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Nutrient content of canopy throughfall in three Minnesota forests

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Calcium, magnesium, nitrogen and phosphorus were measured in throughfall of an oak, marginal fen, and white cedar swamp forest in east-central Minnesota, U.S.A. Annual totals of calcium in throughfall of the oak, fen and swamp forest were 7.6, 10.5, and 10.7 kg/ha respectively. Totals for magnesium were 3.1, 3.8 and 3.7; for ammonia and organic-nitrogen, 5.5, 5.5, and 6.0; and for phosphorus, 0.7, 0.6, and 0.5 kg/ha. These totals were comparable with data in the literature. Calcium depositions in throughfall as per cents of the sum of throughfall and litter fall were 13, 10, and 10 per cent in the oak, fen and swamp forests respectively. Similar percentages for magnesium were 23, 22, and 23; for nitrogen, 11, 10, and 12; and for phosphorus, 11, 8, and 7.

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Определяли содержание кальция, магния, азота и фосфора в лесном опаде в дубовом лесу, на болоте и в заболоченном кедровом лесу, на востоке центральной Миннесоты (США). Годичное содержание кальция в исследованных учатках составляло соответственно 7,6, 10,5 и 10,7кг/га. Количество магния – 3,1, 3,8 и 3,7; количество аммония и органического азота – 5,5, 5,5 и 6,0 и фосфора – 0,7, 0,6 и 0,5кг/га. Полученные результаты согласуются с имеющимися литературными данными.
Содержание кальция в десном опаде в процентах от суммы опада и листовой подстилки составляло 13, 10 и 10% в указанных местообитаниях. Процентное содержание магния – 23, 22 и 23%, азота – 11, 10 и 12% и фосфора – 11, 8 и 7%

Manuscript accepted February 1971

1. Introduction

Element deposition from the atmosphere in rainfall and dry fallout has been studied for many years as an aspect of geochemistry (Junge 1963, Gorham 1961), an aspect of growing concern with the dispersion of exotic airborne materials such as DDT, mercury, lead and radioactive particles. Atmospheric deposition is also receiving increasing attention as an input of ecosystem nutrient budgets. Studies by Nye (1961), Carlisle et al. (1966), Cole et al. (1967), Likens et al. (1967), Juang and Johnson (1967), Chapman (1967), and Fisher et al. (1968) indicate the importance and variability of such nutrient input into various ecosystems.

Nutrients deposited on foliar surfaces through rainfall or dry fallout may be carried downward in throughfall, or may be adsorbed or absorbed by plants (Carlisle et al. 1966). Nutrients may also be leached from foliar surfaces by precipitation (Stenlid 1958) and together with atmospheric input, deposited as enriched solutions of throughfall on forest floors (Tamm 1953). Canopy throughfall therefore represents an important nutrient pathway in terrestrial ecosystems, combining input of new nutrients with the cycling of old nutrients which had been carried up to the crowns to be subsequently leached down. Carlisle et al. (1966) showed that throughfall represented 42 per cent of the calcium, 71 per cent of the magnesium, 18 per cent of the nitrogen, and 37 per cent of the phosphorus in the combined pathways of litter fall and throughfall in a British oak woodland.

The objectives of this study were 1) to estimate the atmospheric contribution of calcium, magnesium, nitrogen and phosphorus in combined precipitation and dry fallout, and 2) to compare the flux of these four elements as throughfall in three Minnesota forests.

The three forests studied are located in Cedar Creek Natural History Area in east-central Minnesota (Fig. 1). They lie along a topographic gradient extending from a sandy upland peninsula down into a peat-filled basin (see Lindeman (1941) for a general description of this area). Northern pin oak *Quercus ellipsoidalis* E. J. Hill dominates the upland portion of the gradient and white cedar *Thuja occidentalis* L. dominates the basin forest. Between these is a transitional forest termed a marginal fen including black ash *Fraxinus nigra* Marsh, red maple *Acer rubrum* L., American elm *Ulmus americana* L. and others. The sites and forests are described in more detail in Reiners and Anderson (1968), Reiners (1968), and Reiners and Reiners (1970).

2. Methods

2.1. Sampling procedure

Rainwater and dry fallout (termed bulk precipitation after Whitehead and Feth 1964) and throughfall samples were collected monthly from September 1967 through August 1968. During the months of December through March, bulk precipitation (primarily snow) and throughfall were collected in polyethylene buckets, 24.1 cm in diameter. In the other months, collectors similar to those of Carlisle et al. (1966) were used. These consisted of 4.2 liter polyethylene bottles with funnels fixed in

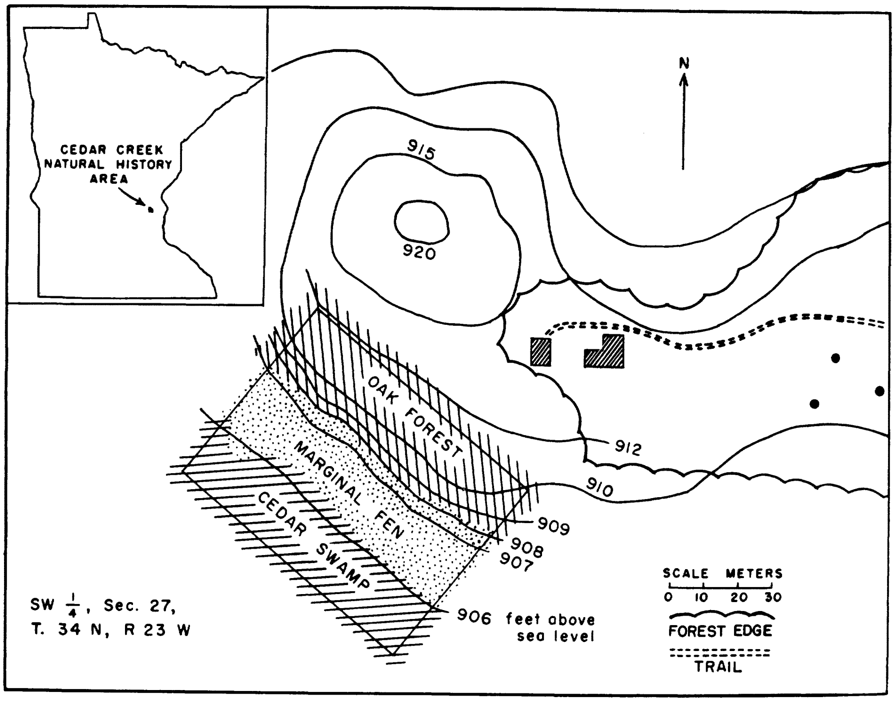

Fig. 1. Map of the study area located in Cedar Creek Natural History Area, Anoka Co., Minnesota. The three forests were sampled within the delimited zones along the topographic gradient. Solid circles indicate locations of the bulk precipitation collectors.

the mouths. The funnels used to collect bulk precipitation were 12.0 cm in diameter and those used to collect throughfall were 20.0 cm in diameter. The funnels were covered with 0.25 mm mesh nylon filters to prevent entry of macroscopic litter and invertebrates, and the bottles were iodine-treated as described by Heron (1962) to prevent surface fixation of nitrogen and phosphorus by microorganisms.

Three bulk precipitation collectors were located in an open, abandoned field 100 m NE of the throughfall collectors (Fig. 1). Eight throughfall collectors were placed in each of the three forests in stratified-random fashion. The collectors were checked and the nylon filters were cleaned of macroscopic debris with a nylon brush weekly. With three exceptions, the collectors were picked up for processing at the end of each month. Collectors were not processed in November or February as they were dry due to low precipitation; collectors were picked up twice in June because heavy precipitation would have overflowed the collectors.

Nutrient deposition in bulk precipitation and throughfall were estimated on the basis of the nutrient concentration and volume in each collecting vessel. Incident precipitation was also measured with a standard rain gauge, for correlative purposes, at a site approximately 400 m SE of the study area.

2.2. Sample processing

At the end of each collection period, sample volumes were measured, thoroughly shaken, 250 ml aliquots removed, and the balance of volumes of the samples measured. The aliquots were treated with 2 cc concentrated H_2SO_4 and boiled down to approximately 100 ml. These concentrated samples were sealed in plastic bottles and shipped to Hanover, New Hampshire, where they were frozen until analyzed. The collection bottles and filters were washed in tap water, then rinsed with deionized water, and returned to the field.

Tab. 1. Incident precipitation (cm) and calcium, magnesium, nitrogen and phosphorus deposited by throughfall in three forests (kg/ha). Throughfall data are means of eight replicates and standard errors are given in parentheses. Significant differences between forests in throughfall deposition are denoted by: (a) oak-fen, (b) fen-swamp, (c) oak-swamp.

Month	Incident Precipitation	Forest	Calcium	Magnesium	Nitrogen	Phosphorus
Jan.	1.68	oak	0.31 (0.02)	0.11 (0.004)	0.20 (0.01)	0.03 (0.009)
1968		fen	0.40 (0.03)	0.16 (0.02)	0.21 (0.03)	0.02 (0.01)
		swamp	0.46 (0.04) (c)	0.16 (0.02)	0.19 (0.03)	0.01 (0.002)
Feb.	0.56		n.a.	n.a.	n.a.	n.a.
March	4.95	oak	0.77 (0.07)	0.41 (0.03)	0.70 (0.08)	0.10 (0.03)
		fen	1.78 (1.87)	0.55 (0.46)	0.92 (0.14)	0.06 (0.02)
		swamp	1.63 (0.34)	0.57 (0.09)	1.20 (0.24)	0.04 (0.01)
April	10.16	oak	1.18 (0.16)	0.35 (0.05)	0.64 (0.07)	0.02 (0.005)
		fen	1.39 (0.29)	0.36 (0.05)	0.63 (0.05)	0.03 (0.008)
		swamp	1.92 (0.36)	0.46 (0.08)	0.85 (0.10)	0.02 (0.005)
May	8.97	oak	0.86 (0.04)	0.44 (0.10)	0.58 (0.10)	0.08 (0.03)
		fen	1.20 (0.20)	0.36 (0.04)	0.46 (0.07)	0.05 (0.03)
		swamp	1.37 (0.09) (c)	0.38 (0.03)	0.52 (0.05)	0.02 (0.004)
June	18.72	oak	1.49 (0.10)	0.57 (0.05) (a)	0.98 (0.14)	0.10 (0.02)
		fen	1.84 (0.15) (b)	0.74 (0.05) (b)	1.09 (0.07)	0.10 (0.02)
		swamp	1.42 (0.12)	0.51 (0.04)	0.82 (0.10)	0.06 (0.007)
July	5.94	oak	0.96 (0.05) (a)	0.33 (0.03)	0.74 (0.04)	0.06 (0.005)
		fen	1.26 (0.11)	0.43 (0.04)	0.60 (0.10)	0.07 (0.008)
		swamp	1.28 (0.09) (c)	0.45 (0.11)	0.61 (0.09)	0.07 (0.006)
August	4.55	oak	0.45 (0.02) (a)	0.17 (0.01)	0.42 (0.04)	0.03 (0.007)
		fen	0.66 (0.10)	0.22 (0.02)	0.43 (0.05)	0.04 (0.01)
		swamp	0.49 (0.05)	0.28 (0.07)	0.45 (0.10)	0.04 (0.01)
Sept.	1.78	oak	0.67 (0.16)	0.29 (0.03)	0.46 (0.03)	0.06 (0.003)
1967		fen	1.03 (0.95)	0.59 (0.23)	0.48 (0.05)	0.08 (0.02)
		swamp	0.78 (0.08)	0.35 (0.04)	0.48 (0.02)	0.08 (0.01)
Oct.	3.43	oak	0.65 (0.05)	0.29 (0.01)	0.60 (0.04)	0.12 (0.02)
		fen	0.70 (0.31)	0.29 (0.10)	0.47 (0.05) (b)	0.11 (0.04)
		swamp	0.94 (0.09)	0.40 (0.10)	0.66 (0.05)	0.14 (0.02)
Nov.	0		n.a.	n.a.	n.a.	n.a.
Dec.	1.65	oak	0.24 (0.04)	0.10 (0.02)	0.22 (0.04)	0.06 (0.01) (a)
		fen	0.26 (0.14)	0.08 (0.03)	0.21 (0.04)	0.02 (0.006)
		swamp	0.40 (0.07)	0.12 (0.02)	0.27 (0.05)	0.03 (0.005)
Total	62.39	oak	7.59 (0.36) (a)	3.07 (0.22)	5.54 (0.29)	0.66 (0.07)
for year		fen	10.52 (1.39)	3.78 (0.34)	5.49 (0.43)	0.59 (0.11)
		swamp	10.69 (0.64) (c)	3.68 (0.30)	6.05 (0.42)	0.51 (0.05)

n. a. = not analyzed

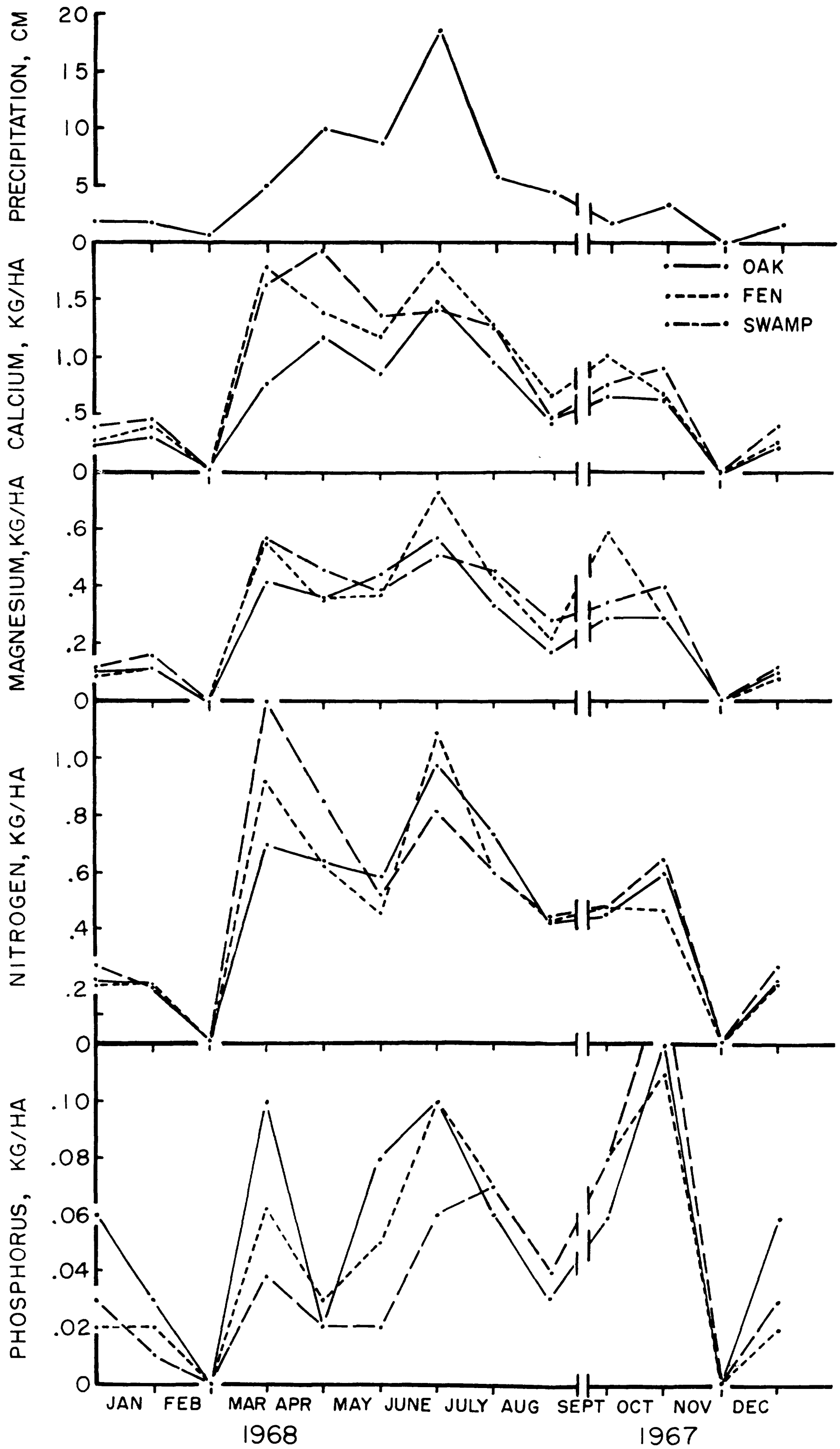

Fig. 2. Gross precipitation and deposition of nutrients via throughfall in the three forest types from September 1967 through August 1968.

2.3. Chemical methods

2.3.1. Calcium and magnesium

Aliquots of the concentrated samples were treated with 5 ml of 30 per cent H_2O_2 for four days over a low temperature sandbath to oxidize organic compounds. These treated samples were analyzed on a Perkin Elmer Model 303 Atomic Absorption Spectrophotometer. Appropriate amounts of La_2O_3 and HCl were added to prevent interferences (Likens et al. 1967).

2.3.2. Nitrogen

Ammonia- and organic-nitrogen were analyzed by Kjeldahl extraction and Nessler colorimetry (Rainwater and Thatcher 1960: 223). Colorimetry was performed with a Spectronic 20 Spectrophotometer.

Nitrate-nitrogen was not analyzed as much of it was probably driven off as HNO_3 while boiling during the concentration process. Furthermore, sample coloration caused by iodine treatment of the collection bottles interfered with the preferred method of nitrate analysis.

2.3.3. Phosphorus

Twenty ml sample aliquots were diluted with 20 ml 0.1 N HCL, and 4 ml 70 per cent $HClO_4$ were added to digest organic matter. A color complex was generated with ammonium molybdate and 1,2,4-aminonapthol-sulfonic acid. Colorimetry was performed with a Spectronic 20 Spectrophotometer.

2.4. Statistical methods

The variances of throughfall samples were calculated with estimates of covariance between concentrations and volumes. Tests for significant differences between forests were made at the 0.90 confidence level with Scheffé's range test (Scheffé 1959). Regression analyses of relationships between gross precipitation and nutrient deposition via throughfall were performed by standard methods (Steel and Torrie 1960) and levels of tests of significance are given in Tab. 2.

3. Results and discussion

3.1. Bulk precipitation

Annual nutrient totals for bulk precipitation were comparable with values for similar continental environments. However, they were considerably higher than the nutrient totals of throughfall collected concurrently in the adjacent forests. While precipitation waters are diluted to some extent in some elements as they pass through tree crowns (Miller 1963, Carlisle et al. 1966), the net change is generally toward enrichment. As a result, I was forced to the conclusion that the bulk precipitation samples were contaminated, possibly by road dust and/or grass pollen. These data were therefore discarded.

3.2. Throughfall

Variation in throughfall is a function of nutrient input by bulk precipitation, leaching potential by the volume of precipitation, and the state of the vegetation. Although bulk precipitation collections seemed to be contaminated, the data did show a correlation between bulk precipitation and incident precipitation. It was useful, therefore, to compare throughfall data with incident precipitation because of the correlation of the latter with atmospheric deposition as well as the leaching potential of rainfall. A graph of monthly precipitation totals which were collected by the standard raingauge is included in Fig. 2, and regression statistics for nutrient fluxes in throughfall as functions of precipitation are provided in Tab. 2.

3.2.1. Calcium

Calcium flux in throughfall correlated with precipitation rather well, particularly in the oak forest (Tab. 1, Fig. 2). Slopes for the calcium regression of all three forests were essentially identical but intercepts increased in the order oak, fen and swamp, indicating generally higher fluxes of calcium in throughfall of the wetland forests (Tab. 2). In fact, throughfall calcium was significantly higher in the fen and swamp than in the oak forest in individual months and in the annual total (Tab. 1). Such differences might be expected on the basis of mass of calcium available in the tree canopy. Total weights of calcium in summer tree canopies of the oak, fen, and swamp forests respectively, were 27, 71, and 143 kg/ha (unpublished data).

A distinct pattern of diminishing correlations between precipitation and throughfall in the same rank order of oak, fen, and swamp forests was revealed in Tab. 2. Confidence levels for regression slopes and standard errors increased while correlation coefficients and F-ratios decreased from upland to lowland forests. This pattern reflected marked deviations of fen and swamp throughfall from precipitation in the spring and autumn.

These deviations may have had several causes. Inspection of raw March data revealed unusually high concentrations of calcium in one fen collector and two swamp collectors. Open buckets were used as collectors in March and unusual contaminants such as bark fragments were recorded for that month. These may have led to aberrant concentrations in these three collectors. If mean concentrations from the other collectors in the same forest are substituted for these three aberrant collectors, total March calcium throughfall in the fen is 1.14 rather than 1.78 kg/ha, and in the swamp is 1.36 rather than 1.63 kg/ha. These adjusted values bring the throughfall graph for calcium into better accordance with the precipitation graph (Fig. 2) but values still are relatively high in March. It is possible that March rains washed down large amounts of dry fallout which had accumulated in the canopy over the winter when the predominant form of precipitation was snow. Furthermore, such accumulation might have been exaggerated in the fen and swamp in which cedar foliage may have been more efficient at capturing dry fallout than the leafless branches of deciduous trees.

Tab. 2. Linear regression statistics for relationships between monthly deposition of nutrients in throughfall as functions of monthly precipitation. Confidence limits for slopes are calculated at the 0.95 confidence level.

Forest	Y-intercept	slope	correlation coefficient	standard error of estimate	F-ratio for slope
		Calcium			
Oak	0.35	0.06 ± 0.008	0.90	0.18	34.36**
Fen	0.59	0.07 ± 0.018	0.73	0.39	9.10*
Swamp	0.67	0.06 ± 0.020	0.64	0.43	5.52*
		Magnesium			
Oak	0.16	0.02 ± 0.004	0.82	0.09	17.02**
Fen	0.23	0.02 ± 0.008	0.62	0.17	5.08
Swamp	0.27	0.02 ± 0.006	0.59	0.12	4.32
		Nitrogen			
Oak	0.33	0.04 ± 0.007	0.80	0.15	14.66**
Fen	0.30	0.04 ± 0.009	0.76	0.19	11.14*
Swamp	0.44	0.03 ± 0.013	0.48	0.28	2.33
		Phosphorus			
Oak	0.06	0.001 ± 0.002	0.23	0.03	0.44
Fen	0.04	0.002 ± 0.001	0.34	0.03	1.06
Swamp	0.05	−0.0006 ± 0.002	−0.09	0.04	0.06

* significant at the 0.95 confidence level.
** significant at the 0.99 confidence level.

The high March values may also have been enhanced by the accumulation of evaporate deposited in the collectors from the slight precipitation and dry fallout of February which was added to March totals. Such an effect would not explain the marked differences between forests, however.

Unexpectedly high levels of calcium throughfall in all three forests in September and October may have been caused by senescence and higher leaching rates (Miller 1963).

Total depositions of calcium by throughfall for all three forests were low to intermediate in comparison with other data in the literature (Tab. 3).

3.2.2. Magnesium

The patterns of magnesium deposition were very similar to those of calcium (Tab. 1, Fig. 2). Regression intercepts (Tab. 2) again reflected higher deposition in the fen and swamp than oak forest but differences were not significant except in the month of June. The mass of magnesium held in summer tree foliage of the oak, fen and swamp forests respectively was 8, 15 and 22 kg/ha (unpublished data) which paralleled differences in throughfall. Annual totals in throughfall were low in comparison with other studies (Tab. 3).

Only the oak forest regression was significant (Tab. 2) and correlation coefficients, confidence limits, and standard errors all indicated poorer relationships between magnesium throughfall and precipitation than was the case with calcium. As with calcium, the relationship between magnesium throughfall and precipitation became poorer through the rank order of oak, fen and swamp.

Deviations from a correlation between throughfall and precipitation were greatest in March, September and October (Fig. 2), probably for the same reasons described for calcium. By applying similar adjustments to March data as described for calcium, the March high was reduced only slightly. Magnesium throughfall in the fen was reduced from 0.55 to 0.40 kg/ha, and in the swamp from 0.57 to 0.50 kg/ha. The especially high peak for the fen in September may have been caused by earlier leaf senescence and consequent leaching. Leaves drop nearly a month earlier in the fen than in the other two forests (Reiners and Reiners 1970) and autumn leaf senescence may have been earlier as well. The same phenomenon is also suggested in the calcium throughfall graph but not in the graphs for nitrogen and phosphorus.

3.2.3. Nitrogen

Patterns of nitrogen deposition in throughfall were also similar to those described for calcium but there were few differences between forests. Slopes and intercepts of the regressions were similar among forests and regression lines actually crossed (Tab. 2). Total nitrogen throughfall was highest in the swamp, due principally to the very high March total. The fen and oak totals were virtually identical. Only one significant difference between forests was found throughout the year: nitrogen in swamp throughfall was greater than that of fen in October. Masses of nitrogen in the summer foliage of

Tab. 3. Nutrient deposition by throughfall in kg/ha/yr in this and comparable studies.

Location	Reference	Ca	Mg	N	P
Minnesota, USA	present study[1]				
oak forest		7.6	3.1	5.5	0.7
marginal fen		10.5	3.8	5.5	0.6
cedar swamp		10.7	3.7	6.0	0.5
Washington, USA	Cole et al. 1967[2]	4.3	–	2.6	0.3
New Zealand	Will 1959[3]				
Pinus radiata D. Don site B		4.8	–	–	0.6
Pinus radiata site C		3.1	–	–	1.2
Pseudotsuga taxifolia (Poir) Britt.		5.6	–	–	4.6
Skåne, Sweden	Nihlgård 1970				
Fagus sylvatica L.		9.0	3.0	8.5	0.1
Picea abies L.		14.7	5.2	21.5	0.4
New Zealand	Miller 1963[4]	13.4	13.4	3.3	0.6
Lancashire, UK	Carlisle et al. 1966	17.2	9.4	8.8	1.3
Southeastern England	Madgwick and Ovington 1959[3]	24.2	9.5	–	–
Kade, Ghana	Nye 1961	41.6	29.1	26.4	4.1

[1] ammonia- and organic – N only
[2] leachate from canopy plus litter in collecting screens
[3] samples filtered during collection and before analysis
[4] samples filtered before analysis

the oak, fen and swamp forests, respectively, were 70, 56, and 90 kg/ha.

Although NO_3^--N was not analyzed, total nitrogen in throughfall was intermediate among the comparative totals in Tab. 3. Some measure of the underestimate resulting from this procedure can be drawn from the nata of Carlisle et al. (1966). Forty-three per cent of oitrogen throughfall in their oak woodland was in-drganic (NH_4^+, NO_3^-, NO_2^-). The proportion of this which was NO_3-N was not published, but approximately 35 per cent of nitrogen in incident rainfall in western Britain is NO_3–N (S. E. Allen, pers. comm.), and since trees not only absorbed inorganic nitrogen in the Carlisle et al. study, but also are unlikely to contribute NO_3-N to throughfall, throughfall nitrogen is likely to be less than 15 per cent of the total. On the basis that throughfall of this study is similar to that of the forest studied by Carlisle et al., the underestimate resulting from failing to conserve or analyze NO_3-N is probably less than 15 per cent.

As with calcium and magnesium, the correlations between nitrogen throughfall and precipitation declined through the rank order of oak, fen and swamp forests. Linear regressions were significant in the oak and fen forests but not in the swamp.

Deviations from such a relationship occurred, again, primarily in the spring and autumn. By applying adjustments for March data as described for calcium, the March spike was reduced from 1.2 to 1.09 kg/ha in the swamp but was actually raised slightly in the fen. The March spike was most prominent in the swamp, due perhaps to the influence of *Thuja occidentalis*, an evergreen species. These evergreen crowns may be comparatively susceptible to nitrogen leaching in the leafless season, or they may be aerodynamically superior in capturing dry fallout, a particularly important factor in March when heavy silt deposits were found in all collectors. Presumbly, the same factors described for calcium contributed to high nitrogen content of throughfall in autumn.

3.2.4. *Phosphorus*

Phosphorus deposition in throughfall was the most unique of the four elements studied. There were no significant correlations between phosphorus in throughfall and precipitation (Tab. 2). There was only one significant difference in phosphorus throughfall between forests during any sampling period and none among the totals, but the oak forests showed higher mean values than the other forests. This was the only element among the four for which this was true. Total values for all forests were intermediate among the comparisons in Tab. 3.

As with the other nutrients, the March spike in phosphorus was probably caused by factors discussed above. Unlike the other nutrients, however, the highest March spike was in the oak forest rather than the fen or swamp. Adjustment of March values for contamination in the fen and swamp reduced March values only slightly: from 0.062 to 0.059 kg/ha in the fen, and from 0.039 to 0.031 kg/ha in the swamp.

Phosphorus was also unusual among the elements studied in having the highest amount of deposition in October rather than March or June. Variations for phosphorus collections were not unusually high in October, thereby supporting the reality of this spike, but except for the possibility of unusually high rates of leaching, the cause is unknown.

3.3. Comparisons between forests

Two patterns emerged in comparisons between the three forests with respect to nutrient fluxes in throughfall. First, except for calcium, there were no significant differences between forests in total deposition. This was somewhat surprising in view of the evident contrasts in physiognomy, species composition, and site characteristics of the forests. More significant differences might have appeared had more numerous collectors been used and variation of means reduced, but similarities in total nutrient deposition by throughfall in elements other than calcium might be real and expected. Whereas there was a 5.3-fold difference in calcium held in oak versus swamp summer foliage, the difference was only 2.7-fold for magnesium, and only 1.3-fold for nitrogen. Thus the amounts of magnesium and nitrogen available for foliar leaching were more similar among the three forests. The absence of significant differences between phosphorus throughfall may be attributed to both high variations compared with means, and to very small differences in summer foliage phosphorus content: 7, 6 and 10 kg/ha for oak, fen and swamp forests respectively (unpublished data).

The second major pattern arising from comparison of the three forests was a systematic decline (excluding phosphorus) in correlations between nutrient flux via throughfall and incident precipitation (Tab. 2). The decline in correlation coefficients and associated statistics followed the order of oak, fen and swamp forests. This pattern may be attributed, in large part, to the proportion of deciduous tree foliage in each forest. In Minnesota, most of the annual precipitation falls during the growing season (Fig. 2) when deciduous trees display their foliage. Deciduous foliage accounted for 100, 61 and 27 per cent of tree foliage mass in the oak, fen and swamp forests (unpublished data). Thus, deciduous tree foliage, most prominent in the oak forest and least prominent in the swamp, was exposed to leaching by precipitation during those months in which precipitation was concentrated. Such synchrony could contribute to higher correlations of nutrient flux in throughfall with incident precipitation. On the other hand, to the extent that evergreen *Thuja* occurred, it diminished correlations by trapping dry fallout, and by providing leachates during the low precipitation months when deciduous trees were leafless.

3.4. Comparison of throughfall with litter fall

The return of nutrients from aerial portions of plants to the detritus pool may follow several pathways including litter fall, stem-flow, and leaching loss in throughfall. Stem-flow was not measured in this study because of the many species involved, and because stem-flow is probably a minor component of the total flux of nutrients from shoots to the ground. The amount of incident precipitation reaching the ground as stem-flow varies widely among species and between storms. The range of stem-flow as a percentage of incident precipitation under conifers is from 0.7 to 6.7 on an annual basis (Rothacher 1963, Kittredge et al. 1941, Delfs 1967, Nihlgård 1970). Among American hardwoods, stem-flow as a percentage of incident precipitation ranges from 0.5 to 8.7 (Helvey and Patric 1965). Stem-flow waters are relatively rich in nutrients, however, so nutrient fluxes by this pathway are more important than hydrological data indicate. Tree stem-flow as a percentage of combined nutrient flux by stem-flow and throughfall have been estimated by Carlisle et al. (1967) in a British oak woodland, and by Nihlgård (1970) in Swedish beech and spruce forests. These percentages, in the order calcium, magnesium, nitrogen and phosphorus, were 9.6, 5.8, 1.4 and 1.2 in the oak woodland; 10.9, 11.5, 4.5, and 9.1 in the beech forest; and, 15.5, 14.6, 10.8 and 14.2 in the spruce forest. According to these data, the elimination of stem-flow data in this study leads to an underestimate of nutrient flux by rainwashing of the order of 10 per cent for all of these elements.

Stem-flow may be even less important than estimated

Tab. 4. Comparisons of the relative importance of throughfall and litter fall in the return of nutrients to forest floors of three forests, and recalculated turnover times for forest floors with the addition of throughfall deposition.

Element	Forest	$\overline{X}$ pool in forest floor (kgm/ha) (A)	Litter fall Total (kgm/ha) (B)	Litter fall % of total flux	Turnover time (years) (A/B)	Throughfall Total (kgm/ha) (C)	Throughfall % of total flux	Total flux (kgm/ha) (B + C)	Turnover time (years) (A/(B + C))
calcium	oak	485.3	50.5	86.9	9.6	7.6	13.1	58.2	8.3
	fen	8366.8	90.8	89.7	92.2	10.5	10.3	101.5	82.4
	swamp	28863.4	92.4	89.6	312.4	10.7	10.4	103.3	279.4
magnesium	oak	103.2	10.3	77.0	10.0	3.1	23.0	13.5	7.6
	fen	988.0	12.9	77.6	76.1	3.8	22.4	17.0	57.9
	swamp	1793.3	12.7	77.4	141.2	3.7	22.6	16.4	109.3
nitrogen	oak	1728.1	44.6	89.0	38.7	5.5	11.0	50.1	34.5
	fen	8591.4	48.6	89.8	176.9	5.5	10.1	54.2	158.5
	swamp	21949.0	43.6	87.9	503.1	6.0	12.1	49.5	443.4
phosphorus	oak	154.1	5.6	88.7	27.4	0.7	11.3	6.2	24.8
	fen	710.4	6.6	92.0	108.2	0.6	8.0	7.5	94.7
	swamp	1207.2	6.2	92.8	193.8	0.5	7.2	6.9	175.0

above in terms of nutrient flux to forest floors because a large proportion flows deep into the soil along root channels rather than on to the surface of the forest floor (Voigt 1960).

Reiners and Reiners (1970) described litter fall and forest floor nutrient pools for the forests of this study, and by dividing average standing states by inputs via litter deposition, calculated average residence times, or "turnover times" for the detritus pools. Because throughfall also enters the forest floor, it may be summed with litter fall and revised turnover times calculated (Tab. 4).

The addition of throughfall to this combined input was most important in the case of magnesium in which about 22 per cent was contributed by throughfall. Calcium, nitrogen and phosphorus throughfall all ranged around 10 per cent of combined input. These values are considerably lower than the values of 42, 71, 18 and 37 per cent of calcium, magnesium, nitrogen and phosphorus reported in the Carlisle et al. (1966) study of an oak woodland. In this present study, throughfall contribution to total flux usually was greatest under the oak canopy; contributions in the fen and swamp were less and virtually equal to each other.

The addition of throughfall to litter flux reduced turnover times in proportion to the amount added to the total by throughfall. Thus, turnover times of calcium were reduced by about 10 per cent, of magnesium by 22 per cent, of nitrogen by 11 per cent and of phosphorus by about 9 per cent. Based on the literature reviewed above, the addition of stem-flow waters would reduce these turnover times further by one to two per cent.

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