands at the H. J. Andrews Experimental Forest. The following are the results of the data analyses. Elemental concentrations contained in throughfall samples varied throughout the year and tended to follow a seasonal cycle. Concentrations were lowest during the winter when precipitation was greatest and highest during the summer months when precipitation was lowest. Nutrient return in throughfall generally followed the same trend as did the concentration curves. The general mobility of the various mineral elements was demonstrated. For example 12% of the N, 39% of the P, 74% of the K, 9% of the Ca, and 37% of the Mg was returned in the leaf and litter wash. Average litter production for all stands during the 2 years was 5.520 metric tons/hectare. Litterfall was maximum during the winter months. The average total kg/hectare return of nutrients in litterfall was N 26.7, P 4.6, K 75., Ca 49.9, and Mg 3.8. The greatest portion,

63% of the nutrient return, came through needle litterfall. Together, the needle, cone, and twig litterfall accounted for 84% of the total nutrient input through litterfall.

Nutrient Cycling Under

450-Year-Old

Douglas-fir Stands

by

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TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

Nutrient Cycling Under 450-Year-Old Douglas-fir Stands

INTRODUCTION

Forest ecosystems can reduce the loss of available nutrients in the soil, especially when the biological activities of the soil are favored. Approximately four-fifths of the nutrients assimilated by forest trees are returned to the soil through litterfall, leaf wash, and stem flow (Tamm, 1951; Madgwick, 1959; Will, 1959). Litterfall also has a marked affect upon the physiological condition of the soil. The litter layer absorbs and returns moisture, prevents rapid evaporation, and also has a protective influence against erosion of mineral soil.

Precipitation, as it penetrates the tree crowns, removes considerable quantities of inorganic nutrients as well as numerous organic substances from the trees as both leaf wash and stem flow.

The objective of this study was to measure the movement of nutrients in canopy throughfall and litterfall in several association types of natural, old-growth Douglas-fir stands.

REVIEW OF LITERATURE

The Leaching[1] Phenomenon

The removal of substances from plants by precipitation is now well documented. The review by Arnes (1934) is especially useful for its extensive evaluation of the literature concerning the leaching of substances from plants prior to 1930. Stephen Hales (1727) alluded to nutrient losses by leaching in "vegetable staticks"; but it remained for de Saussure (1804) to be the first to show experimentally that unwashed leaves contained more of "certain" materials than did washed leaves. Gaudichand (1841) and Sachs (1892) observed that water droplets on leaves became alkaline. Le Clerc and Breazeale (1908) exposed crop plants to artificial rainfall and noted that 27 to 32% of the total nitrogen in wheat was lost. Data from oat plants subjected to rainfall at various times during the growing season suggest that the amount of material leached increased with age. However, these reports did not gain universal acceptance. Despite the excellent papers of Le Clerc and Breazeale (1908) and Arens (1934), full and adequate proof seemingly was not provided until radioisotope techniques were adapted to the problem. By the use of labeled materials, it became possible to show conclusively that some metabolites which were introduced into the plants could be removed by leaching. Mes (1954) was the first to utilize radioisotope techniques

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[1]leaching - the removal of substances from plants by the action of rain, dew, mist and fog (Tukey, 1970).

in studying leaching. Mes found that soaking was less effective than rain in removing nutrients from crop plants. She also reported that the majority of labelled phosphorus could be removed from soaked, detached plant material. Other authors (Long, _et al._, 1956; Tukey and Amling, 1958; Tukey, _et al._, 1958; Morgan and Tukey, 1964; Muller and Muller, 1964; and Yamada, _et al._, 1964) have demonstrated that rainfall may remove substantial quantities of nutrient elements from plants.

Tukey (1970) compiled a review of his own research and the general literature on leaching of substances from plants and formulated several generalizations:

1) Leaching and uptake through foliage appear to be reversible, nonmetabolic processes.
2) All inorganic nutrients, as well as organic substances, the essential amino acids, sugars, organic acids, and gibberellins, have been identified in leachates.
3) No plant has yet been studied which cannot be leached to some degree.
4) As the maturity of the leaf increases, the susceptibility to nutrient loss increases, reaching a peak at senescence.
5) Other plant parts besides foliage are susceptible to leaching.
6) Stomata are not the primary pathway of nutrient loss.
7) The intensity and volume of rain affect the efficiency of leaching. Rain which falls as a light drizzle, continuously bathing the foliage, will remove considerable more nutrients than will a greater quantity of water which falls in a

shorter period of time.

8) Results of foliage analyses to determine the nutritional status of plants should be interpreted with the knowledge of the previous precipitation, the techniques of sampling, and processing.

All of the above studies, however, were concerned with the removal of substances from horticultural plants.

Composition of Throughfall

In a more definitive study of forest species in Sweden, Tamm (1951) compared open-area precipitation and throughfall beneath spruce and pine trees and reported that two to three kg/hectare of Ca, Na and K were leached within 1 1/2 months. Similar results were found by Will (1955) in New Zealand. He observed that the nutrients returned to the soil beneath radiata pine and Douglas-fir trees, as calculated in milliequivalent/m^2, was Ca 4.7, Mg 12.6, and K 21.5. Thirty yards from the trees in an open area, values were Ca 1.3, Mg 1.4, and K 2.2.

Will (1959) in New Zealand found that annual rainfall reaching the ground under Douglas-fir contains two times as much K and approximately the same amount of P in comparison with radiata pine. Maximum removal of nutrients from the tree crowns was in the late summer and fall.

Madgwick and Ovington (1959) in England determined the chemical composition of the precipitation in three open plots and under thirteen different forest canopies for a two-year period in southeast

England. They found that the average contents of Na, K, Ca and Mg in precipitation collected in the open are 19, 3, 11, and less than 4 kg per hectare per annum respectively, compared with 33, 24, 24, and 10 under the forest canopies. They also found that deciduous trees (*Quercus*, *Nanofagus*, and hardwood coppice stand) lose more nutrients than do conifers (*Picea*, *Larix*, *Abies*, *Pseudotsuga*, *Chamaecyparis*, and *Thuja*) during the spring and summer months, but that conifers continue to lose nutrients throughout the winter. Similar studies in forest stands (Carlisle, *et al.*, 1966-Lancashire, *Quercus*; Will, 1964-New Zealand, *Pinus*; and Duvigneaud and Deneayer, 1967-Belgium, *Fagus*, *Carpinus*, *Prunus*, and *Quercus*) demonstrated that rainwater which passes through tree crowns contains significantly higher quantities of many nutrient elements than rainfall collected in adjacent openings.

Many investigations in the past have tended to regard nutrients in tree litterfall as the total nutrient fall. If the rainfall nutrients are omitted, this can lead to serious errors. The same applies to the contributions from the woodland ground flora unless the latter is very sparse. Carlisle, *et al.*, (1967) found that *Pteridium aquilinum* intercepted 3.7% of the total annual incident rainfall. Carlisle also found that *Pteridium* ground flora played an important role in the potassium cycle. Its total contribution of K in both litter and rainfall leachate was 31.4% of the total K falling from all sources.

Finally, in the Pacific Northwest, studies reported by Rahman (1964-Washington, Douglas-fir and alder), Tarrant, *et al.*, (1968-Oregon, open area), Lavender (personal communication-Oregon, Douglas fir) and Cole and Gessel (1968-Washington, Douglas-fir) yielded data which describe the movement of nutrients from the atmosphere and tree crowns to the forest floor by precipitation.

Inasmuch as above-ground plant parts can lose substances through leaching and gain substances through absorption, Tukey (1966) suggested that above-ground interchanges play an ecologically significant role within the plant community.

Amount of Litterfall

Litterfall is the amount of organic matter that is added to the soil surface by the vegetation on it. The worldwide interest of scientists in litterfall production during the past century was shown by Bray and Gorham (1964) in their review of litter production in the forests of the world, with Europeans as the primary contributors. Research in this area has increased in North America in recent years and is expanding even more with the advent of the International Biological Program.

The methodology cited by Bray and Gorham included reports which range from utilization of randomly located collection devices of varied design; separation, oven drying, and chemical analysis of several litter components; to merely raking up and air drying the litter on a unit area basis.

The consensus of the literature concerned with levels of litter production (Table 1) was that the rate of accumulation of litter varied from year to year and from species to species in different

Table 1. Litterfall amounts of several selected studies.

Authority	Date	Location	Plant Community	Age	Litterfall Metric tons/ha/yr
Alway & Zon	1930	Minnesota	Red pine Jack pine White pine	30-250	2.20
Sims	1932	N. Carolina S. Appalachians	Mixed pine and oak forest		2.92-3.48
Heyward & Barnette	1934	Florida	Long-leaf and slash pine	all ages	2.70-3.94
Kittredge	1940	California	Canary pine plantation	30	6.68
Chandler	1941	Central New York	Hardwoods 2nd growth		2.72-3.39
	1944	Southern New England	White pine & Norway pine		2.24-3.36
Kittredge	1948	California	Canyon oak & manzanita	16-55	2.04-2.78
Tarrant	1951	Pacific Northwest	Lodgepole pine Western red cedar		.29 2.15
Owen	1954		Sitka spruce	30	2.05
Scott	1955	Connecticut	Central hardwood forest		2.07

Table 1 (cont.) Litterfall amounts of several selected studies.

Authority	Date	Location	Plant Community	Age	Litterfall Metric tons/ha/yr
Puri	1956	Great Britain			.90-1.77
Miller	1957	New Zealand	Hard-beech stand		6.07
Dimock	1958	Wash. state	Douglas-fir	45	
			unthinned		1.8
			light thinned		1.6
			med. thinned		1.4
			heavy thinned		1.1
Will	1959	New Zealand	Radiata pine		5.57
			Corsican pine		7.08
			Douglas-fir		2.59
			European larch		3.29
Hurd	1971	Juneau, Alaska	Alder-willow	21	2.53
			Poplar-spruce	28	2.89
			Spruce	62	3.04
			Hemlock-spruce	148	2.94
Zavitkovski & Newton	1971	Oregon	Red alder	2-33	7.39
Gosz, J. R. *et al*.	1972	New Hampshire	Northern Hardwood forest	mature	5.70

seasons within a given year. Annual litterfall was dependent upon stand density, species involved, site, age, etc.; the accumulation of litter on the forest floor, however, was dependent upon all of these as well as all other factors of the environment, such as temperature, humidity, and rainfall, which influence the decomposition of organic material.

Kittredge (1948) concluded that in even-aged, well-stocked stands on an average site, there was not much difference between the total annual litterfall accumulation of spruce, beech and pine, coniferous and deciduous species, or between light and heavy-crowned species. He summarized his own work and all the data which was published up to that date in the following paragraphs:

> 1) The oven-dry weight of the annual accumulation of forest litter is a function of the stand and varies from over 3.5 to less than 0.5 metric ton per acre in a moderately well stocked stand.
>
> 2) Litterfall varies widely in the same stand in different years to such a degree that the maximum in one year may be as much as three times the minimum in another.
>
> 3) Differences between species and types, between deciduous and coniferous or between light and heavy-crowned species are not all defined.
>
> 4) The annual fall is smaller on poor than on good soil.
>
> 5) The heaviest annual fall in well-stocked stands occurs about the age of culmination of the current annual increment and is less at older and at younger ages.

Due to the great number of influencing agencies which affected total annual litterfall accumulation, the variations in accumulation of unincorporated organic matter were even more extreme than were the variations in annual leaf fall.

Cole and Gessel (1968) yielded data which described the movement of nutrients from the atmosphere and young Douglas-fir tree crowns to the forest floor by precipitation, stem flow, and litterfall in Washington. They found a total return of N and Ca was 14.56 and 19.00 kg/hectare respectively. The return for each pathway was:

	N	Ca
Litter	12.54	11.09
Crown wash	1.79	6.38
Stemflow	.23	1.57
Total	14.55	19.04

Composition of Litter

When examining the nutrient content of forest litter and the nutrient input through litterfall, one must be aware of the different factors which can influence nutrient concentration in litterfall.

The chemical composition of tree leaves depended upon site condition and the individual tree species. Great differences occurred between species growing under different soil and climatic conditions (Table 2). Ovington (1956), for instance, found that the surface organic matter under a hardwood stand had a distinctively different chemical composition than that under softwood stands. Scott (1955) found that the litter of conifer trees contained less N and Ca than hardwood trees.

Mitchell (1936) made an analysis of some forest trees during the growing season and found that the leaves of deciduous species continued to increase in weight as long as they remained green.

Table 2. Litterfall composition (kg/hectare/year)

Author	Date	Species	N	P	K	Ca	Mg	Sulphate
Chandler	1941	White cedar Balsam fir Norway spruce	26.43	2.02	7.28	29.68	5.04	
Alway & Zon	1930	Red pine Jack pine White pine	12.54	2.46	2.91	19.27		3.81
Tarrant	1951	Lodgepone pine	2.8-	.22-	1.2-	1.57-		
		Western red cedar	13.33	1.9	16.69	47.94		
Owen	1954	Sitka spruce	22.29	5.15	5.82	7.50		
Miller	1957	Beech	36.96	4.48	6.72	61.60		
Will	1959	Radiata pine Corsican pine Douglas-fir European larch	34.72	3.36	14.00	20.72		

Concentrations of N, P and K in the leaves became relatively constant for the month previous to initial yellowing. After yellowing, the absolute amount of N, P, and K decreased, implying a movement of these elements out of the leaf.

White (1954) confirmed the decline of K, N, and P in needle tissue from an early summer maximum to a fairly constant base level during the winter months. White recommended late fall and winter sampling for foliar analysis since the needles were likely to be least affected by confounding physiological changes.

Tarrant (1951) observed that leaf nutrient content of some Pacific Northwest tree species varied during the growing season and that the litter composition was greatly influenced by environment, especially the soil and the amount of litterfall, which varies markedly from year to year.

Owen (1954) stated that there was a seasonal variation in the nutrient content of sitka spruce litter.

McVickar (1949) observed that the Ca composition of white oak leaves increased as the growing season advanced; nitrogen, K, and P decreased, whereas magnesium remained fairly constant throughout the growing season.

Lavender and Carmichael (1966) found that the content of N, P, K, Ca, and Mg in Douglas-fir foliage varied with season of collection, foliage age, and the level in the crown of the foliage sample. Therefore, when comparing the nutrient status of Douglas-fir trees, the foliage samples analyzed should be composed of needles of the same age, and harvested from the same level in the crown during the same season.

All of the studies cited in the above review, save that of Tarrant *et al*. (1951), however, were concerned with litterfall and nutrient movement through relatively young stands. 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 is scarce (Kira-Shidei, 1967).

STUDY AREA

The H. J. Andrews Experimental Forest occupies strongly dissected topography characteristic of the west side of the Cascade Range (Figure 1). The experimental forest encompasses 610 meters, 80 percent of which are steep slopes and the remainder, gentle slopes or benches. Elevations within the forest vary from 460 meters to more than 1520 meters. Precipitation is heavy, varying from 230 cm per year at lower elevations to as much as 360 cm per year along the highest ridges. A considerable snowpack develops during the winter months at the mid- and high-elevation slopes, while rain predominates at the lower elevations. Mean temperatures within the forest range from 3°C in January to 18°C in midsummer (Berntsen and Rothacher, 1959).

U. S. Forest Service scientists have recognized a series of over twenty plant communities on the H. J. Andrews Experimental Forest (Figure 2). These stands span the range of environments found on the forest from the "*Pseudotsuga menziesii*-*Holodiscus discolor*" community, found on relatively warm, dry sites at 460 meters to a "*Abies*-*Tiarella*" community growing on cool, moist areas at 1500 meters. These communities were used as guides to locate the plots for the nutrient cycling study over the range of environments found on the experimental forest.

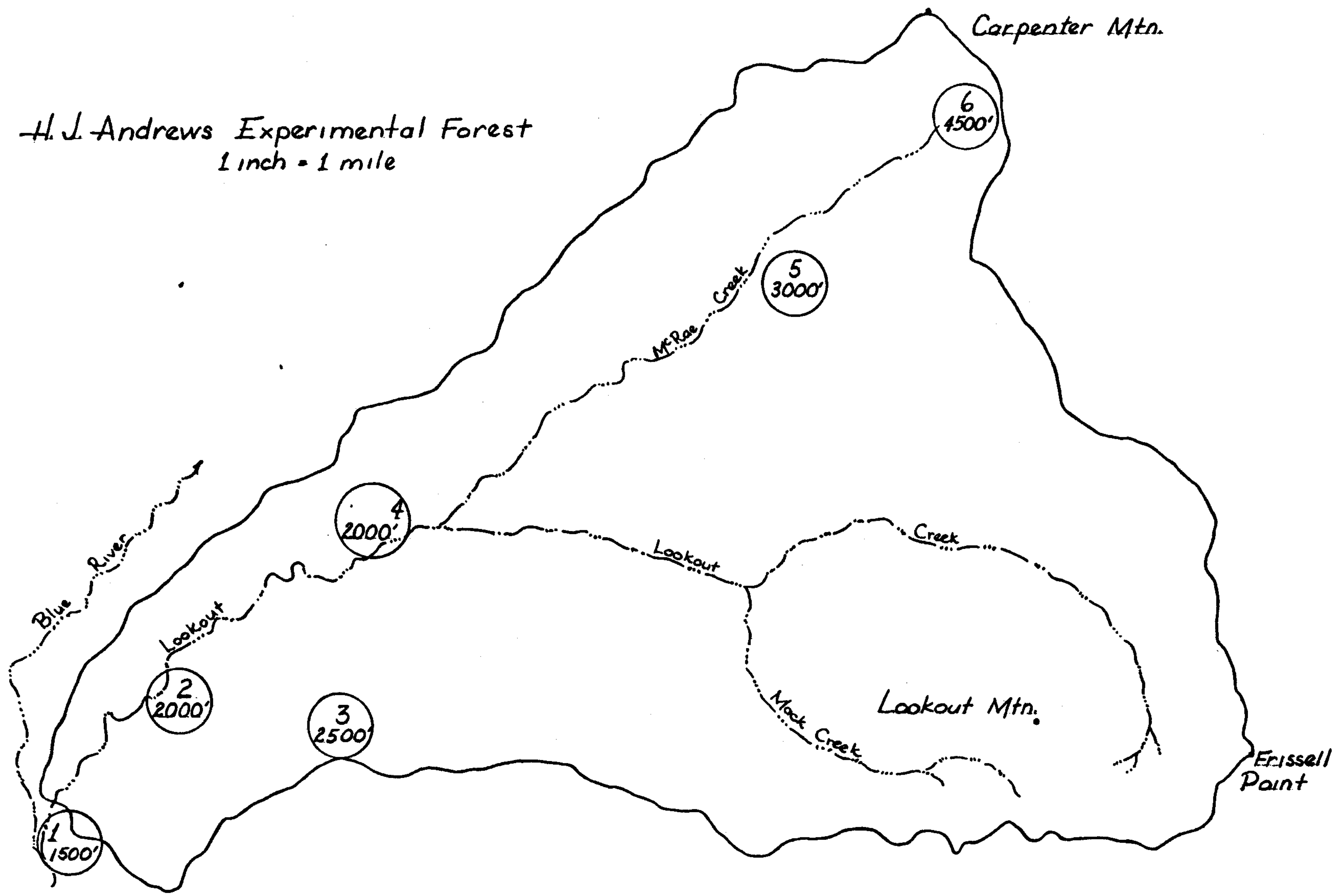


Figure 1. Map of the H. J. Andrews Experimental Forest.

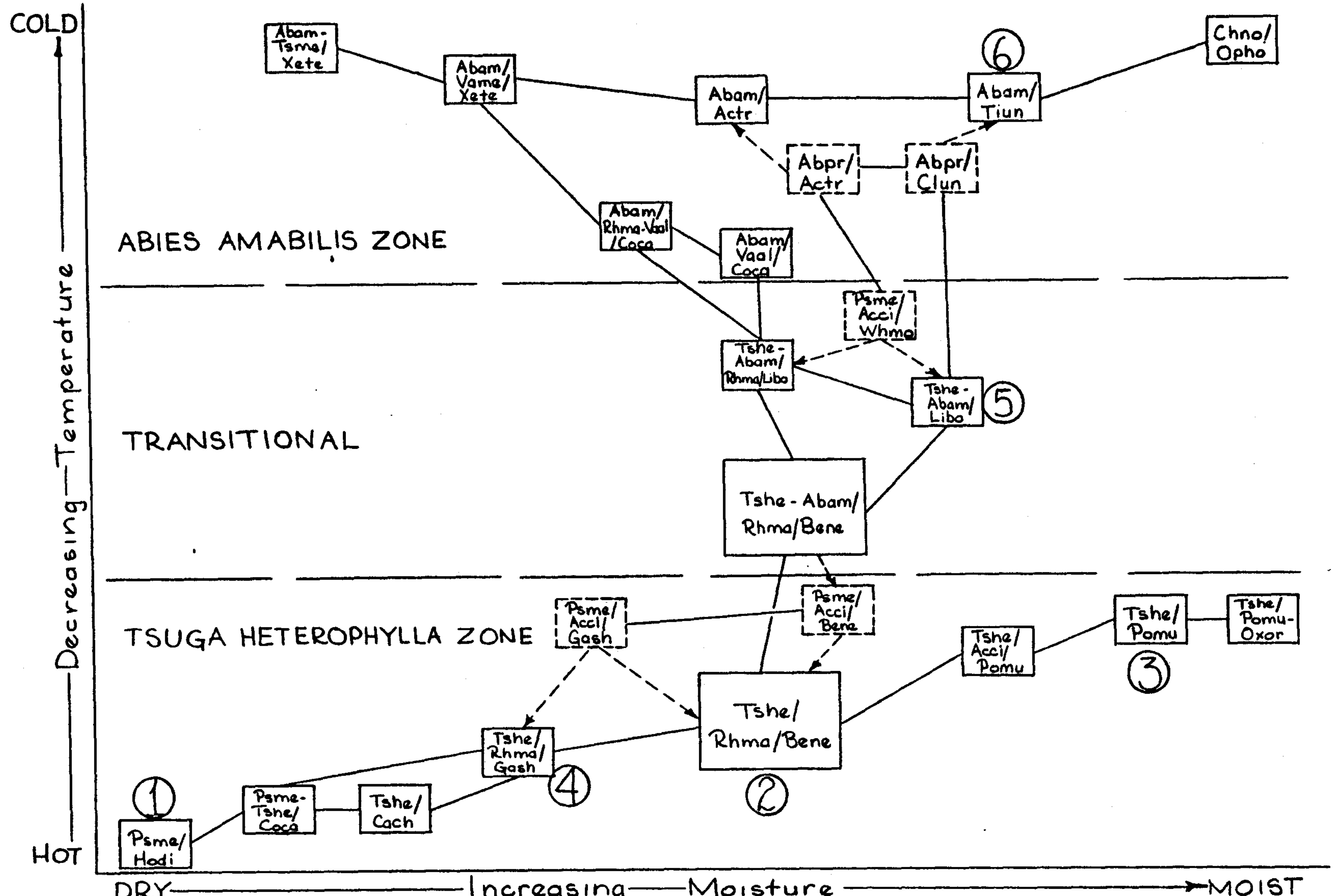


Figure 2. Series of plant communities found on the H. J. Andrews Experimental Forest.

METHODS

Six plant communities were chosen (Table 3), 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 was one-fifth hectare in size and was equipped with eight litter traps, each 2,600 cm^2, located randomly in each plot.

Litter was collected every four to six weeks during the snowfree months of 1970-72. Heavy snow pack prevented litter collection during much of the winter of 1970-71. Therefore, data describing nutrient movement in the litter for this period are weak because: (1) the necessarily infrequent collections did not permit accurate assessment of the rate of litterfall, and (2) litter which remained in the traps for long periods was subjected to leaching.

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, twigs, cones, branches, bark, hardwoods, lichens and mosses), and weighed. Prior to chemical analysis, litter from the eight litter traps per plot was composited into two samples, each representing four traps. A portion of the combined samples for each component was ground in a micro-Wiley mill to pass through a 20-mesh screen. The ground material was stored in screw-cap glass bottles until samples were drawn for chemical analysis.

Table 3. Characteristics of study plots.

Plot	Elecation	Precipitation/ year	% species composition[1]		Diameter range	Average d.b.h.	Basal area[2]	Stems/ hectare
	meters	centimeters			centimeters			
1. Pseudotsuga-Holodiscus	457	233	Psme	89.3	11 - 163	46.7	83.06	277
			Tsme	5.4				
			Tabr	3.6				
			Acci	1.7				
2. Tsuga-Rhododendron-Berberis	488	247	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	237	Psme	26.5	10 - 213	68.1	120.87	168
			Tsme	61.8				
			Tabr	8.8				
			Thpl	2.9				
4. Tsuga-Rhododendron-Gaultheria	610	270	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				

Table 3 (cont.) Characteristics of study plots.

Plot	Elevation	Precipitation/ year	% species composition[1]		Diameter range	Average d.b.h.	Basal area[2]	Stems/ hectare
	meters	centimeters				centimeters		
5. Tsuga-Abies-Linneae	975	269	Psme	16.1	8 - 173	66.3	129.60	277
			Tsme	46.4				
			Thpl	33.9				
			Tabr	3.6				
6. Abies-Tiarella	1,311	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.

Chemical analyses for litterfall were done as follows: one subsample for each litter component sample was analyzed for nitrogen by the Kjeldahl-Wilforth-Gunning method (Association of Official Agricultural Chemists, 1950). A second subsample was digested with nitric acid-sulphuric acid-hydrogen peroxide (Ulrich, et al., 1959), and analyzed on a Beckman DO spectrophotometer equipped with flame attachment and photo-multiplier for the following: phosphorus by the molybdate blue procedure (Fiske and Subbarow, 1925), and potassium and calcium by flame emission. Magnesium determinations were done by atomic absorption following addition of lanthanum as a masking agent.

Control samples with known amounts of each element were done simultaneously with litter samples. After chemical analysis, the two composited samples were averaged to determine nutrient input in litterfall.

In addition to the litter traps, each plot was equipped with four 20-inch-high rain gages lined with polyethylene bags which were periodically replaced. 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). Plots located on higher elevations also contained a rain gage on a platform 3 meters above 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 through Whatmas #45 filter paper, and stored at -12°C until thawed for analysis. For analysis, the four samples per plot were combined into two samples and chemical analyses were done as follows: potassium by flame emission; calcium and magnesium by atomic absorption following addition of lanthanum as a masking agent; ammonium and dissolved organic nitrogen by Macro Kjeldahl on 1/2-liter samples and detection by Nesslerization; nitrite by sulphanilamide method; nitrate by reduction and detection as nitrite; orthophosphorus by the molybdate blue method; total phosphorus by the molybdate blue method following a persulfate-sulfuric acid digestion in the autoclave.

Mercuric chloride was added to the rain gages in the summer and fall 1970 to keep microorganism activity to a minimum. However, the mercuric chloride interferred with the phosphorus analysis and was discontinued. 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. Since canopy development tends to remain constant in old-growth defective stands, basal area and volume poorly describe intercepting crown cover; hence direct estimates were attempted. Photographs were taken above each sampling point with a 35-mm camera. Each picture was shown over a spherical dot grid to give a means of comparing crown densities.

Precipitation data are missing for the high elevation plots during the winter months. These data were estimated by expressing the measured throughfall values for each plot as a percentage of the actual amount of precipitation that fell on an open area. Precipitation here was measured daily by personnel of the Pacific

Northwest Experiment Station. This percentage was multiplied times the actual amount of precipitation that fell over the time period where data are missing, as a means of estimating net precipitation under the canopy for the individual plot.

The concentrations of the chemical elements contained in leafwash varied throughout the year and tended to follow a seasonal cycle. These cycles were similar for each plot. Consequently, nutrient concentrations for high elevation plots for the winter months were estimated by averaging the measured concentrations from the lower elevation plots. It must be realized, however, that the above provides only an estimation of nutrient return. The relative effectiveness of snow as a leaching agent as compared to rain is questionable.

RESULTS AND DISCUSSION

The return of elements to the forest floor was stratified into two component parts: litterfall and throughfall. Stemflow was not determined as Rothacher (1963) found for dense stands of old-growth Douglas-fir and associated species typical of Douglas-fir forests, that stemflow was relatively unimportant for nearly all species.

Throughfall Results

The concentrations of the chemical elements contained in throughfall varied throughout the year and tended to follow a seasonal cycle (Table 4). The cycles were similar for all plots; however, even though yearly averages were comparable, differences between years and plots obscured any real differences between community types. Nutrient concentrations in throughfall for N, P, K, Ca, and Mg were highest during the summer months when precipitation was minimal (Figure 3). 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. The NO_3 concentration did not seem to follow a seasonal pattern as did the other elements (Figure 4). Rather, NO_3 concentration increased from autumn of 1970 to spring 1971, then decreased slowly to winter 1971, and again slightly increased to spring 1972.

Table 4. Concentration PPM in Throughfall.

		N		NO_3[1]		P		K		Ca		Mg	
		Year		Year		Year		Year		Year		Year	
		1	2	1	2	1	2	1	2	1	2	1	2
1	F	.336	.147	3.1	5.1	.307	.351	2.050	1.606	.664	.476	.371	.245
	W	.164	.032	5.9	3.3	.038	.038	.225	.086	.208	.076	.117	.047
	Sp	.205	.165	9.2	9.5	.109	.082	.840	.683	.362	.400	.150	.019
	Su	.436	.739	7.8	3.0	.345	.425	2.480	2.100	.928	.630	.423	.450
Average		.285	.271	6.5	5.2	.200	.224	1.399	1.119	.541	.396	.265	.190
2	F	.222	.222	1.6	4.5	.220	.422	1.300	1.726	.243	.456	.198	.259
	W	.149	.108	5.0	5.4	.026	.048	.204	.073	.162	.253	.080	.086
	Sp	.239	.136	7.2	4.0	.110	.126	1.500	.430	.379	.143	.137	.025
	Su	.377	.280	5.5	2.0	.451	.350	1.955	1.230	.968	.500	.327	.330
Average		.247	.187	4.8	4.0	.202	.237	1.240	.865	.438	.338	.186	.175
3	F	.275	.232	3.5	4.6	.238	.437	1.951	2.509	.294	.478	.193	.274
	W	.172	.107	5.4	1.2	.052	.050	.356	.080	.119	.152	.068	.042
	Sp	.280	.191	5.0	12.0	.216	.048	2.522	.577	.331	.617	.175	.079
	Su	.439	.360	5.2	13.5	.343	.073	2.487	2.580	.627	1.530	.308	.450
Average		.292	.223	4.8	7.8	.212	.152	1.829	1.437	.343	.694	.186	.211
4	F	.215	.169	2.1	4.3	.223	.684	2.095	2.933	.378	.534	.184	.335
	W	.137	.066	5.9	4.5	.032	.060	.261	.943	.119	.292	.080	.034
	Sp	.151	.143	4.9	3.7	.206	.065	.803	.630	.492	.233	.144	.024
	Su	.335	.278	6.1	ND	.692	.500	3.792	1.400	1.230	.400	.474	.300
Average		.210	.164	4.8	3.1	.288	.327	1.738	1.477	.555	.365	.221	.173
5	F	.254	.207	3.8	4.8	.159	.510	1.511	2.548	.369	.513	.177	.266
	W	.140	.137	6.7	3.4	.034	.070	.235	.420	.154	.240	.080	.031
	Sp	.224	.175	6.6	4.2	.158	.063	1.482	.930	.435	.245	.173	.017
	Su	.344	.242	5.0	ND	.396	.320	2.428	1.200	.860	.130	.318	.500
Average		.241	.190	5.5	3.1	.187	.241	1.414	1.275	.455	.282	.187	.204
6	F	.201	.202	6.0	5.6	.184	.263	1.139	1.668	.257	.438	.171	.202
	W	.159	.131	7.7	1.5	.033	.065	.234	.308	.150	.173	.085	.030
	Sp	.224	.198	6.5	3.9	.158	.115	1.482	.712	.435	.332	.173	.041
	Su	.362	.242	5.6	ND	.299	.334	2.113	1.316	.780	.638	.311	.406
Average		.237	.193	6.5	2.8	.169	.194	1.242	1.001	.381	.395	.185	.170

[1] 1×10^{-3}

ND - Non detectable

F - September, October, and November
W - December, January, and February
Sp - March, April, and May
Su - June, July, and August

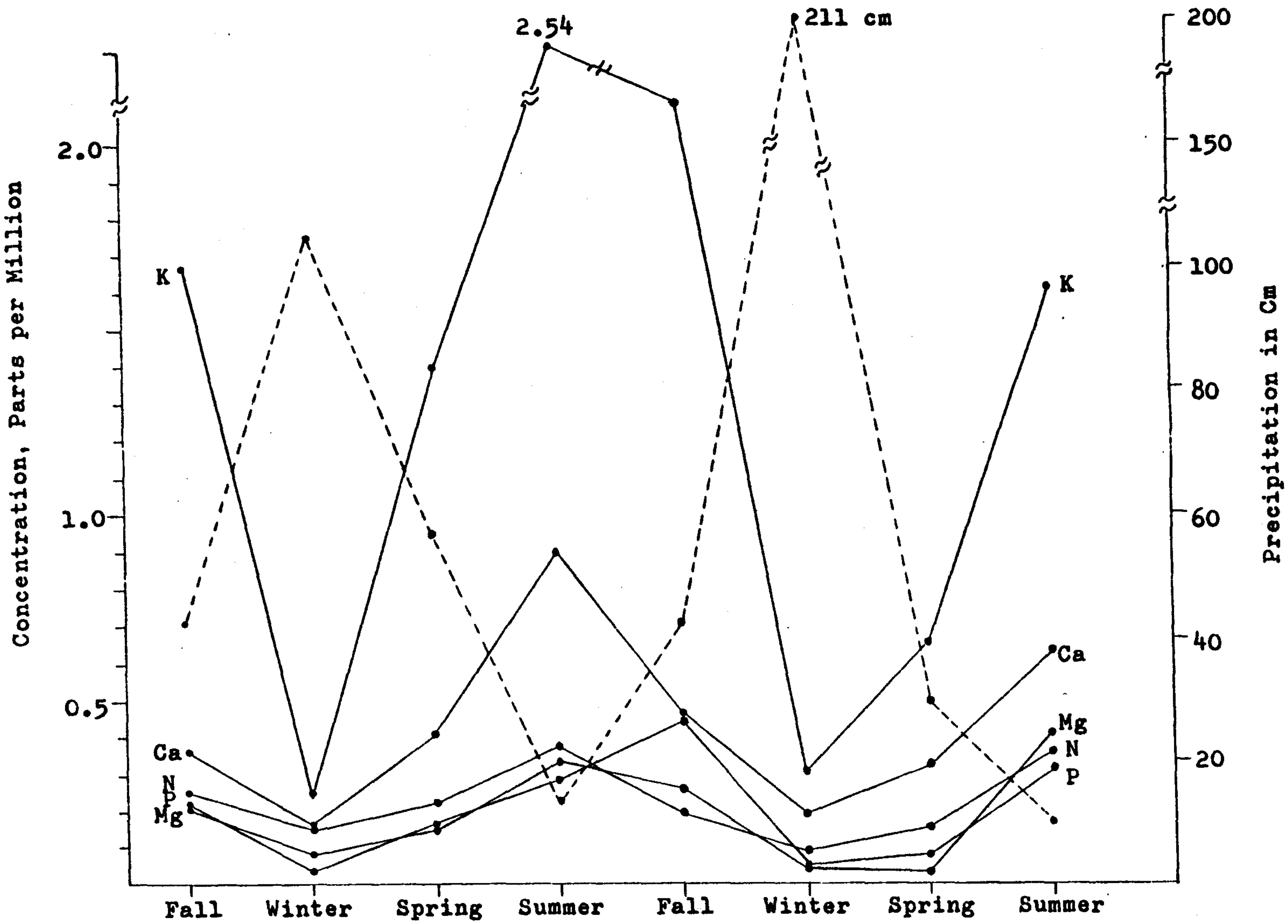


Figure 3. Average nutrient concentrations of plots 1-6 for each element by season.

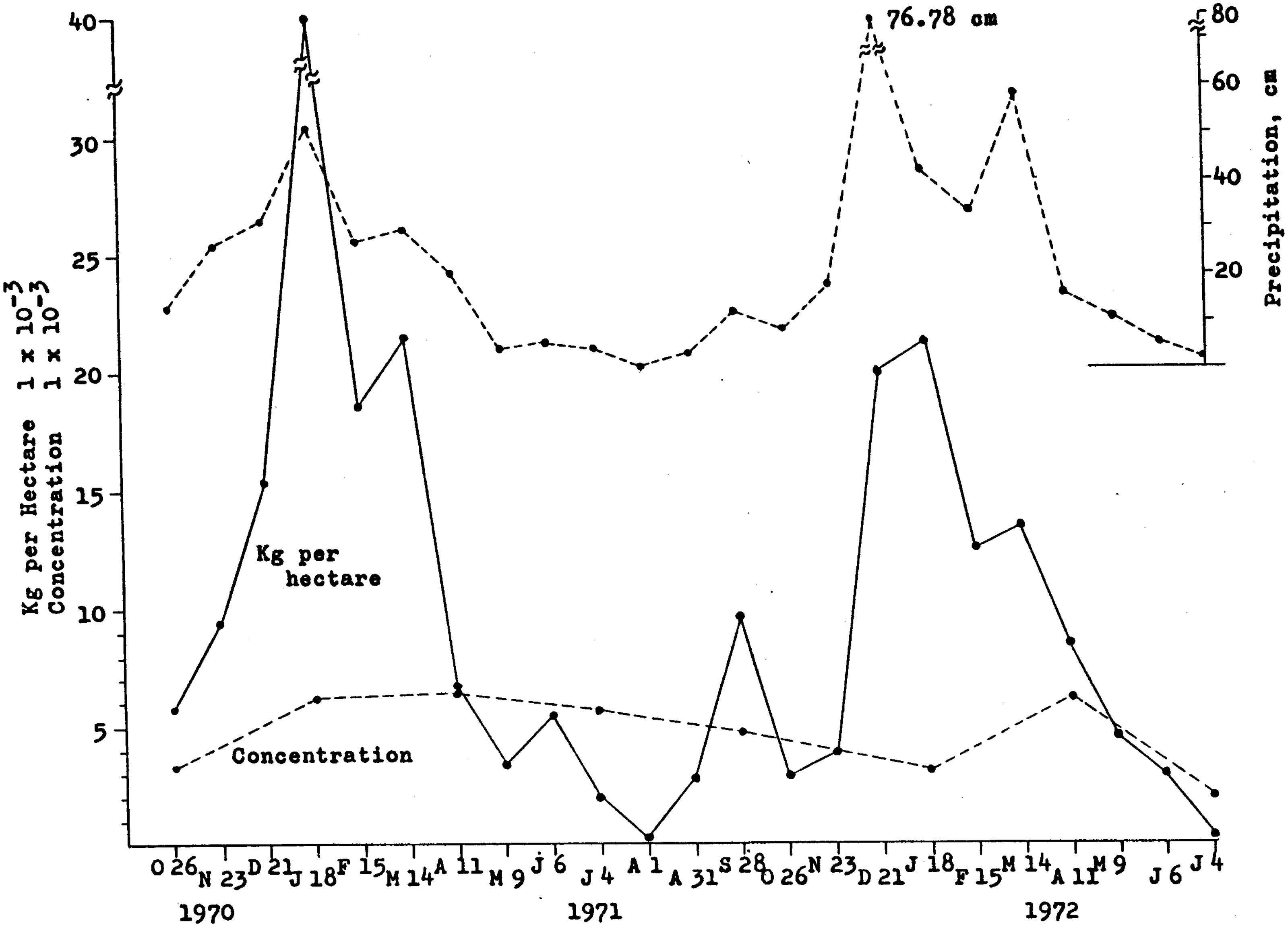


Figure 4. Average concentration and kg per hectare of nitrate for plots 1-6.

Total cm of precipitation for each plot (Table 5) generally followed the elevational gradient found in Figure 2. Precipitation was greatest during the winter months. During this time approximately 51% of the total precipitation fell.

Unlike N and NO_3, the average total input of P, Mg, Ca, and K generally followed the same trend as did the concentration curves (Figures 5 and 6). The greatest amount of each element was moved from the crowns to the forest floor during the fall when precipitation first washes the canopy. Minimal amounts were moved late in the summer when precipitation was minimal. For the two years, potassium input decreased from autumn to winter, increased from winter to spring, and dropped sharply from spring to summer. Calcium was quite variable for both years. Generally, however, calcium decreased from fall to winter, increased from winter to spring, and decreased from spring to a summer low. Phosphorus decreased to a low point in mid-summer for both years. Magnesium input was greatest from fall to winter, generally decreasing from the winter months to a low point in the summer. For the year 1970-71, N input slightly increased from fall to winter, decreased from winter to a low in August. Second year data for N was similar except that two high peaks occurred, one in December and the other in March. It is interesting to note that the N curve generally followed the precipitation curve. Nitrate input was greatest during the winter and spring months and lowest during the fall and summer (Figure 4).

Differences in terms of net kg per hectare per year (Table 6) existed between years and plots; however, average yearly values for

Table 5. Seasonal distribution of precipitation for 2 years (centimeters).

	1	2	3	4	5	6	Average
F	34	43	41	42	44	51	42
W	99	107	106	120	109	150	115
Sp	49	54	40	60	61	77	57
Su	11	12	11	10	18	20	14
Total	193	216	198	232	232	298	228
F	44	41	39	46	40	45	43
W	189	195	198	217	203	264	211
Sp	28	25	24	26	44	32	30
Su	11	16	14	19	18	23	17
Total	272	277	275	308	305	364	301
Average Total	233	247	237	270	269	331	265

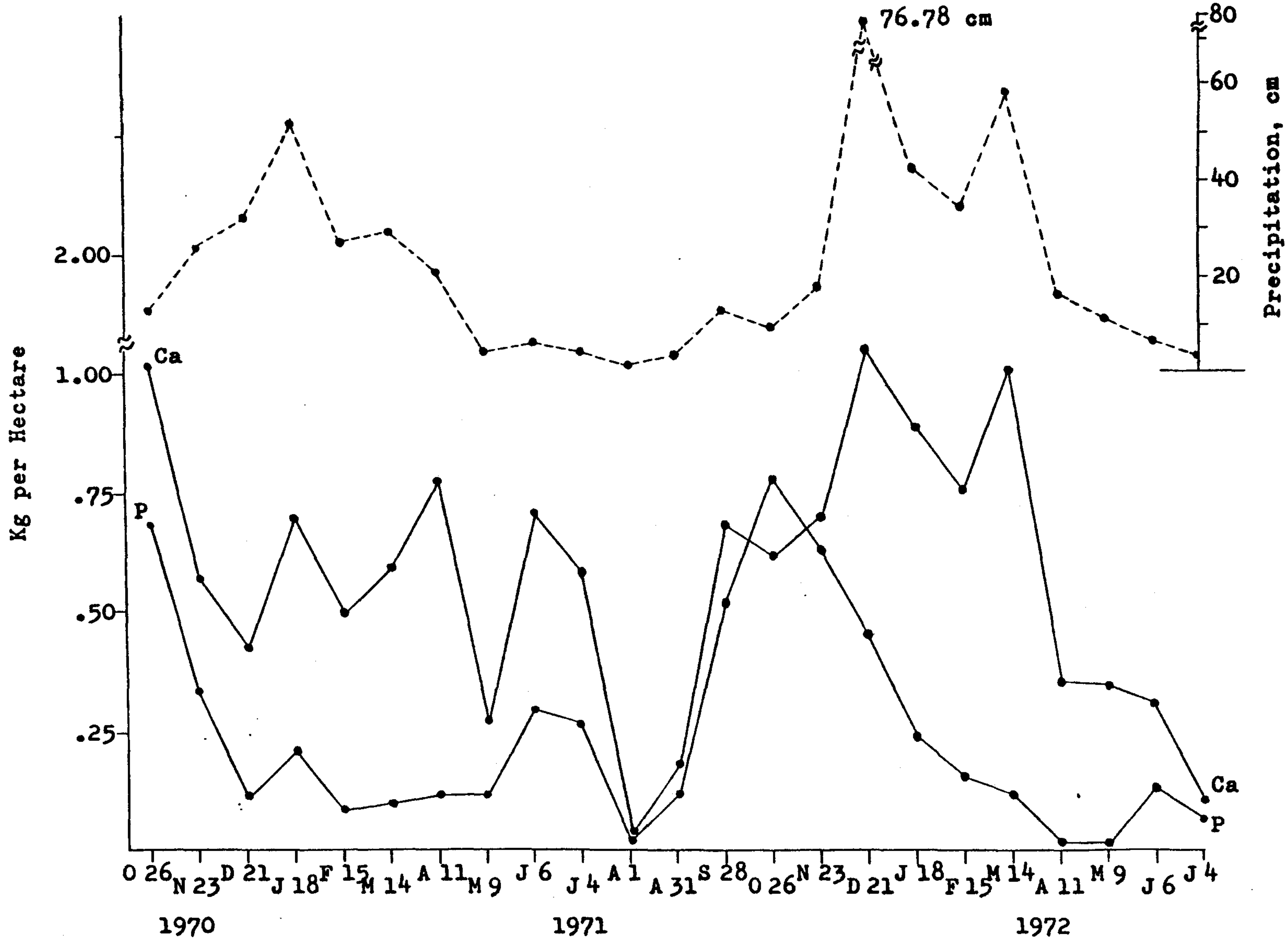


Figure 5. Average kg per hectare of Calcium and Phosphorus for plots 1-6.

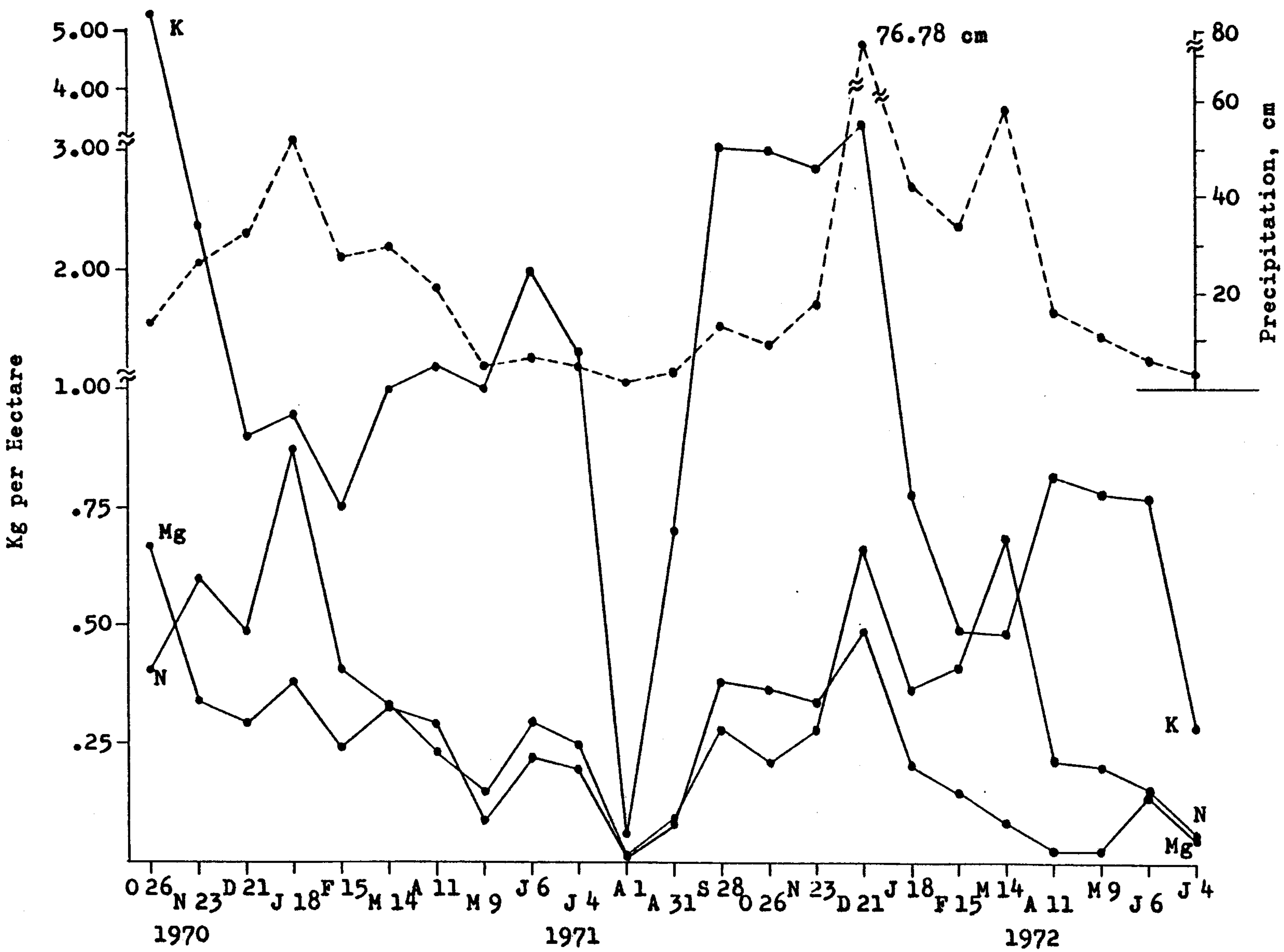


Figure 6. Average kg per hectare of Nitrogen, Magnesium and Potassium for plots 1-6.

Table 6. Total nutrient input in throughfall for 2 years (kg/hectare).

Plot	Year	N	NO_3	P	K	Ca	Mg
1	1	4.38	.12	2.49	17.14	7.88	4.06
	2	1.64	.08	3.08	8.69	3.98	2.46
	Average	3.01	.10	2.79	12.92	5.93	3.26
2	1	4.05	.11	2.62	15.85	6.43	3.31
	2	3.44	.12	3.84	8.55	7.40	3.12
	Average	3.75	.12	3.23	12.20	6.92	3.22
3	1	4.29	.10	3.07	24.49	4.61	2.84
	2	3.59	.06	2.91	10.70	8.50	2.72
	Average	3.94	.08	2.99	17.60	6.56	2.78
4	1	3.89	.14	3.81	23.83	7.83	3.61
	2	2.81	.11	5.97	20.61	9.53	2.41
	Average	3.35	.12	4.89	22.22	8.68	3.01
5	1	4.35	.15	3.04	22.97	7.71	3.63
	2	4.45	.11	3.74	19.63	9.30	1.95
	Average	4.40	.13	3.39	21.30	8.51	2.79
6	1	5.54	.23	3.31	22.29	8.05	4.08
	2	5.43	.06	3.65	18.13	8.56	2.73
	Average	5.49	.14	3.48	20.21	8.31	3.41

ATMOSPHERIC INPUT*

N	P	K	Ca	Mg
.90	.27	.11	2.33	1.32

*Fredriksen, 1972. To determine net throughfall return, the atmospheric input values for each nutrient must be subtracted from the average values in Table 6.

each element appeared to be comparable between plots.

Throughfall Discussion

The return of elements by throughfall was adjusted (Figure 7) to take into consideration elemental additions from the atmosphere during periods of precipitation.

The general mobility of the various mineral elements was demonstrated in Figure 7. For example, 12% of the N, 39% of the P, 74% of the K, 9% of the Ca, and 37% of the Mg was returned in the leaf and litter wash. This high transfer rate in throughfall has been observed in many other ecosystems (Will, 1955, 1959; Tamm, 1951; Madgwick and Ovington, 1959; and Cole, *et al.*, 1967).

In general, the nutrient concentrations and total nutrient input in throughfall samples were highest during the fall and summer months. This was the period when rainfall was minimal. Once the rains started in the fall, the majority of each nutrient was leached out. As the rains increased in quantity and duration, the available fraction of removable nutrients was decreased.

Another supply of nutrients can come from the tree crowns catching aerosols (Ericksson, 1955) and dust (Tamm and Treodsson, 1955), which are washed off the branches and leaves during periods of rain.

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

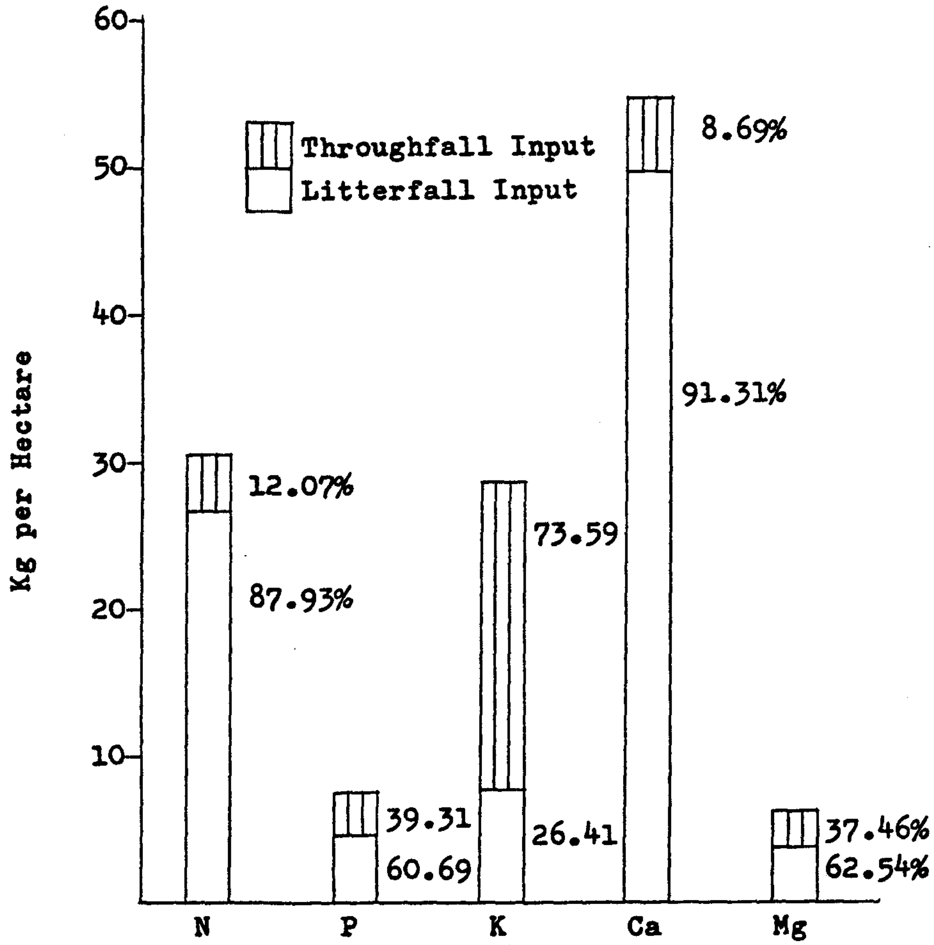


Figure 7. Average total nutrient return in throughfall and litterfall for plots 1-6.

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

An interesting result was the detectable presence of nitrate in the throughfall samples during the winter and spring months. During this time period temperatures were cold and microorganism activity was thought to be at a minimum. No previous study has reported an analysis for nitrate in canopy throughfall, and therefore no comparisons of amounts can be made. A possible explanation could be the catabolic processes of microorganisms on the foliage, during the winter months. Also, a study by Miller and Abee[2] suggested that nitrate could be removed from live foliage of Douglas-fir trees through leaching. They noted that more nitrate was removed from old tissue than young. The significance of the biological presence of nitrate within the foliage is open to speculation.

No close relationship existed between the species composition in the different plots and the difference in the amounts of plant nutrients contained in the throughfall samples. Since many other factors beside leaf composition must affect the loss of elements from the tree canopies by leaching, i.e. soils, canopy density, leaf shape, and morphology, and the relative mobility of different ions, this was not surprising. Mann and Walker (1925) found that 86.4

[2]Miller and Abee, unpublished data.

percent of the K could be leached from apple leaves of the Bramley variety and 99.7 percent for the Cox. It was interesting, in view of this, that of all the elements that were determined in the throughfall samples, the greatest return was for potassium.

Frequent summer and fall collections are suggested to keep microorganism activity to a minimum. However, analytical samples can be consolidated if done on a proportional basis. Winter and spring collections can be less frequent as temperatures are cold and concentrations are minimal during this time.

Litterfall Results

Litterfall production varied from stand to stand and from year to year so that if any real differences existed they were not apparent from the data, despite the marked differences in stand characteristics shown in Table 3. Average litter production for all stands during the 2 years was 5,520 kg/ha (Table 7). This was approximately 1 1/2 times the average 3.5 metric tons per hectare reported by Bray and Gorham (1964) for cool, temperature forests, but closer to the yield they reported for a latitude comparable to our study. From worldwide data, these authors reported that nonleaf litter averaged from 27 to 31 percent of total litter production. The stands reported here averaged 48 percent nonleaf (woody) litter for the first year (Table 8). Average leaf litter for all plots was 2.$\overset{7}{6}$8 metric tons/hectare for the two years.

In terms of total kg/hectare of litter, the vast majority fell

Table 7. Litter production (kilograms per hectare) for six plots.

	PLOT							
Year	1	2	3	4	5	5a[1]	6	Average[2]
Total Litter								
1970-1971	5614	5878	6428	5086	4816	16,919	7060	5810
1971-1972	5475	4599	7269	5537	4355		4138	5229
Average	5545	5239	6849	5303	4586		5599	5520
Standard dev.	115	128	246	99	47		96	13.47
Coefficient of variation (%)	34	40	59	31	17		28	13.47
Non Woody								
1970-1971	2015	2247	2953	3204	2538		3727	2781
1971-1972	2133	2236	2906	3101	2483		2689	2591
Average	2047	2242	2930	3153	2511		3208	2682
Standard dev.	8	5	15	11	9		17	487
Coefficient of variation (%)	16	9	20	13	13		19	18.15

Note: In plot 5, an extremely large slab of bark from a nearby snag fell into a trap causing high values for total kg/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 ignored.

[1]Excluding extreme bark sample

[2]Excluding 5a

Table 8. Distribution of metric tons/hectare between litter components by plot for 1970-71.

Plot	1	2	3	4	5a	5b[1]	6	Average[2]
Needles	2.015	2.247	2.953	3.204	2.538	2.538	3.727	2.781
% of total	35.65	37.76	46.20	62.25	52.86	52.86	52.79	47.67
Twigs	.988	.760	.864	.705	.748	.748	1.011	.846
% of total	17.48	12.78	13.53	13.72	15.60	15.60	14.32	14.51
Branches	.852	1.364	.294	.106	.069	.069	1.257	.657
% of total	15.07	22.93	4.60	2.06	1.44	1.44	17.80	11.27
Bark	.418	.527	.720	.221	12.753	.628	.351	.478
% of total	7.40	8.86	11.27	4.30	13.10	13.10	4.97	8.20
Cones	.873	.871	1.281	.742	.545	.545	.528	.807
% of total	15.07	14.64	20.06	14.44	11.37	11.37	7.48	13.84
Hardwoods	.409	.031	.072	.091	.146	.146	.016	.128
% of total	7.24	0.52	1.13	1.77	3.05	3.05	0.23	2.20
Mosses & lichens	.097	.149	.205	.075	.124	.124	.170	.137
% of total	1.72	2.51	3.21	1.46	2.59	2.59	2.41	2.35
Total	5.652	5.949	6.390	5.143	16.919	4.798	7.060	5.832

[1]Excluding extreme bark sample.

[2]Excluding 5a.

during the winter months (Figure 8). This was the period when snowfall was greatest; consequently, much litter in the trees broke under the weight of the snow. Needle cast was greatest in the fall, decreased during the winter, and gradually increased during the spring months. Woody material and cone litterfall was greatest during the winter months. Hardwood litter was greatest during the fall, and decreased throughout the rest of the year. Moss and lichen litterfall increased from a low in the fall to a winter and spring maximum, then decreased slowly from spring to summer.

Maximum and minimum concentrations of the various litterfall components varied considerably among plots (Table 9). Generally, nutrient concentrations were highest for hardwoods and moss and lichens, and lowest for branch litterfall. However, total kg/hectare of nutrient input for each plot appear comparable (Table 10).

The maximum return of N, K, and Mg in litterfall occurred on plot 6, while P and Ca return was greatest on plot 3. The average total kg/hectare of nutrient input (Table 11) were N 26.7, P 4.6, K 7.5, Ca 49.9, and Mg 3.8. The greatest portion, 63%, of the nutrient input came through needle litterfall. Cone litterfall (including flowers) accounted for 10 percent while twig litterfall accounted for 11 percent of the total. Together, the needle, cone, and twig litterfall account for 84% of the total nutrient input through litterfall.

Plots 1-4 were chosen to represent the range of concentrations (Figure 9A, B, C, D, and E) and nutrient return values (Figures 10, 11, 12, 13 and 14) that can be found through litterfall components during

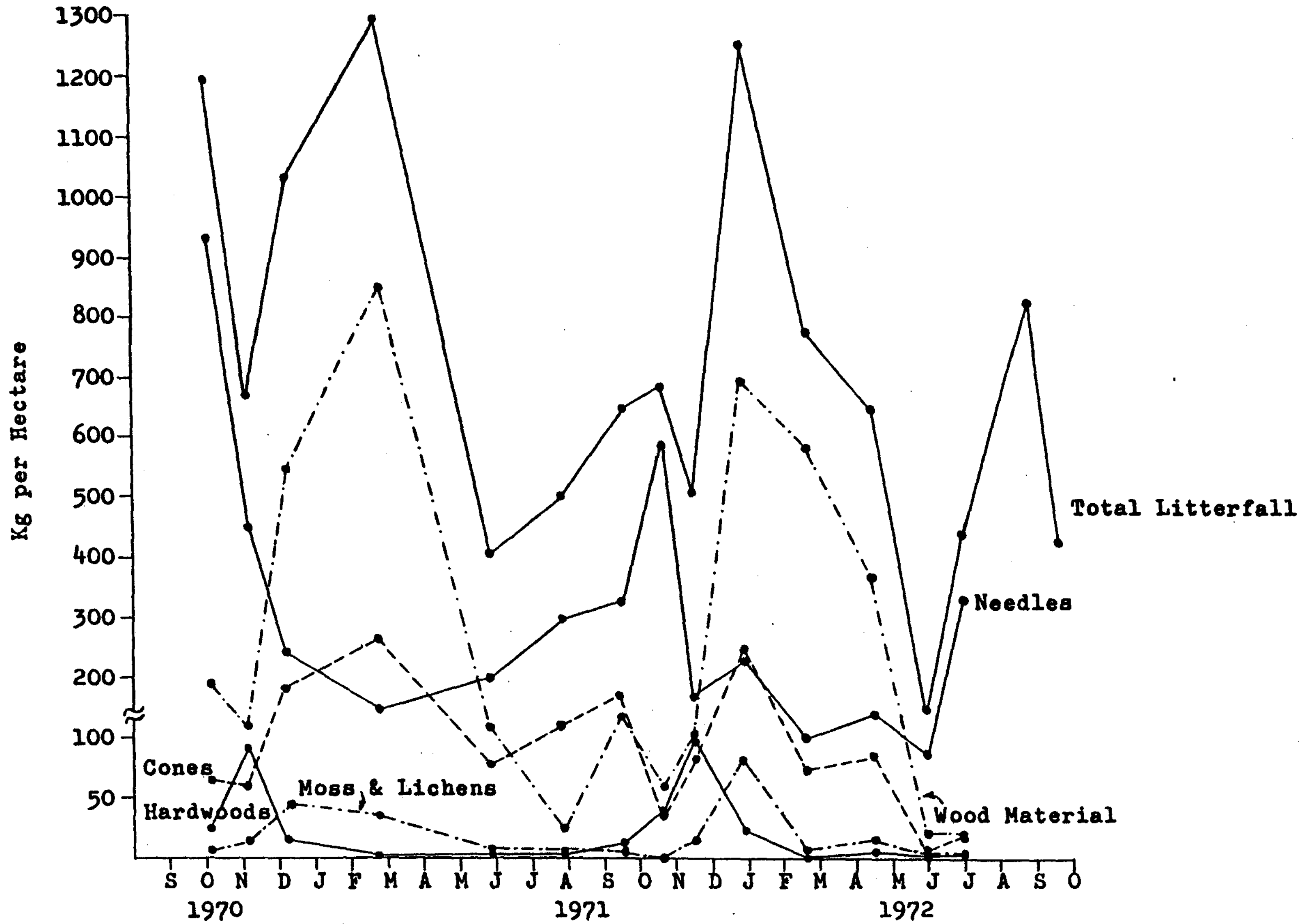


Figure 8. Average kg per hectare by collection date and litter component for plots 1-4.

Table 9. Maximum and minimum concentrations (%) for each component for year 1970-71.

	1		2		3		4		5		6		Average	
	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN
N														
Needles	.767	.320	.776	.343	.847	.466	.681	.401	.851	.411	1.093	.426	.836	.395
Cones	.615	.218	.902	.309	.656	.430	.778	.338	.461	.265	.790	.519	.700	.347
Twigs	.471	.284	.356	.260	.491	.397	.423	.276	.442	.250	.612	.362	.466	.305
Branches	.302	.154	.189	.119	.328	.113	.175	.129	.303		.287	.101	.264	.123
Bark	.560	.225	.760	.385	.644	.335	2.327	.449	.497	.248	.615	.446	.901	.348
Hardwoods	.820	.603	1.349	.340	1.658	.634	.732	.429	1.212	.412	1.607	1.192	1.230	.602
Mosses & lichens	2.016	.463	1.964	.897	1.999	.710	2.622	.521	1.557	.509	.902	.579	1.843	.613
P														
Needles	.167	.054	.170	.063	.179	.059	.189	.057	.138	.063	.138	.072	.164	.061
Cones	.084	.024	.111	.032	.074	.033	.119	.027	.068	.018	.078	.068	.091	.034
Twigs	.072	.028	.050	.008	.055	.032	.064	.034	.052	.032	.056	.044	.058	.030
Branches	.021	.013	.017	.008	.039	.007	.012	.008	.021		.032	.002	.024	.008
Bark	.041	.012	.068	.033	.080	.028	.114	.039	.051	.026	.060	.034	.069	.029
Hardwoods	.144	.059	.168	.047	.162	.086	.281	.070	.113	.041	.242	.181	.185	.081
Mosses & lichens	.119	.053	.113	.069	.142	.092	.263	.073	.112	.049	.138	.079	.148	.069
K														
Needles	.229	.053	.230	.049	.280	.055	.212	.064	.262	.075	.357	.107	.262	.067
Cones	.183	.031	.182	.031	.220	.051	.156	.030	.159	.034	.204	.086	.184	.044
Twigs	.135	.050	.112	.035	.170	.046	.187	.059	.206	.054	.165	.097	.163	.057
Branches	.080	.021	.051	.014	.082	.025	.043	.021	.029		.098	.012	.064	.019
Bark	.086	.038	.083	.046	.214	.051	.227	.071	.110	.029	.110	.050	.138	.047
Hardwoods	.309	.055	.575	.113	.815	.134	.895	.152	.635	.076	1.015	.356	.707	.148
Mosses & lichens	.304	.117	.130	.073	1.034	.192	.553	.199	.330	.097	.290	.117	.474	.133

Table 9 (cont.). Maximum and minimum concentrations (%) for each component for year 1970-71.

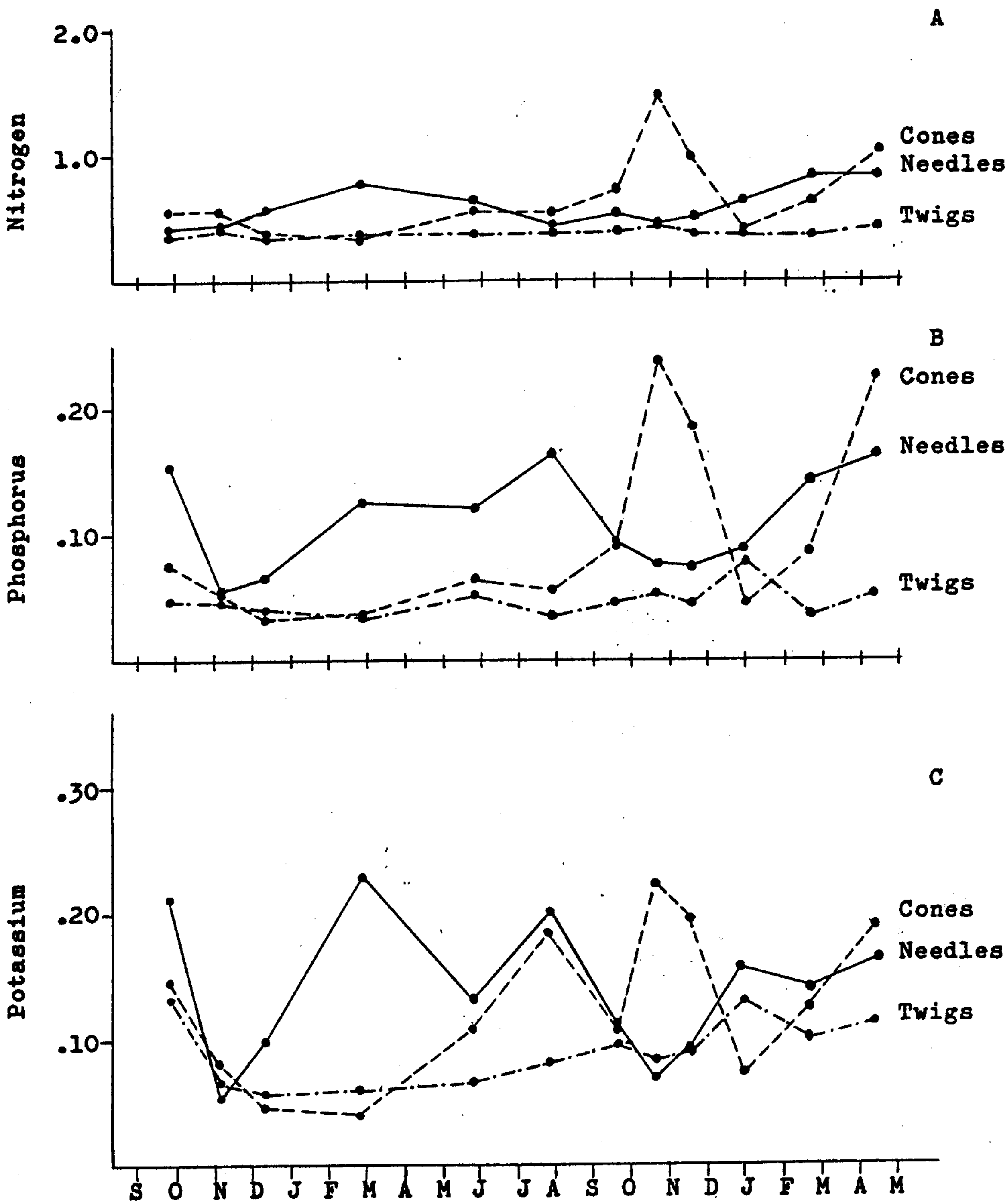
	1		2		3		4		5		6		Average	
	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN
Ca														
Needles	2.035	1.241	1.875	.899	1.850	1.103	1.679	.112	2.182	.825	1.026	.673	1.775	.809
Cones	.397	.109	1.378	.080	.229	.126	.395	.070	.428	.128	.295	.082	.520	.099
Twigs	1.299	.711	1.311	.311	1.122	.823	1.978	.673	1.948	.581	1.174	.562	1.472	.610
Branches	.828	.598	.948	.168	.843	.338	.453	.073	.385		.625	.058	.680	.247
Bark	1.122	.542	.673	.408	.605	.300	.700	.251	.641	.330	.739	.344	.747	.363
Hardwoods	2.978	1.484	4.950	1.643	2.530	1.633	3.343	.684	1.555	.780	2.434	1.687	2.965	1.318
Mosses & lichens		.049	3.571	.176	3.029	.297	.906	.175	.595	.274	.551	.290	1.563	.210
Mg														
Needles	.150	.033	.118	.039	.129	.055	.105	.026	.108	.054	.114	.063	.121	.045
Cones	.205	.047	.089	.036	.075	.045	.121	.038	.061	.031	.071	.042	.104	.040
Twigs	.064	.028	.066	.020	.074	.034	.072	.038	.082	.036	.097	.042	.076	.033
Branches	.027	.013	.040	.019	.025	.010	.019	.015	.018		.052	.005	.030	.012
Bark	.058	.037	.104	.029	.058	.036	.062	.030	.039	.021	.040	.019	.060	.029
Hardwoods	.296	.069	.460	.149	.246	.118	.440	.081	.284	.142	.276	.133	.334	.115
Mosses & lichens		.062	.064	.020	.324	.064	.124	.058	.068	.030	.076	.057	.126	.049

Table 10. Total kg/hectare per year for year 1970-71 in litterfall.

		1	2	3	4	5	5a	6
	N	8.75	11.48	16.55	14.67	12.41	12.41	22.46
	P	2.33	2.59	3.82	4.18	2.48	2.48	4.01
Needles	K	3.16	3.07	5.91	5.28	3.61	3.61	7.92
	Ca	34.15	33.35	36.95	38.11	33.24	33.24	28.51
	Mg	1.94	1.68	2.68	2.43	1.90	1.90	3.07
	N	3.14	3.92	7.06	2.40	2.18	2.18	3.12
	P	.35	.51	.69	.36	.23	.23	.35
Cones	K	.74	.66	1.43	.62	.49	.49	.60
	Ca	.91	2.62	2.06	1.13	1.10	1.10	.69
	Mg	.72	.46	.70	.45	.26	.26	.29
	N	3.94	2.29	3.88	2.19	2.11	2.11	4.98
	P	.54	.29	.33	.28	.27	.27	.52
Twigs	K	.65	.42	.88	.57	.72	.72	1.38
	Ca	3.88	6.95	9.56	7.84	7.85	7.85	6.21
	Mg	.45	.32	.45	.31	.35	.35	.64
	N	2.19	1.81	.91	.14	.21	.21	1.69
	P	.26	.13	.13	.01	.01	.01	.14
Branches	K	.74	.33	.29	.02	.02	.02	.43
	Ca	2.06	2.82	2.15	.13	.26	.26	2.75
	Mg	.25	.28	.11	.02	.01	.01	.34
	N	1.82	2.30	3.23	1.27	1.70	16.00	1.97
	P	.13	.20	.28	.11	.16	2.46	.19
Bark	K	.21	.28	.47	.17	.23	2.05	.28
	Ca	2.03	2.71	3.20	.96	3.06	75.81	2.31
	Mg	.17	.22	.00	.10	.29	.63	.06
	N	2.62	.13	.42	.42	.46	.46	.09
	P	.36	.03	.06	.12	.07	.07	.02
Hardwoods	K	.68	.08	.11	.31	.52	.52	.04
	Ca	10.33	.91	1.54	2.15	1.23	1.23	.15
	Mg	.71	.06	.09	.18	.19	.19	.02
	N	1.25	1.44	3.18	1.21	.74	.74	1.20
	P	.19	.09	.29	.09	.08	.08	.17
Moss &	K	.13	.16	.92	.24	.16	.16	.27
Lichens	Ca	.20	1.39	.91	.17	.41	.41	.67
	Mg	.06	.05	.19	.04	.05	.05	.11
	N	23.70	23.39	35.23	23.30	19.82	34.12	35.53
	P	4.15	3.85	5.60	5.15	.329	5.60	5.38
Total	K	6.32	5.01	10.01	7.21	5.74	7.56	10.32
	Ca	53.57	50.76	56.36	50.50	47.16	119.91	41.30
	Mg	4.31	3.08	4.22	3.52	3.06	3.40	4.53

Table 11. Average kg per hectare per year for plots 1-6 for each litterfall component.

	N	P	K	Ca	Mg	Average %
Needles	14.39	3.23	4.82	34.05	2.28	
Percent	53.98	70.68	64.01	68.18	60.16	63.40
Cones	3.64	.42	.76	1.42	.48	
Percent	13.65	9.19	10.09	2.84	12.67	9.69
Twigs	3.23	.37	.77	7.05	.42	
Percent	12.13	8.10	10.23	14.12	11.08	11.13
Branches	1.16	.11	.31	1.70	.17	
Percent	4.35	2.41	4.12	3.40	4.49	3.75
Bark	2.05	.18	.27	2.38	.14	
Percent	7.69	3.94	3.49	4.77	3.95	4.79
Hardwoods	.69	.11	.29	2.72	.21	
Percent	2.59	2.41	3.85	5.45	5.54	3.97
Moss & Lichens	1.50	.15	.31	.63	.08	
Percent	5.63	3.28	4.12	1.26	2.11	3.28
Total Average Input	26.66	4.57	7.53	49.94	3.79	


A
2.0
1.0
Nitrogen
Cones
Needles
Twigs
B
.20
.10
Phosphorus
Cones
Needles
Twigs
C
.30
.20
.10
Potassium
Cones
Needles
Twigs
S O N D J F M A M J J A S O N D J F M A M

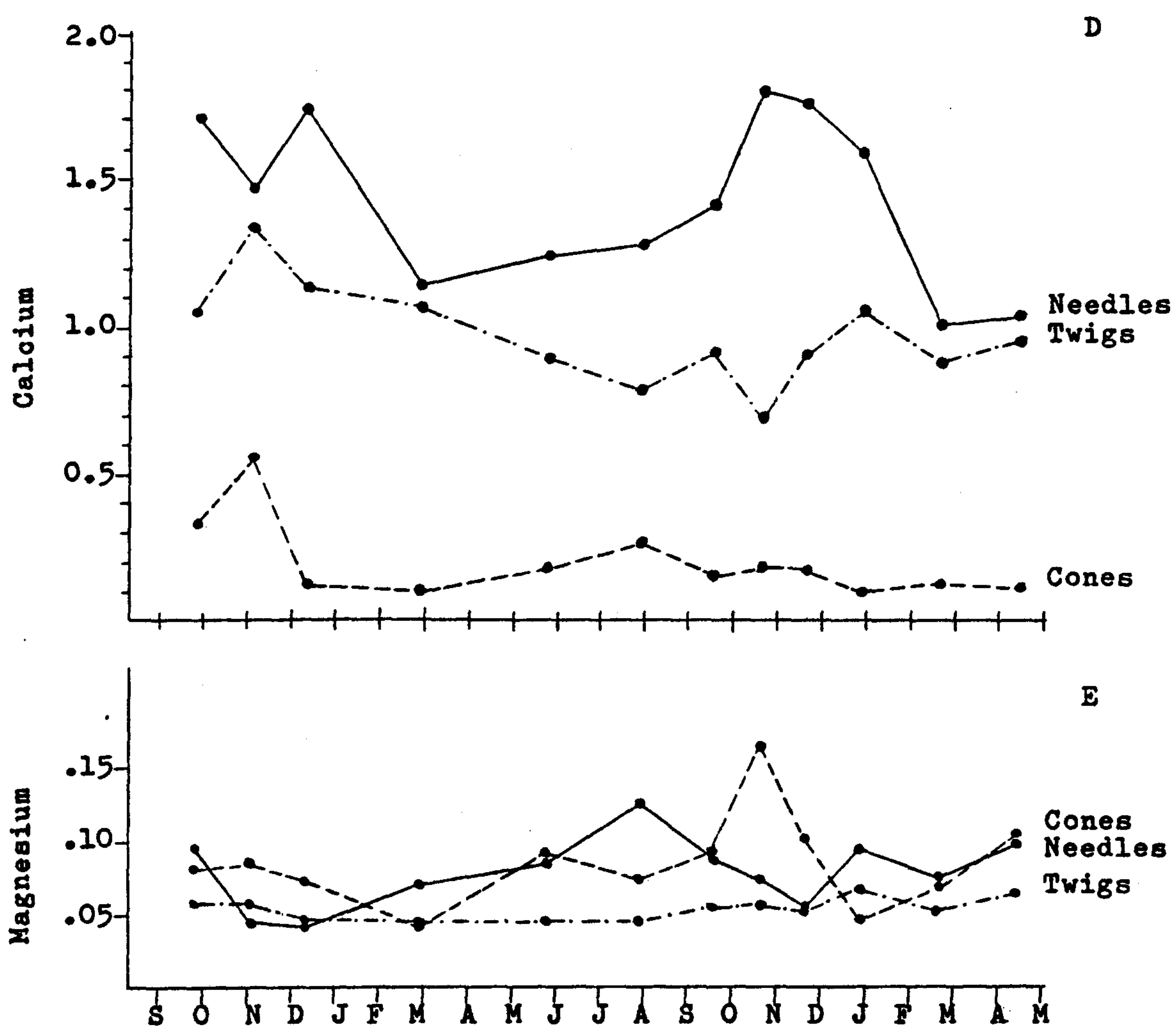


Figure 9. Average litterfall concentrations (per cent) by mid-collection date for Nitrogen (A), Phosphorus (B), Potassium (C), Calcium (D), and Magnesium (E).

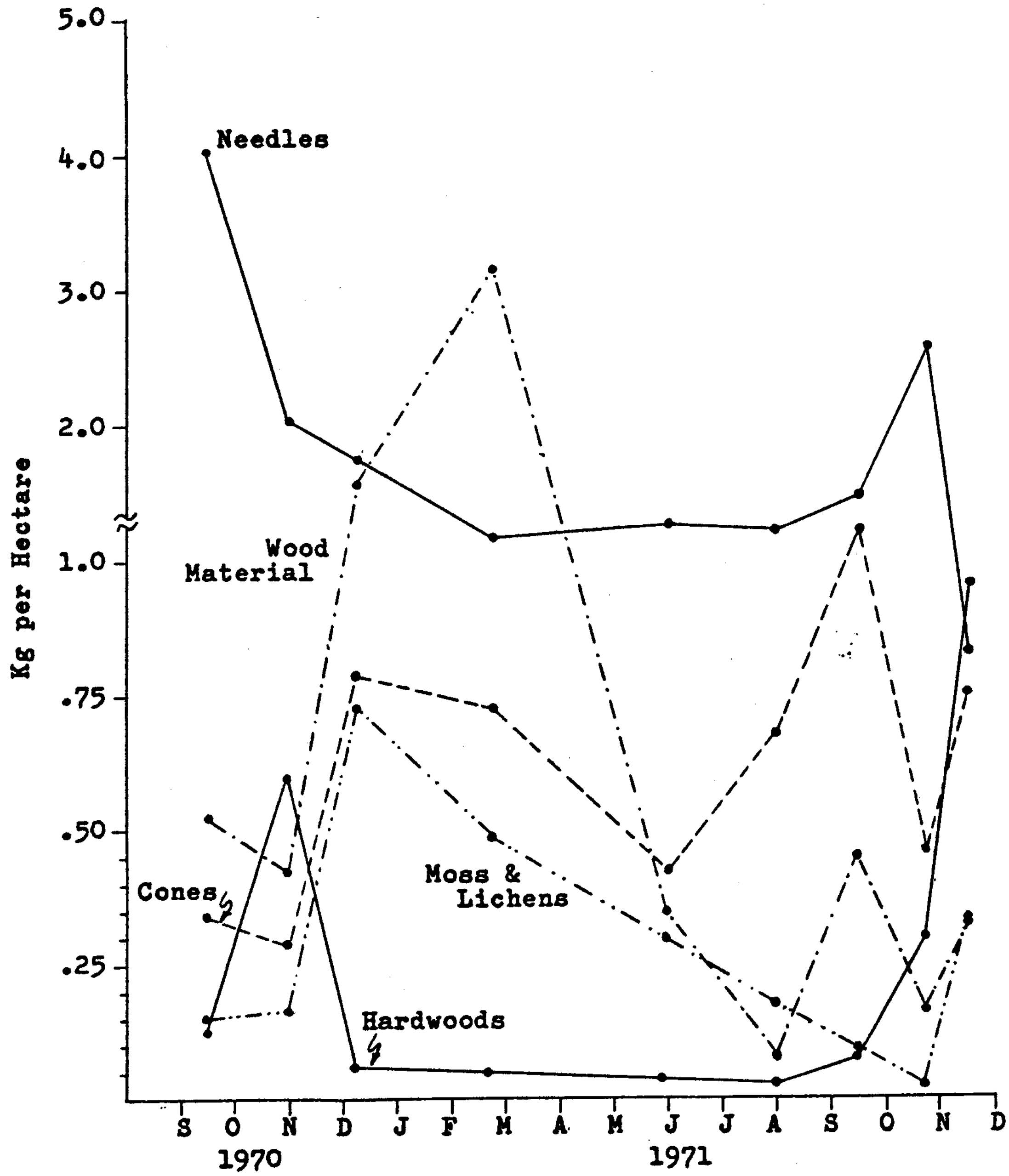


Figure 10. Average return of Nitrogen (Kg per hectare) by litter component and mid-collection date for plots 1-4.

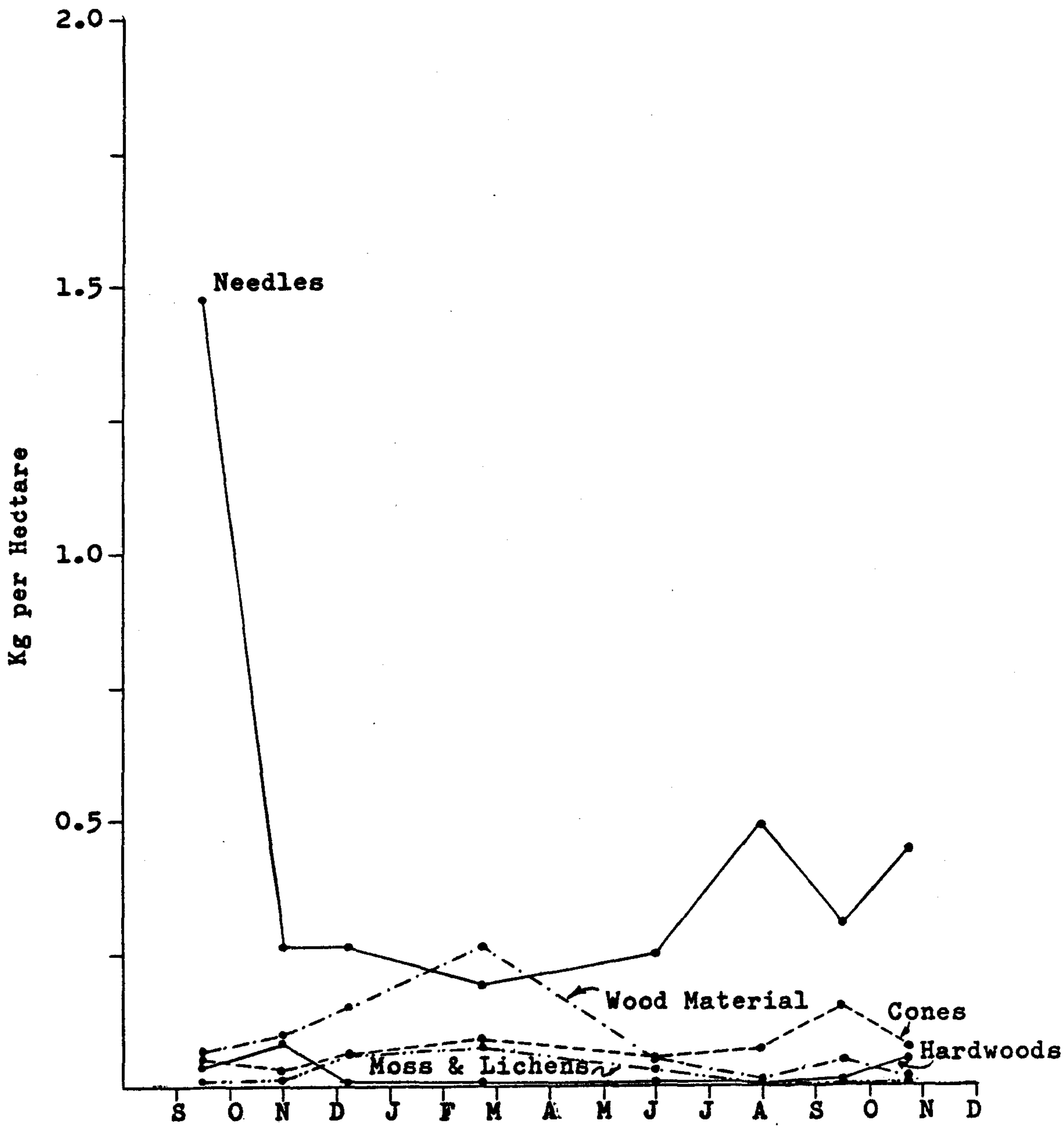


Figure 11. Average return of Phosphorus (Kg per hectare) by litter component and mid-collection date for plots 1-4.

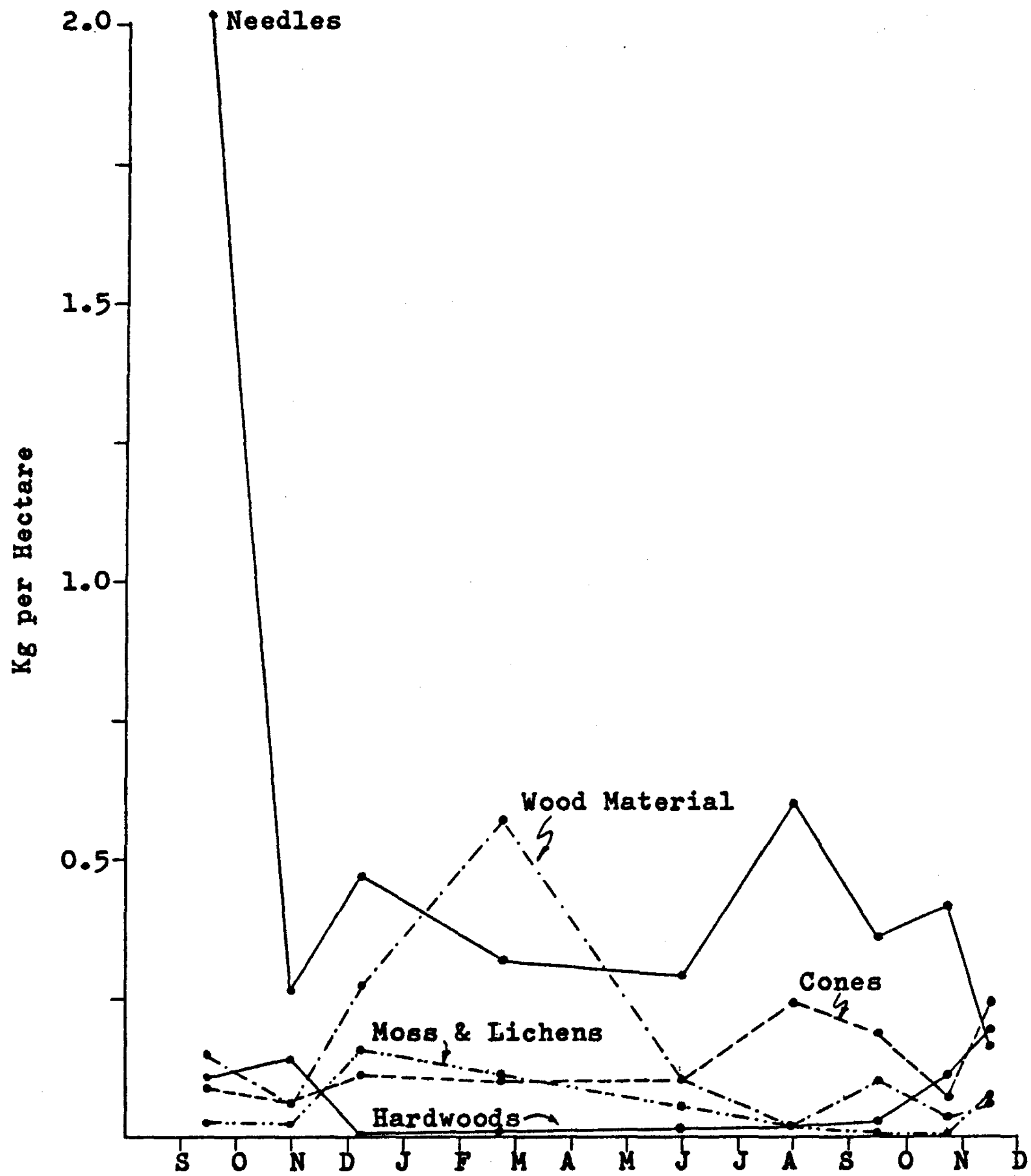


Figure 12. Average return of Potassium (Kg per hectare) by litter component and mid-collection date for plots 1-4.

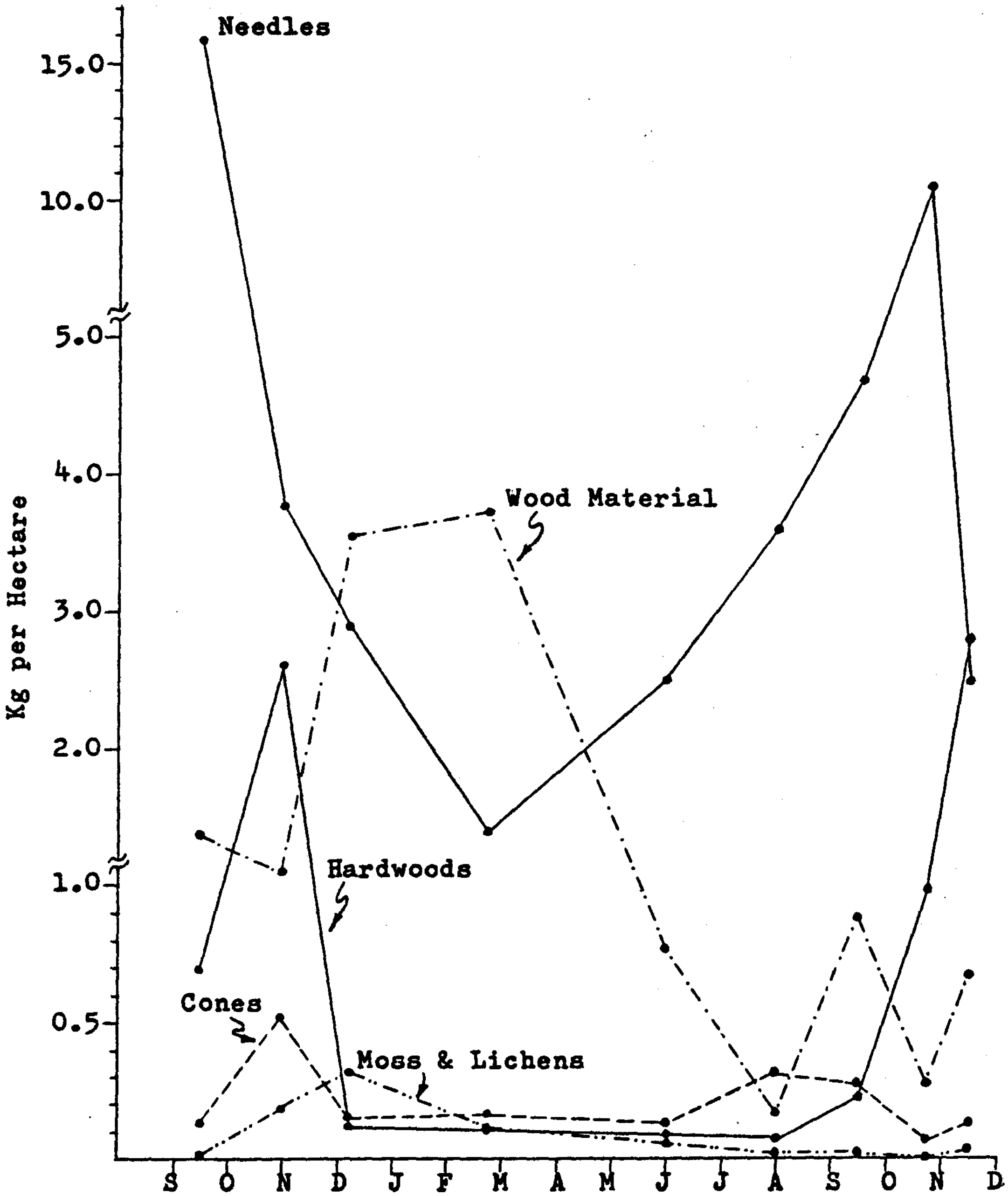


Figure 13. Average return of Calcium (Kg per hectare) by litter component and mid-collection date for plots 1-4.

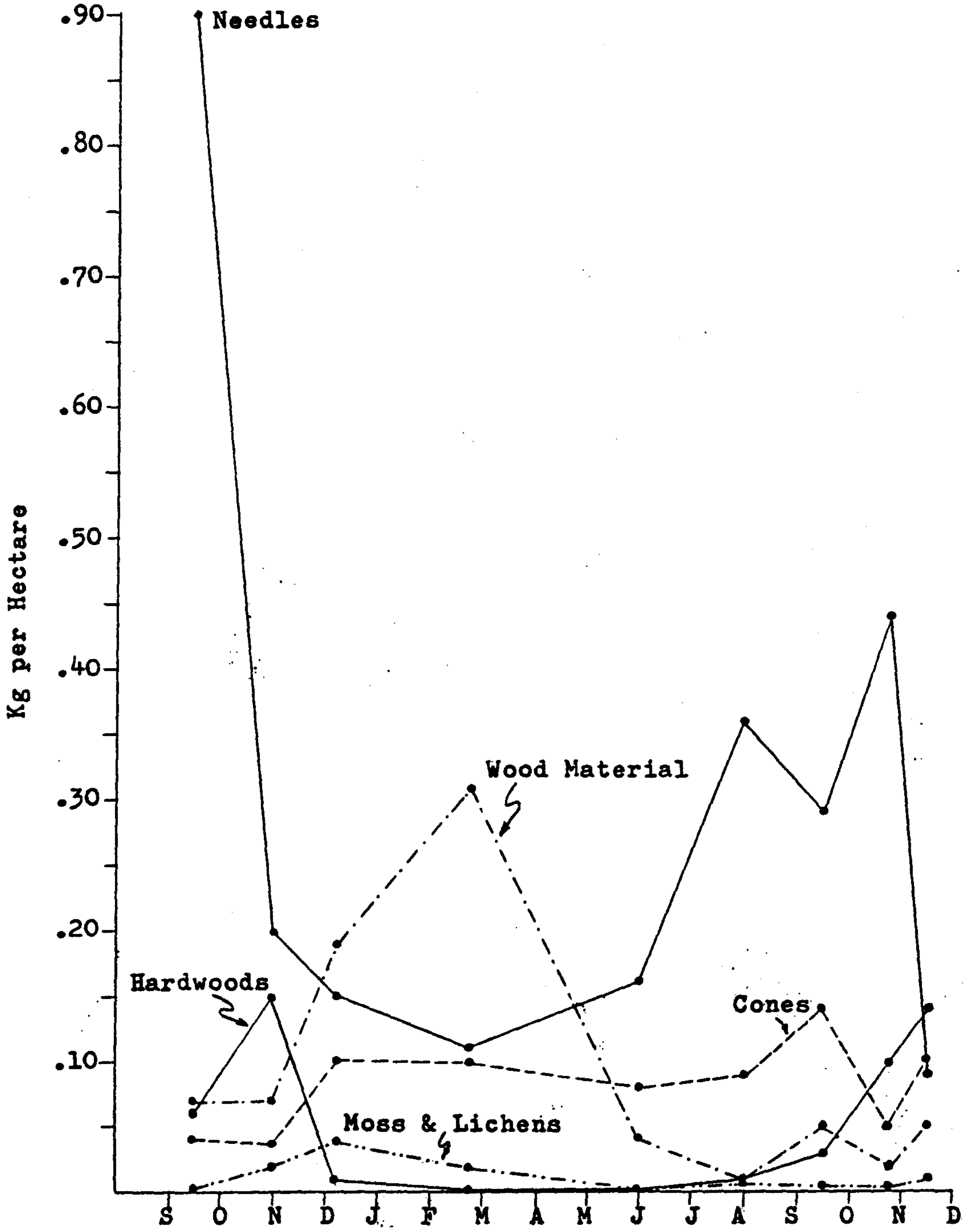


Figure 14. Average return of Magnesium (Kg per hectare) by litter component and mid-collection date for plots 1-4.

the year 1970-71. Nutrient concentrations varied among elements with respect to time for any one litter component. Twig concentrations varied less than did needle and cone concentrations for any one nutrient.

Nutrient return in litterfall components generally followed the same trend as did litterfall return by weight (Figure 8). Nutrient return through woody material was greatest during the winter months while nutrient return through needle litter was greatest during the fall. For cones, Mg return was greatest during the winter months; Ca and P return was greatest in the fall; N return reached a high during the winter and fall months while K return was greatest during the summer months.

The results of our efforts to describe crown density are presented in Table 12. The order of density was 2 > 3 > 6 > 1 > 4 > 5. No consistent relationship was found between total litterfall and density or woody material and density for any one year. However, average total litterfall values generally followed the density index results.

Litterfall Discussion

The annual nonwoody leaf-litter production for a stand varied less than total litter production (Table 7). This was attributed to trap size and sampling time. Nye (1961) in Ghana, observed that timberfall (*Diospyros* spp.) over a small area was very eratic and

Table 12. Order of density for plots 1-6.

Density	2	>	3	>	6	>	1	>	4	>	5
Total Litter											
Year 1	6	>	3	>	2	>	1	>	4	>	5
2	3	>	4	>	1	>	2	>	5	>	6
Average	3	>	6	>	1	>	4	>	2	>	5
Woody material											
Year 1	2	>	3	>	6	>	1	>	5	>	4
2	3	>	1	>	4	>	2	>	5	>	6
Average	3	>	1	>	2	>	6	>	4	>	5

difficult to measure, since it was influenced greatly by the fall of even a single tree. Woody litter, bark and branches in particular, were not as uniformly distributed as leaf litter. Part of a relatively large slab of bark across a trap frame could add significantly to the total weight of litter production from that stand. This was found in Table 7 for plot 5. Although lack of similar incidents in other stands caused disparity among the stands for the first year, such incidents apparently will offset each other between stands over long periods of time. Alway and Zon (1930) showed that a considerable difference existed between experimental sample plots during the same year and between years on the same plot, in the latter case, up to 24 percent. Kittredge (1948) found 100 percent difference in weight in successive years in the Ceanothus-chamise type in California. Since all investigations seem to point to a substantial variation in litterfall within a given stand and from year to year, and since the magnitude of these variations is difficult to explain on sampling grounds alone, it seems certain that the amount of organic matter reaching the forest floor from year to year is not a constant value.

The efficiency of forest ecosystems to utilize available energy can be expressed as foliage production (Ovington, 1962). In view of this, stands 6, 4, and 3 seemed to be more efficient in using available energy to produce an annual crop of foliage expressed as leaf litter (Table 7). However, second year data indicated that the order of foliage production for those 3 plots is 4, 3, and 6. When net primary production is considered to be the total amount of organic matter synthesized by plants, foliage becomes only a part of the organic matter produced. A more substantial part is the woody matrix superficially described by basal area, and stems per acre (Table 1). In terms of total net primary production, the energy-capturing efficiency of each stand was beyond the scope of the study.

Variations in nutrient concentration found between litterfall components among plots and seasons can be expected if foliage characteristics such as age, morphology, and species are not constant. We also observed that the age of the tissue, and when it falls, varied throughout the year for each plot. For example, N concentration increased during the winter months for needles (Figure 7) while Ca concentration decreased during this same period of time (Figure 9D). Since calcium tends to increase in concentration with age, and N concentration is greater in young foliage than old, these data suggested that the needle foliage of a given sample was younger in the winter than in the fall. This was primarily due to environmental parameters such as wind action, rainstorms, and snowfall.

Differences between total nutrient input through litterfall (Table 10) were affected by the distribution of litter components within the total. Even where two plots seemed to produce comparable total quantities on a yearly basis, amounts of the various litter components were important. The amounts of each litter component were important because concentrations of nutrient elements varied for each litter component. For example, Table 8 shows that the greatest difference between plots 1 and 3 in terms of kg/hectare of litterfall occurred between needles and woody material. Plot 3 produced approximately

940 kg/hectare more of needles than plot 1, while plot 1 produced 560 kg/hectare more of woody material than plot 3. However, Table 9 shows that the average concentration of nitrogen, for example, was much higher in needles than it was in woody material; consequently, variations such as found in Table 8 were brought about.

More amounts of N, P, Ca, and Mg were transferred to the soil through litterfall than through throughfall, while more K was added to the soil through throughfall (Figure 7).

By examining the nutrient return data in litterfall and throughfall, a general indication of the rate of elemental turnover by the forest component of the ecosystem was established. Based on the data of Figure 7, a turnover progression of Ca > N > K > P > Mg was evident in this particular ecosystem. Cole, et al., (their Table 5, 1967) found a similar progression in a second-growth Douglas-fir ecosystem.

The poor relationship between woody material and the density index (Figure 7) was probably due to the amount of variability that is present in deteriorating, old-growth stands. However, with the exception of plot 2, the average of the total litterfall return for the 2 years followed the same order as did density.

It was obvious from the data in Figures 9A, B, C, D, and E, that there was a great deal of variability between elements in terms of concentration for any one litter component. These differences in concentration for the various components as suggested earlier were affected by growing season, environmental parameters, leaching, soils, species, etc. It was also demonstrated that the amount of litterfall varied markedly in a given year and from year to year. In light

of these variables, the importance of periodic, long-term sampling stands out. However, field samples collected frequently in the fall can be consolidated into one sample for chemical analysis if the analytical sample is proportional to the total amount that fell during any one period of time. Frequent sampling is suggested during the winter months. Will (1967) in New Zealand has shown that most of the K in *Pinus radiata* litter was leached out within the first three months; about half the phosphorus was also removed in the same time. During the winter months, field samples should not be consolidated for analytical purposes if data describing seasonal variability in nutrient concentration and nutrient return is desired.

CONCLUSIONS

To investigate the movement of elements from the tree crowns by natural litterfall and leaf wash, plots were established on six 450 year-old growth stands at the H. J. Andrews Experiment Forest.

Litterfall and throughfall collections were taken periodically (throughfall every two weeks, litterfall every four to six weeks - during snow free months) from September 1970 to October 1972, and analyzed for N, P, K, Ca, and Mg.

The following conclusions were derived as a result of the data analysis.

1) Elemental concentrations contained in throughfall samples varied throughout the year and tended to follow a seasonal cycle. Concentrations were lowest during the winter when precipitation was greatest and highest during the summer months when precipitation was lowest.

2) The average total kg/hectare elemental input in throughfall generally followed the same trend as did the concentration curves. The greatest amount of each element was removed from the crowns to the forest floor during the fall when precipitation first washed the canopy. Minimal amounts were moved late in the summer when precipitation was minimal. Nitrate return was greatest during the winter and spring months and lowest during the fall and summer.

3) The general mobility of the various mineral elements was demonstrated. For example, 12% of the N, 39% of the P, 74% of the K, 9% of the Ca, and 37% of the Mg was returned in the leaf and litter

wash.

4) No close relationship existed between species composition in the different plots and the differences in the amounts of plant nutrients contained in the throughfall samples.

5) Frequent summer and fall throughfall collections are suggested to keep microorganism activity to a minimum. Winter and spring collections can be less frequent. However, amalytical samples can be consolidated if done on a proportional basis for each season.

6) Litterfall production varied from stand to stand and from year to year so that if any real differences existed they were not apparent from the data. Average litter production for all stands during the 2 years was 5,520 kg/hectare. In terms of total kg/hectare of litter, the vast majority fell during the winter months.

7) Nutrient concentrations of the various litterfall components varied considerably among plots. Generally, nutrient concentrations were highest for hardwoods and moss and lichens and lowest for branch litterfall.

8) The average total kg/hectare of nutrient return in litterfall was N 26.7, P 4.6, K 7.5, Ca 49.9, and Mg 3.8. The greatest portion, 63% of the nutrient return, came through needle litterfall. Together, the needle, cone, and twig litterfall accounted for 84% of the total nutrient input through litterfall.

9) By examining the total nutrient return in throughfall and litterfall, a turnover progression of Ca > N > K > P > Mg was evident in this particular ecosystem.

10) Fall litterfall samples can be consolidated into one sample

for chemical analysis if the analytical sample is proportional to the total amount that fell during any one period of time. Frequent sampling is suggested during the winter months. Winter samples should not be consolidated for analytical purposes if data describing seasonal variability in nutrient concentration and nutrient return is desired.

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