posed to *C. fulgens*, which is soil borne (2, 7). Why white pine, ponderosa pine, and amabilis fir seeds were not diseased is unknown.

The chi-square test results (Table 2) showed that all seed lots, and especially those of spruce, originating from squirrel-cache cone collections had a significantly higher incidence of *C. fulgens*. This is probably because the cool, moist conditions within caches, especially older ones, are ideal for *C. fulgens* spread (4). Since squirrels frequently cache repeatedly in the same locality, the fungus may be perpetual within caches. Overall, significantly fewer *C. fulgens* infested seed lots originated from slash-picked cones than from cones from other sources. This is expected because fewer slash-picked cones contact the ground, and then only briefly.

The Mann–Whitney U test results showed that the percentage of infected seeds, within fungus-infested seed lots, was significantly ($P = 0.05$) higher in partial squirrel-cache than in squirrel-cache cone collections of white × Engelmann spruce (see Table 2 for numbers of cone collections in each category) and also higher in partial squirrel-caches than in slash-picked cone collections of white × Engelmann spruce, total (all *Picea* spp.) spruce and all species (total spruce plus Douglas-fir plus grand fir). Since these differences do not follow any logical pattern, it is concluded that the percentage of diseased seeds within infested seed lots is unrelated to the origin of ground-collected cones.

1. DOBBS, R. C., D. G. W. EDWARDS, J. KONISHI, and D. WALLINGER. 1976. Guideline to collecting cones of B.C. conifers. B.C. For. Serv. – Can. For. Serv. Jt. Rep. No. 3.
2. PADEN, J. W., J. R. SUTHERLAND, and T. A. D. WOODS. *Caloscypha fulgens* (Ascomycetidae, Pezizales): the perfect state of the conifer seed pathogen *Geniculodendron pyriforme* (Deuteromycotina, Hyphomycetes). Can. J. Bot. **56**: 2375–2379.
3. SALT, G. A. 1970. Conifer seedling pathology. *In* Report on Forest Research for the year ended March, 1970 For. Comm. Her Majesty's Stationery Office, London. pp. 174–175.
4. SALT, G. A. 1974. Etiology and morphology of *Geniculodendron pyriforme* gen. et sp. nov., a pathogen of conifer seeds. Trans. Br. Mycol. Soc. **63**: 339–351.
5. SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
6. SNEDECOR, G. W. 1956. Statistical methods. 5th ed. Iowa State University Press, Ames, IA. p. 228.
7. SUTHERLAND, J. R., and T. A. D. WOODS. 1978. The fungus *Geniculodendron pyriforme* in stored Sitka spruce seeds: effects of seed extraction and cone collection methods on disease incidence. Phytopathology, **68**: 747–750.

# Decomposition and nutrient release in Douglas-fir needle litter in relation to stand development

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Decomposition rates and changes in the nutrient content of needle litter were examined in an age sequence of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in western Washington. The stands at the initiation of the study were 11, 24, 44, 75, and 97 years old. Nylon litter bags (1 mm mesh) containing needles from the 44-year-old stand were placed in the stands in February 1975. Bags were collected after 3, 6, 12, and 24 months, weighed, and analyzed for N, P, K, Ca, Mg, Mn, and lignin. Decomposition constants ($k$ values) were determined. After 2 years, maximum decomposition rate occurred in the 24-year-old stand, where temperature and moisture conditions were most favorable. Low litter moisture tended to inhibit decomposition in summer. Values of $k$ determined from 1-year weight loss data and percent needle lignin after 2 years were significantly different between stands. Values of $k$ determined from weight loss were greater than those determined from litter fall weight : forest floor weight ratios. Loss of elements from litter bags after 2 years was in the following sequence in all stands, N < Mn < Ca < Mg < P < K. Annual stand net productivity was strongly correlated to N + K loss from litter bags ($r = 0.96$).

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EDMONDS, R. L. 1979. Decomposition and nutrient release in Douglas-fir needle litter in relation to stand development. Can. J. For. Res. 9: 132–140.

L'auteur a étudié le taux de décomposition et le changement de la teneur en éléments de la litière de feuilles dans des peuplements d'âges progressifs de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco), dans l'ouest de l'Etat de Washington. Les peuplements étaient âgés, au début de l'expérience, de 11, 24, 44, 75 et 97 ans. Des sachets de nylon (grillage de 1 mm) contenant des aiguilles du peuplement de 44 ans furent placés dans les peuplements en février 1975. Les sachets furent recueillis après 3, 6, 12 et 24 mois, pesés, et analysés pour N, P, K, Ca, Mg, Mn et la lignine. L'auteur a pu ainsi mesurer les constantes de décomposition (valeurs de $k$). Après 2 ans, le taux maximum de décomposition fut observé dans le peuplement de 24 ans où les conditions de température et d'humidité étaient plus favorables. La faible humidité de la litière en été défavorisait sa décomposition. Les valeurs de $k$ mesurées à partir des pertes de poids après 1 an, et de la teneur en lignine après 2 ans, différaient d'une façon significative entre les peuplements. Les valeurs de $k$ déterminées à partir des pertes de poids étaient plus élevées que celles obtenues du ratio masse des aiguilles tombées : masse de la couverture d'humus. Les pertes d'éléments mesurées après 2 ans se présentaient dans l'ordre suivant: N < Mn < Ca < Mg < P < K. La productivité annuelle nette des peuplements étaient fortement corrélée aux pertes de N + K des sachets ($r$ = 0.96).

[Traduit par le journal]

## Introduction

Many studies have been conducted on the decomposition of tree litter and the subsequent release of nutrients (Attiwell 1968; Bocock 1963; Hayes 1965; Howard and Howard 1974; Gosz et al. 1973; Will 1967), but few attempts have been made to relate litter decomposition rates to stand development or age. Turner and Long (1975), however, indicate that rates of litter decomposition, as well as stand net annual productivity, are not constant as stands develop. In addition, Van Cleve and Noonan (1975) indicate that forest floor nutrient turnover rates also change as stands age.

This study was initiated to examine relationships between litter decomposition, nutrient release, and productivity in an age sequence of Douglas-fir stands. The specific objectives of the study were to (1) determine decomposition rates of Douglas-fir needles in a series of stands ranging in age from 11 to 97 years in relation to environmental variables, (2) examine seasonal patterns of decomposition, (3) determine patterns of release of N, P, K, Mg, Mn, and Ca, and (4) relate stand productivity to litter decomposition rates and to changes in nutrient content of litter in litter bags.

## Materials and Methods

### *Site Description*

The study was conducted in and around the A. E. Thompson Research Center of the College of Forest Resources, University of Washington, which is located approximately 50 km west of Seattle in the City of Seattle's Cedar River Watershed, Washington, U.S.A. The mean annual rainfall is 144 cm with a winter maximum. Summers are dry. Mean annual air temperature is 9.4°C.

Overstory vegetation is primarily Douglas-fir with an understory dominated by salal (*Gaultheria shallon* Pursh.). The gravelly glacial outwash soil is of the Everett series (Typic Haplorthod, U.S. Soil Classification System). One square (0.045 ha) plot was set up in each of five stands as described by Turner and Long (1975) and Turner (1975). Four of the five stands selected were naturally regenerated after fires and at the initiation of the study were 24, 44, 75, and 97 years old. The fifth stand, which was 11 years old at the initiation of the study, was a plantation in which the forest floor had not been burnt. The stands were site quality IV (King 1966). Stand density ranged from 644 to 2756 stems/ha with a general trend toward decreasing densities in the older stands. All stands were located at an elevation of approximately 210 m on generally level terrain.

### *Needle Litter Decomposition*

Litter bags measuring 25.4 × 17.8 cm (0.045 $m^2$) with a mesh size of 1.0 mm (Nylon Net Co., Tennessee) were constructed. In the late fall and winter of 1974 canvas sheets were placed in the 44-year-old stand and needle litter fall was collected. Needles were then air dried. Ovendry weight (48 h at 75°C) was determined on a subsample. The equivalent of 10 g ovendry weight of needles was placed in each litter bag. A 3 × 3 m area was laid out in each plot and 20 litter bags were placed in a randomized block design within this area on February 14, 1975. Five replicate bags were sampled at each collection time (3, 6, 12, and 24 months). The needles were dried at 75°C for 48 h and weight loss was determined. An examination of the needle litter fall from each stand revealed that the quality of needles varied little from stand to stand. Average needle litter N concentration in the stands was 0.89% with a range from 0.7 to 1.1% (Turner 1975).

### *Chemical Analyses*

Three of the five replicate bags collected at each sample time were randomly selected for chemical analyses. Needles were ground in a Wiley mill to pass through a No. 20 stainless-steel mesh and analyzed for C, N, P, K, Ca, Mg, and Mn. Ground litter was digested using the wet oxidation method (Parkinson and Allen 1975). Nitrogen and P concentrations were then determined on an autoanalyzer (Technicon Auto Analyzer II). Potassium, Ca, Mg, and Mn were determined on an atomic absorption spectrophotometer (IL 353). Carbon was determined on a Leco carbon analyzer. Absolute weights of elements in the litter bags were calculated in grams per square metre as follows: (element con-

TABLE 1. Decomposition constants ($k$) for Douglas-fir needles determined from litter bags after 1 and 2 years and from the litter fall : forest floor weight ratio, percent needle lignin after 2 years decomposition, average, maximum, and minimum air temperatures, and average and minimum litter moisture in a sequence of stands ranging from 11 to 97 years

| Stand age, years | Litter bag[a] | | Litter fall : forest floor weight ratio[b] | % lignin after 2 years[c] | Air temperature, °C | | | Litter moisture, % | |
|---|---|---|---|---|---|---|---|---|---|
| | Year 1[d] | Year 2 | | | Minimum | Maximum | Average | Minimum | Average |
| 13 | 0.48±0.09[e] | 0.41±0.16[e] | 0.093 | 36.6±1.9[e] | −8.0 | 35.0 | 10.2 | 25.8 | 68.6 |
| 24 | 0.69±0.10 | 0.56±0.06 | 0.126 | 27.2±2.6 | −6.0 | 28.0 | 8.8 | 37.8 | 67.3 |
| 44 | 0.57±0.05 | 0.49±0.12 | 0.105 | 37.8±5.6 | −6.0 | 37.0 | 10.8 | 28.0 | 64.3 |
| 75 | 0.53±0.02 | 0.53±0.05 | 0.048 | 31.8±4.3 | −10.0 | 31.0 | 9.0 | 35.9 | 68.7 |
| 97 | 0.56±0.06 | 0.40±0.03 | 0.054 | 39.6±3.8 | −8.0 | 26.0 | 10.0 | 31.0 | 65.4 |

[a]Based on litter bag weight loss and calculated according to $x = x_0e^{-kt}$, where $x_0$ is the initial weight of needles and $x$ is the weight of needles after time $t$ (years) (Olson 1963).
[b]Decomposition constants based on data from Turner and Long (1975) and Turner (1975).
[c]Significant difference between stands at 95% level, LSD = 6.63. Initial percent lignin in all bags was 18.3%.
[d]Decomposition constants values significantly different at the 99% level between stands after 1 year's decomposition, LSD(0.05) = 0.12 and LSD (0.01) = 0.20.
[e]Mean ± standard deviation.

centration (in parts per million) / $10^6$ × dry weight (in grams)) / litter bag area (0.045 $m^2$).

Lignin content was determined for the initial sample (0 months) and for the 24-month samples using the Van Soest (1963) technique.

*Temperature, Moisture, and Rainfall Determinations*

Air temperatures were determined weekly with shielded maximum–minimum thermometers (Taylor) placed in each stand approximately 30 cm above the forest floor. Litter temperatures were determined weekly using a soil thermometer (Taylor). Litter moisture was determined gravimetrically by taking three replicate samples weekly. Litter was dried at 75°C for 48 h and moisture was expressed on a wet weight basis.

## Results

*Decomposition as a Function of Stand Age*

Needle weight loss varied from 38.3 ± 5.4 to 50.0 ± 4.7% in the various aged stands after 1 year and from 54.9 ± 12.7 to 66.9 ± 4.3% after 2 years. There was no significant difference in weight loss between stands.

However, the decomposition constants ($k$ values) calculated from the weight loss data were significantly different at the 99% level between stands after 1 year (Table 1). The highest $k$ value (0.69 ± 0.10), i.e., the fastest decomposition, occurred in the 24-year-old stand and the lowest value (0.48 ± 0.09) occurred in the 11-year-old stand. After 2 years there was no significant difference in the $k$ values between stands. A decrease in $k$ values occurred from year 1 to year 2 and the litter bag $k$ values were generally higher than $k$ values calculated from the ratio of litter fall to forest floor weight (Table 1).

There was also a significant difference between stands at the 95% level for percent lignin in the needles after 2 years decomposition (Table 1). The lowest percent needle lignin occurred in the 24-year-old stand.

Average air temperature was the coolest (8.8°C, Table 1) in the 24-year-old stand. The temperature range in this stand was also less extreme than in other stands (Table 1). Litter temperatures showed a similar trend to air temperatures and ranged from −2.2 to 17.2°C during the study period. The 24-year-old stand also had the highest minimum litter moisture (37.8%). There was little difference in average litter moisture between stands (Table 1).

The decomposition constants ($k$) based on 2 years of weight loss data were most highly correlated with minimum litter moisture ($r = 0.91$, significant at the 95% level) and minimum litter moisture plus average air temperature ($r = 0.98$, significant at the 99% level using stepwise multiple linear regression analysis).

*Decomposition as a Function of Season*

Seasonal rates of decomposition in the age sequence of stands are shown in Fig. 1. There was very little difference in the rates of needle decomposition between the stands in the winter and early spring period from February to May 1975. Weight loss in this period no doubt includes some leaching loss (Nkyvist 1963). During the late spring and summer months, however, there were apparent differences in decomposition rates in the stands. Needle weight losses in the 11- and 97-year-old stands were slight while loss was considerable in the other stands, particularly in the 24-year-old stand which had the greatest loss in this period.

During the period from May to August 1975, the 11-year-old stand was drier than the other stands

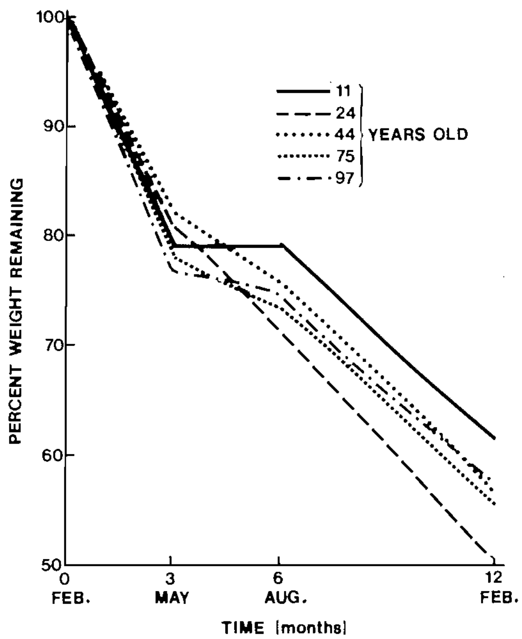


FIG. 1. Percent weight of needles in litter bags remaining after 3, 6, and 12 months in the age sequence of Douglas-fir stands.

with minimum litter moisture being 25.8% (Table 1). The 24-year-old stand was moister and cooler in the summer than other stands. The rate of decomposition increased in all stands in the period from August 1975 to February 1976 with the patterns established in the summer essentially controlling the annual weight loss.

*Release of Nutrients from Litter Bags*

Concentrations of nutrients in the needles in decomposition bags for the various collection dates are shown in Table 2. The nitrogen concentrations of the needles increased in comparison with the initial concentrations in all stands throughout the 24-month period. Maximum concentration was 2.14% in the 75-year-old stand after 12 months. Carbon: nitrogen ratios fell during the study period from 49.8 to 22.4 in the 24-year-old stand after 24 months. Concentrations of P, K, Ca, and Mg also fell. Manganese concentrations after 24 months exceeded the initial concentration of 1450 ppm in the 24-year-old stand (1484 ppm) and the 75-year-old stand (1486 ppm).

Patterns of release of N, P, K, and Ca from the litter bags during the 24-month period in the various stands, however, are best seen in Figs. 2*a* to 2*d*, respectively, where absolute losses are presented in terms of grams per square metre. Absolute nitrogen weights in the litter bags increased in all stands in the first 3 months (Fig. 2*a*) with a sharp initial increase in the 97-year-old stand. However, after this time weights of N in the needles in this stand fell. In general, absolute increases in N were greatest in the older stands with the 75-year-old stand showing the greatest increase at 12 months. Needles in all stands showed an absolute loss after 24 months (Fig. 2*a*). Maximum N loss after 24 months occurred in the 24-year-old stand and least loss occurred in the 11-year-old stand. The first indication of net N mineralization occurred between 3 and 6 months in the 24- and 97-year-old stands, between 6 and 12 months in the 11- and 44-year-old stands, and between 12 and 24 months in the 75-year-old stand (Fig. 2*a*).

Phosphorus loss was very similar in all stands with a rapid initial loss in the first 3 months (Fig. 2*b*) and little loss after this time. Least loss, however, was in the 11-year-old stand and greatest loss was in the 75-year-old stand. Ratios of N:P started at 4.5 and averaged 16.4 after 12 months and 17.2 after 24 months.

Potassium was lost most readily from the litter bags. Leaching losses in the first 3 months accounted for most of the total loss recorded after 24 months (Fig. 2*c*). Greatest loss was in the 24-year-old stand, but there was little difference between stands.

Losses of Ca, Mg, and Mn after 2 years were similar in magnitude in all stands. However, loss of Ca tended to be relatively steady with time (Fig. 2*d*) while loss patterns for Mg and Mn were similar to that for K with most rapid loss in the first 3 months, probably owing to leaching. On average 76.9, 31.7, 31.0, 30.2, 19.4, and 6.7% of the N, Mn, Ca, Mg, P, and K remained in the litter bags after 2 years.

*Litter Decomposition Rates, Nutrient Release, and Stand Productivity*

Correlation coefficients were calculated for linear regressions of total stand net annual productivity (from published data of Turner and Long (1975) and Turner (1975)) and (*a*) needle decomposition rates ($k$ values) and (*b*) elemental losses from litter bags after 2 years. The only significant $r$ value (at the 95% level) for regressions of stand productivity and decomposition rates was that involving litter bag $k$ values based on 12-month data ($r = 0.87$).

For the regressions of stand productivity versus elemental losses none of the correlation coefficients were significant. However, when N and K loss were considered together in a stepwise multiple linear regression, the correlation coefficient was significant at

TABLE 2. Nutrient concentration of litter in decomposition bags (standard deviations in parentheses)

| Collection date | Stand age, years | Duration of decomposition, months | Dry weight, g | C, % | N, % | C:N ratio | P, ppm | K, ppm | Ca, ppm | Mg, ppm | Mn, ppm |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Feb. 14, 1975 | | 0 | 10.0 | 46.8 | 0.94 | 49.8 | 2080 | 4710 | 8660 | 850 | 1450 |
| May 14, 1975 | 11 | 3 | 7.90 (0.21) | 47.8 (0.8) | 1.27 (0.18) | 37.6 | 825 (52) | 5069 (163) | 8038 (571) | 425 (55) | 416 (84) |
| | 24 | | 8.12 (0.09) | 47.9 (1.1) | 1.30 (0.14) | 36.9 | 875 (81) | 551 (260) | 7949 (711) | 450 (73) | 473 (59) |
| | 44 | | 8.23 (0.14) | 48.0 (0.8) | 1.26 (0.16) | 38.1 | 838 (68) | 537 (396) | 7747 (765) | 442 (42) | 525 (41) |
| | 75 | | 7.23 (0.11) | 48.1 (0.6) | 1.38 (0.07) | 34.9 | 829 (60) | 540 (268) | 7535 (547) | 484 (31) | 526 (25) |
| | 97 | | 7.71 (0.14) | 48.4 (0.3) | 1.40 (0.01) | 34.6 | 936 (92) | 702 (234) | 7489 (923) | 462 (48) | 577 (57) |
| Aug. 20, 1975 | 11 | 6 | 7.91 (0.05) | 47.9 (0.7) | 1.38 (0.09) | 34.7 | 747 (60) | 278 (47) | 8108 (351) | 407 (32) | 468 (56) |
| | 24 | | 7.16 (0.11) | 48.6 (1.25) | 1.43 (0.09) | 34.0 | 887 (72) | 827 (254) | 8447 (49) | 449 (59) | 659 (17) |
| | 44 | | 7.35 (0.09) | 45.5 (1.5) | 1.47 (0.06) | 31.0 | 893 (28) | 945 (243) | 8355 (394) | 495 (68) | 651 (30) |
| | 75 | | 7.38 (0.18) | 47.6 (0.8) | 1.42 (0.15) | 33.5 | 828 (106) | 611 (327) | 8113 (169) | 460 (49) | 577 (78) |
| | 97 | | 7.56 (0.15) | 48.7 (1.5) | 1.42 (0.30) | 34.3 | 1002 (59) | 896 (178) | 8033 (300) | 544 (58) | 683 (55) |
| Feb. 14, 1976 | 11 | 12 | 6.17 (0.54) | 48.6 (0.5) | 1.73 (0.16) | 28.1 | 1016 (13) | 672 (138) | 7804 (586) | 456 (15) | 484 (17) |
| | 24 | | 5.00 (0.47) | 47.4 (0.7) | 2.04 (0.15) | 23.2 | 1305 (104) | 1012 (89) | 9047 (122) | 552 (62) | 864 (38) |
| | 44 | | 5.64 (0.24) | 47.3 (1.0) | 1.80 (0.11) | 26.3 | 1136 (28) | 832 (52) | 8410 (235) | 730 (392) | 827 (207) |
| | 75 | | 5.89 (0.12) | 48.4 (0.6) | 2.14 (0.32) | 22.6 | 1154 (53) | 973 (47) | 7744 (323) | 788 (83) | 859 (142) |
| | 97 | | 5.72 (0.37) | 48.3 (0.6) | 1.52 (0.05) | 31.8 | 1011 (109) | 1137 (86) | 7625 (637) | 501 (197) | 739 (143) |
| Feb. 14, 1977 | 11 | 24 | 4.51 (1.27) | 48.4 (0.4) | 1.86 (0.09) | 26.0 | 1085 (45) | 592 (105) | 7288 (497) | 611 (154) | 656 (107) |
| | 24 | | 3.31 (0.43) | 44.6 (1.9) | 1.99 (0.22) | 22.4 | 1129 (175) | 735 (91) | 7798 (2762) | 760 (120) | 1484 (353) |
| | 44 | | 3.85 (0.97) | 47.5 (1.3) | 1.81 (0.04) | 26.2 | 973 (77) | 799 (156) | 6713 (1144) | 675 (192) | 1283 (236) |
| | 75 | | 3.46 (0.38) | 46.6 (0.7) | 1.97 (0.15) | 23.7 | 1217 (558) | 1219 (558) | 6341 (547) | 740 (164) | 1468 (320) |
| | 97 | | 4.14 (0.03) | 47.9 (0.3) | 1.72 (0.26) | 27.8 | 1036 (43) | 840 (280) | 7138 (1364) | 627 (94) | 1320 (205) |

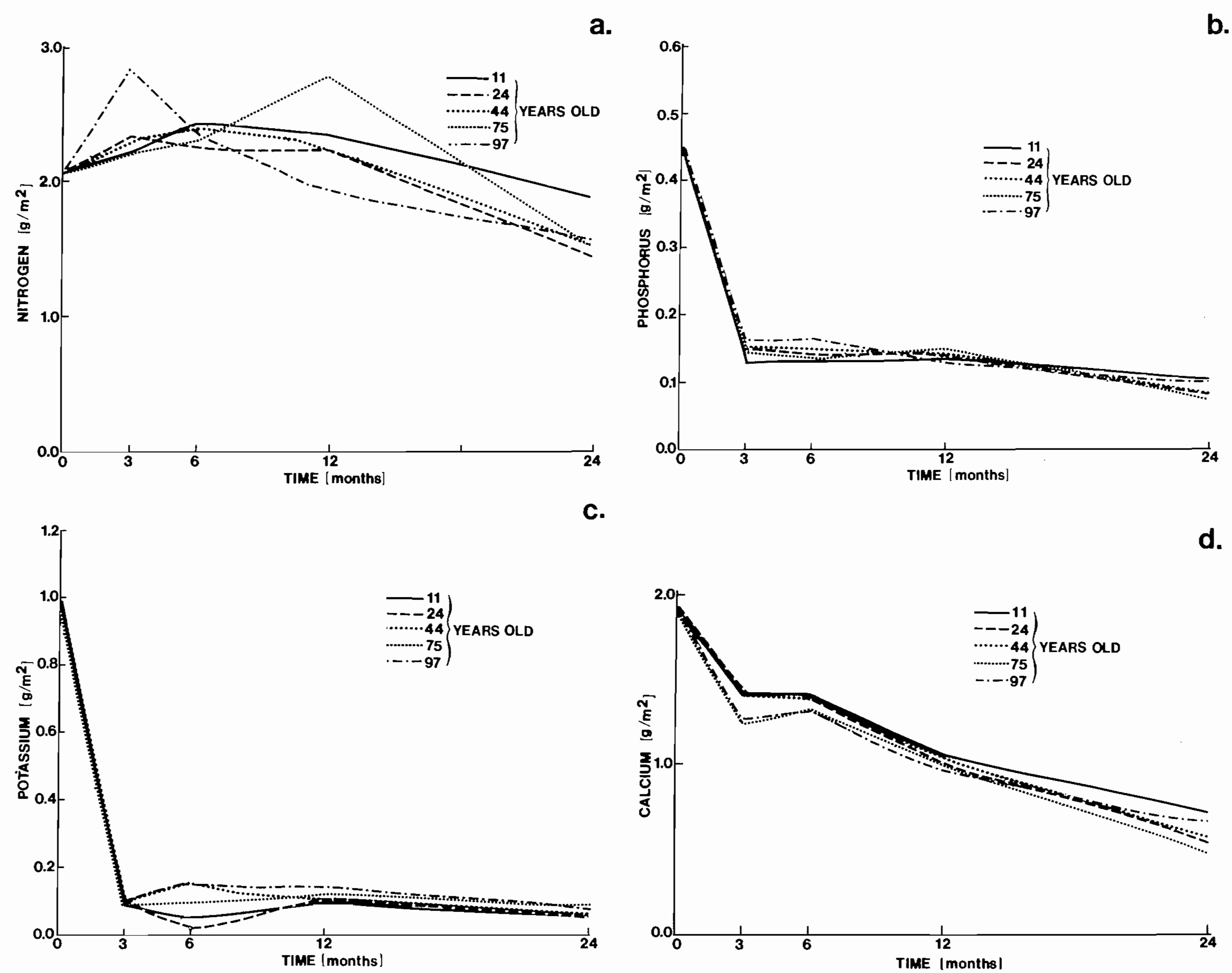


FIG. 2. Weights (grams per square metre) of (*a*) nitrogen, (*b*) phosphorus, (*c*) potassium, and (*d*) calcium in needles in litter bags after 3, 6, 12, and 24 months in the age sequence of Douglas-fir stands.

the 99% level ($r = 0.96$). Inclusion of Mg increased $r$ to 0.98.

## Discussion

Turner and Long (1975) using the production: accumulation ratio found that maximum litter decomposition in Douglas-fir stands occurred at the time of canopy closure, i.e., from age 20 to 30 years. Results from the litter bag study described here support this conclusion in that maximum decomposition occurred in the 24-year-old stand based first on $k$ values after 12 months decomposition and second on change in percent needle lignin after 24 months (Table 1). Decomposition rates were lowest in the 11-year-old stand and rates declined after reaching a peak in the 24-year-old stand.

The litter bag data, however, only partially support Turner and Long's data since needle litter from only one stand was used in all of the stands. Thus litter quality was excluded as a variable. To completely support Turner and Long's data, litter from each stand should be used.

The weight loss of needles after 2 years ranged from 54.9 ± 12.7 to 66.9 ± 4.3%. Similar rates were found by Mikola (1960) in Finland in spruce stands (33.3 to 52.9%) and in pine stands (41.3 to 52.9%). Will (1967) also found 50.6% weight loss of needles after 2 years in *Pinus radiata* plantations in New Zealand.

Mikola noted that temperature is the most important factor regulating the litter decomposition rate in Finland since rainfall is evenly distributed throughout the year. Moisture, however, plays a more important role in determining decomposition rates than temperature in the Pacific Northwest of the United States because of summer drought. This is supported by Fogel and Cromack (1977) who found that annual loss rates in Oregon for Douglas-fir needles were primarily correlated with plant moisture stress and by the author who found that decomposition rates were primarily correlated with minimum litter moisture.

Fogel and Cromack (1977) found $k$ values ranging from 0.22 to 0.38 based on 2 years of litter bag data. In this study $k$ values based on 2 years of data ranged from 0.40 ± 0.03 to 0.56 ± 0.06 (Table 1). Increased summer moisture in Washington probably accounts for the higher $k$ values. Also, Fogel and Cromack's stands were in old-growth forests where decomposition may proceed more slowly.

Although decomposition proceeded slowly in the summer months in most stands, in agreement with Fogel and Cromack (1977), it proceeded relatively rapidly in the 24-year-old stand. This stand had the highest minimum litter moisture, lowest annual air temperature, and the smallest temperature range (Table 1). Interestingly, Daubenmire and Prusso (1963) found that Douglas-fir needles decomposed faster at 10 than at 25 °C. It would appear that favorable combinations of moisture and temperature were operating in the 24-year-old stand to promote the fastest decomposition rate during the summer. Decomposition during the rest of the year was similar in all stands and considerable decomposition appeared to occur during the cool months.

The $k$ values calculated from the production to accumulation ratio were less than those calculated from the exponential decay method (Table 1). Similar results were found by Lousier and Parkinson (1976) for aspen litter in western Canada. This is probably because the ecosystems are not in steady state. In addition, the litter bag $k$ values were not constant but declined from year 1 to year 2. The forest-floor biomass estimates also contain some small woody litter and this would tend to lower the $k$ value estimates based on the production:accumulation ratio.

Many workers (Bocock 1963; Gosz et al. 1973; Hayes 1965; Will 1967) have noted increased N concentrations in needles and leaves during the decomposition process. Similar results were found in this study (Table 2). However, not only did N concentrations increase but absolute gains in weight of N were recorded during the first 12 months of decomposition (Fig. 2*a*). Gosz et al. (1973) also observed this. Saito (1957), Gilbert and Bocock (1960), and Gosz et al. (1973) further indicate that this increase probably arises from external sources such as precipitation and insect frass.

Net N mineralization began after 3 months in two of the stands and had commenced after 12 months in all stands. Lutz and Chandler (1946) report that the critical C:N ratio for N mineralization in forest soils is variable, but it generally ranges from 20:1 to 30:1. In this study net N mineralization was initiated in the 74- and 97-year-old stands when the C:N ratio was > 34 while in the 75-year-old stand it was initiated when the C:N ratio was 22.6 (Table 2; Fig. 2*a*). The C:N ratio is thus of little value in predicting the switch from immobilizing substrate to mineralizing substrate.

Greatest N loss was in the 24-year-old stand which had the highest rate of decomposition and the lowest C:N ratio (22.4) after 2 years (Table 2). Of the original N in the litter bags in this stand

70.5% remained after 2 years. Somewhat similar results were found by Will (1967), who found 120% of the initial N after 24 months in *Pinus radiata* needles litter, but only 70% after 30 months. Least N loss was in the 11-year-old stand which had the slowest rate of decomposition.

Gosz et al. (1973) found that in deciduous litter N and P dynamics were similar with an absolute weight increase of P during the 1st year of decomposition. In Douglas-fir litter, however, P was found to be rapidly lost in the first 3 months, presumably by leaching, and absolute weights never exceeded initial weights (Fig. 2*b*). Patterns were similar in all stands. Similar results were found by Will (1967) for *P. radiata* needles. Phosphorus would thus not appear to be the limiting element, at least to decomposers, in Douglas-fir ecosystems, or in *P. radiata* plantations in New Zealand, as it appears to be in the deciduous ecosystems studied by Gosz et al. (1973).

Potassium (Fig. 2*c*), Mg, and Mn appeared to behave in a similar manner to P with rapid leaching losses in the first 3 months followed by small losses in the period from 3 to 24 months. Calcium losses were relatively steady with time (Fig. 2*d*) and closely resembled dry weight losses.

In general, nutrient loss from the litter bags after 24 months revealed that the loss of elements was in the following sequence $N < Mn < Ca < Mg < P < K$. This sequence was also found by Will (1967) after 2 years of decomposition of *P. radiata* litter with the exception of Mn which he did not include.

A strong relationship existed between stand net annual productivity and $k$ values based on 12 months weight loss ($r = 0.87$ significant at the 95% level). There was no significant relationship based on 2-years' data, however, since the variance in weight loss increased with time.

Using stepwise multiple regression stand net annual productivity was also related to N + K loss from the litter ($r = 0.96$, significant at the 99% level). Although nitrogen is generally considered to be deficient in Douglas-fir ecosystems, it is not known if K may be deficient in some ecosystems. However, K has been shown to be important in the nutrition of *Pinus resinosa* (Stone and Kszystyniak 1977). The correlation coefficient was further improved by the addition of Mg ($r = 0.98$, significant at the 99% level).

The regression analyses indicate that there are strong positive relationships between stand net annual productivity and (*a*) litter decomposition rates and (*b*) nitrogen and potassium release from litter bags. However, the study design does not allow one to draw direct causal relationships.

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ATTIWELL, P. M. 1968. The loss of elements from decomposing litter. Ecology, **49**: 142–145.

BOCOCK, K. L. 1963. Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecol. **52**: 273–284.

DAUBENMIRE, R., and D. C. PRUSSO. 1963. Studies of the decomposition rates of tree litter. Ecology, **44**: 589–592.

FOGEL, R., and K. CROMACK, JR. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Can. J. Bot. **55**: 1632–1640.

GILBERT, O., and K. L. BOCOCK. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. II. Changes in nitrogen content of oak and ash leaf litter. J. Soil Sci. **11**: 10–19.

GOSZ, J. R., G. E. LIKENS, and F. H. BORMANN. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monogr. **43**: 173–191.

HAYES, A. J. 1965. Studies on the decomposition of coniferous leaf litter. 1. Physical and chemical changes. J. Soil Sci. **16**: 121–139.

HOWARD, P. J. A., and D. M. HOWARD. 1974. Microbial decomposition of tree and shrub litter. 1. Weight loss and chemical composition of decomposing litter. Oikos, **25**: 341–352.

KING, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser For. Pap. No. 8.

LOUSIER, J. D., and D. PARKINSON. 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. **54**: 419–436.

LUTZ, H. J., and R. F. CHANDLER, JR. 1946. Forest soils. John Wiley and Sons, Inc., New York.

MIKOLA, P. 1960. Comparative experiment on decomposition rates of forest litter in southern and northern Finland. Oikos, **11**: 161–166.

NYKVIST, N. 1963. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. Stud. For. Suec. **3**: 1–31.

OLSON, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, **44**: 322–331.

PARKINSON, J. A., and S. E. ALLEN. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun. Soil Sci. Plant Anal. **6**(1): 1–11.

SAITO, T. 1957. Chemical changes in beech litter under microbiological decomposition. Ecol. Rev. Tohoku, **14**: 209–216.

STONE, E. L., and R. KSZYSTYNIAK. 1977. Conservation of potassium in the *Pinus resinosa* ecosystem. Science, **198**: 192–194.

TURNER, J. 1975. Nutrient cycling in Douglas-fir with respect to age and nutrient status. Ph.D. Thesis, University of Washington, Seattle.

TURNER, J., and J. N. LONG. 1975. Accumulation of organic matter in a series of Douglas-fir stands. Can. J. For. Res. **5**: 681–690.

VAN CLEVE, K., and L. L. NOONAN. 1975. Litter fall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Can. J. For. Res. **5**: 626–639.

VAN SOEST, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for determination of fiber and lignin. J. Assoc. Off. Anal. Chem. **49**: 546–551.

WILL, G. 1967. Decomposition of *Pinus radiata* litter on the forest floor. Part 1. Changes in dry matter and nutrient content. N.Z. J. Sci. **10**: 1030–1044.



# Erratum: Influence de l'irradiation sur la croissance de plants d'épinette noire en contenants placés dans deux enceintes de culture[1]

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Dans la discussion (p. 320), le deuxième paragraphe les lignes 23 et plus devraient se lire: "Ces résultats indiquent aussi qu'il y a un seuil de saturation énergétique, qui se situe entre 186 et 237 $\mu$einstein $m^{-2}$ $s^{-1}$, au-dessus duquel il n'y a aucun gain appréciable pour nos conditions de culture. Nos propres études d'échanges gazeux montrent de plus que pour une concentration normale de $CO_2$ (environ 330 vpm de $CO_2$), un éclairement énergétique plus faible que 200 $\mu$einstein $m^{-2}$ $s^{-1}$ serait limitatif pour la photosynthèse (D'Aoust, manuscrit en préparation)."

[1]Reçu à CNRC le 7 décembre 1978.

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