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Reprinted from

Canadian Journal of Botany

Réimpression du

Journal canadien de botanique

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Volume 55 • Number 12 • 1977

Pages 1632–1640

National Research Council Canada | Conseil national de recherches Canada

Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon

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Received July 26, 1976

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.

Linear regression models were developed for Douglas fir needle, female cone, branch, and bark decomposition in seven stands representing four mature vegetation types in western Oregon. Rate constants (k) for annual weight loss of needles ranged from 0.22 to 0.31 $year^{-1}$, from 0.047 to 0.083 $year^{-1}$ for cones, from 0.059 to 0.089 $year^{-1}$ for branches, and from 0.005 to 0.040 $year^{-1}$ for bark. The decomposition constant (k) of needles had a negative linear correlation ($P < 0.01$) with maximum plant moisture stress and temperature growth index of the seven stands. In comparing substrate quality of needle and woody litter components, k was more closely correlated with lignin content than with C:N ratio.

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Les auteurs ont établi des modèles de régression linéaire pour la décomposition des aiguilles du sapin de Douglas ainsi que des cônes femelles, des branches et de l'écorce dans sept stations représentant quatre types de végétation adulte dans l'ouest de l'Oregon. Les constantes pour le taux annuel de décomposition des aiguilles se situent entre 0.22 et 0.31 an^{-1}, de 0.047 à 0.083 an^{-1} pour les cônes, de 0.059 à 0.089 an^{-1} pour les branches et de 0.005 à 0.040 an^{-1} pour l'écorce. La constante de décomposition (k) des aiguilles montre une corrélation linéaire négative ($P < 0.01$) avec le déficit maximum en humidité des plantes et de la température index de croissance des sept stations. En comparant la qualité du substrat des aiguilles et des constituants ligneux de la litière, le k s'avère plus étroitement lié au contenu en lignine qu'au rapport C:N.

[Traduit par le journal]

Introduction

Litter fall and its subsequent decomposition account for a substantial amount of the nutrient cycling that occurs during forest stand development. For example, litter fall contained about 60% of the nutrients returned to the forest floor in a mesic, oak-dominated stand (Carlisle *et al.* 1966*a*, 1966*b*). Similarly, Abee and Lavender (1972) reported that 72% of the aboveground nutrient return in a 450-year-old Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand was in litter fall. Consequently, considerable biomass and nutrient capital accumulates in the forest floor if decomposition is slow. Youngberg (1966), for instance, reports that litter biomass, excluding large woody litter, in western Oregon Douglas fir stands ranges from 23.2 t ha^{-1} in a stand with no shrub understory to 86.0 t ha^{-1} in a stand with a salmonberry – sword fern understory. Corresponding nitrogen capital in the forest floor of these stands ranges from 202 to 1345 kg ha^{-1}. Williams (1972), on the basis of similar data, states that nitrogen deficiency in many northern coniferous forests is associated with stand age, possibly because of the slow release of available nitrogen from the forest floor.

Our objectives were to determine the effects of habitat, environment, and substrate quality on decomposition rate of Douglas fir needles, cones, bark, and branches. Habitat differences were recognized by changes in vegetation which reflect among other things the relative depletion of soil water reserves during the summer dry period.

Locality and Habitat Types

The vegetation types selected for this study are representative of the mature forest communities at lower elevations in the Western Cascades of Oregon. The study site was the H. J. Andrews Experimental Forest located about 64 km east of Eugene, Oregon. All communities were dominated by an overstory of old-growth (ca. 450-year-old) Douglas fir averaging 120–140 cm in diameter at breast height (dbh) and 45–75 m in height, with timber volumes averaging 350–750 m^3 ha^{-1} (Dyrness *et al.* 1974).

The climate of the study area, summarized by Dyrness *et al.* (1974), is characterized by warm, dry summers and mild, wet winters without extensive snow cover. The January mean temperature is 2.3°C and the July mean is 20.6°C with temperature extremes ranging from −18 to 38°C. Annual precipitation averages 230 cm, mostly as rain between September and June.

Study sites were located in three replicated and one unreplicated habitat type, representing a wide range in soil-moisture depletion and a lesser range in temperature conditions, to examine the effect of environment on litter decomposition. The following habitats (Table 1), as described by Dyrness *et al.* (1974) and listed in order from the warmest and driest to coolest and most moist, were characterized by: (1) *Pseudotsuga menziesii* – *Holodiscus discolor* (Pursh) Maxim. (Psme–Hodi), (2) *Tsuga heterophylla* (Bong.) Carr. – *Castanopsis chrysophylla* (Dougl.) A. DC. (Tshe–Cach), (3) *Tsuga heterophylla* – *Rhododendron macrophyllum* D. Don – *Berberis nervosa* Pursh (Tshe–Rhma–Bene), and (4) *Tsuga heterophylla* – *Polystichum munitum* (Kaulf) Presl. – *Oxalis oregana* Nutt. (Tshe–Pomu–Oxor).

The Psme–Hodi association represents the driest forest habitat in the Andrews Forest and is the only low elevation community where *Tsuga heterophylla* (western hemlock) is absent. Such communities are generally found on steep, south- and southwest-facing slopes and usually have stony, shallow loam and silt loam soils derived from tuff and breccia parent materials. Rooting depths are generally less than 0.5 m. The overstory of old-growth Douglas fir is rather open (30–60% crown coverage), shrub cover is relatively sparse, and the herb layer is very poorly developed.

The Tshe–Cach association is characteristic of relatively dry, exposed sites similar to those occupied by the Psme–Hodi association. Stands of the former type are generally found on or just below ridge tops. Slopes are steep, have a south or southwest aspect, and have poorly developed soils derived from tuff and breccia parent materials with highly variable stoniness and effective rooting depth. Most soils tend to be shallow and stony. The overstory (48–72% canopy coverage) is dominated by Douglas fir but *Tsuga* reproduction is abundant in the understory of most stands. The Tshe–Cach association characteristically contains large amounts of three shrubs: *Castanopsis chrysophylla*, *Rhododendron macrophyllum*, and *Gaultheria shallon* Pursh. The herb layer is poorly developed because of the heavy shrub layer.

The Tshe–Rhma–Bene association is one of the most commonly occurring habitat types in the study area and approaches a stable community type. Stands are located on gentle to moderate slopes (10–40%) and are dominated by old-growth Douglas fir and western hemlock. Soil profiles are generally low in stone content (5–30%) with loam or silt loam surface horizons and silt loam, silty clay loam, or silty clay textured subsoils developed from tuff and breccia residuum and colluvium, andesite colluvium, and mixed colluvium. The association has a dense overstory (92–103% coverage) with Douglas fir and western hemlock codominant (ca. 45% cover each). The shrub layer is rather sparse because of the dense overstory, and the herb layer is highly variable in cover.

The Tshe–Pomu–Oxor association occurs on a variety of landforms ranging from steep, smooth slopes to alluvial fans, with slope gradients varying from gentle to steep (5–90%). Virtually all aspects are represented. Soils are generally deep, relatively stone free, and moderately fine textured with silt loam surface soil and silty clay loam subsoil. The most frequently encountered parent materials are deep, fine-textured andesite colluvium. Overstory cover ranges from medium to dense (70–110%), while the shrub layer is variable in cover (5–70%). *Oxalis oregana* and *Polystichum munitum* dominate the herb layer which is unusually dense and may approach 100% total cover.

Methods

Litter substrates were placed in consecutively numbered, 20 × 20 cm nylon mesh bags (Crossley and Hoglund 1962). Mesh size was 1 mm, small enough to contain Douglas fir needles, yet large enough to permit aerobic microbial activity and free entry of small soil animals. Substrates studied were (1) *Pseudotsuga menziesii* (Psme) needles, (2) Psme female cones, (3) Psme bark, and (4) Psme branches, ca. 10–15 mm diameter and 20 cm in length. Douglas fir needles were collected in February 1973 from the two oldest age classes on live branches from 20-year-old trees in the H. J. Andrews Experimental Forest, near Blue River, Oregon. Green needles were selected because they are representative of litter inputs during late winter. Unweathered female cones were collected from the ground in an old-growth stand. Outer bark was stripped from old-growth trees in the same stand by prying loose large sections at breast height. Small branches were obtained from a 40-year-old stand near

TABLE 1. A comparison of study plots located on the H. J. Andrews Experimental Forest, Oregon

Association	Site	Elevation, m	Aspect	Depth to C horizon, cm	% cover[a] Mature tree	Shrub	Herb	Bryophyte	Minimum litter moisture 1973, % dry wt.	Minimum soil moisture 1973, % dry wt.	Maximum $PMS^{b,c}$ 1973	$TGI^{b,d}$ 1973
Tshe–Pomu–Oxor	6	460	SW	—[e]	—	—	—	—	37.8	27.4	—	—
Tshe–Pomu–Oxor	7	460	N	80–130	110.0	17.6	41.1	54.8	22.6	29.8	6.2	90.1
Tshe–Rhma–Bene	2	490	W	90–100	103.0	29.6	23.9	53.5	20.9	19.7	9.7	88.2
Tshe–Rhma–Bene	17	490	N	100	92.0	43.0	36.8	43.0	17.3	22.5	9.2	73.8
Tshe–Cach	4	620	W	90	48.0	122.7	14.3	4.9	18.9	11.2	10.1	87.5
Tshe–Cach	16	670	SW	120	72.0	108.0	6.5	14.9	20.4	12.8	10.1	85.1
Psme–Hodi	1	490	SW	50	45.0	45.5	35.8	16.9	6.0	10.8	18.4	97.6

Warmer and drier

[a]W. A. McKee (personal communication).
[b]W. H. Emmingham (personal communication).
[c]*PMS*, predawn plant moisture stress(bars) of understory conifers measured by the pressure bomb technique.
[d]*TGI*, Temperature growth index determined by summing the fractions of optimum growth for Douglas fir for each day of the growing season.
[e]Data not available. Assumed to be the same for mature tree cover, maximum *PMS*, and *TGI* as for site. 7

Philomath, Oregon. Only fresh, non-rotted, small-branch litter was used. Duplicate nutrient and lignin analyses were conducted on bulk samples of all substrates before litter-bag construction.

The following are the weights of substrates placed in the litter bags: 5 g of needles, two cones weighing about 12 g, a branch section weighing about 15 g, and between 30 and 100 g of bark, owing to variability in specific gravity of bark.

Litter bags were placed in different habitats defined by moisture–temperature gradients within the H. J. Andrews Forest. Three replicated habitat types or treatments were selected with each replicate designated as an individual site for each habitat type. Psme needles, cones, branches, and bark were placed on six sites. A fourth, unreplicated, habitat type (Psme–Hodi) was also used for all substrates for comparative purposes, as it is the driest of the low elevation habitat types on the Andrews Forest.

At each site, 15 bags of each substrate were distributed on the forest floor at 1-m intervals in rows 1 m apart. One bag of each substrate was placed at each point in a row. Needle litter bags were placed in the field on March 9th or 10th, 1973, and collected at 7- to 24-week intervals over a 2-year period by randomly selecting 6–15 litter bags per site for analysis and weight loss measurement. Woody substrates were placed in the field on May 11th, 1973, and samples similarly at 6-month intervals. After collection, litter bags were dried at 50°C to a constant weight. The substrate was then removed, weighed, and ground to pass through a 40-mesh screen in preparation for nutrient analysis. Total nitrogen was determined by the micro-Kjeldahl technique (Noonan and Holcombe 1975) and structural carbohydrates by a minor modification of Van Soest's (1963) method (Cromack 1973).

An exponential decay model was used to estimate the rate of annual weight loss:

$$X/X_0 = e^{-kt},$$

where X = weight remaining at time t (days), X_0 = original weight, e is the base of natural logarithms, and k is the decomposition constant (Jenny *et al.* 1949; Olson 1963).

Gravimetric water content of the litter layer and A_1 soil horizon, as percentage dry weight, was determined after drying samples at 60°C to constant weight. Ten samples of each layer were collected whenever a stand was visited, usually biweekly during the summer and monthly during fall and winter after field capacity was reached.

Predawn plant moisture stress (*PMS*), an index of soil water reserves available to roots, was measured on understory conifers at the end of the dry season by the pressure bomb technique (Waring and Cleary 1967). Temperature growth index (*TGI*), or optimum-temperature days of Cleary and Waring (1969), was determined by summing the fractions of optimum growth possible for Douglas fir for each day of the growing season. These indices were used as x–y coordinates for separating vegetation types on the H. J. Andrews Experimental Forest (Zobel *et al.* 1974).

Results

The results of our study are presented by substrate in order of increasing resistance to

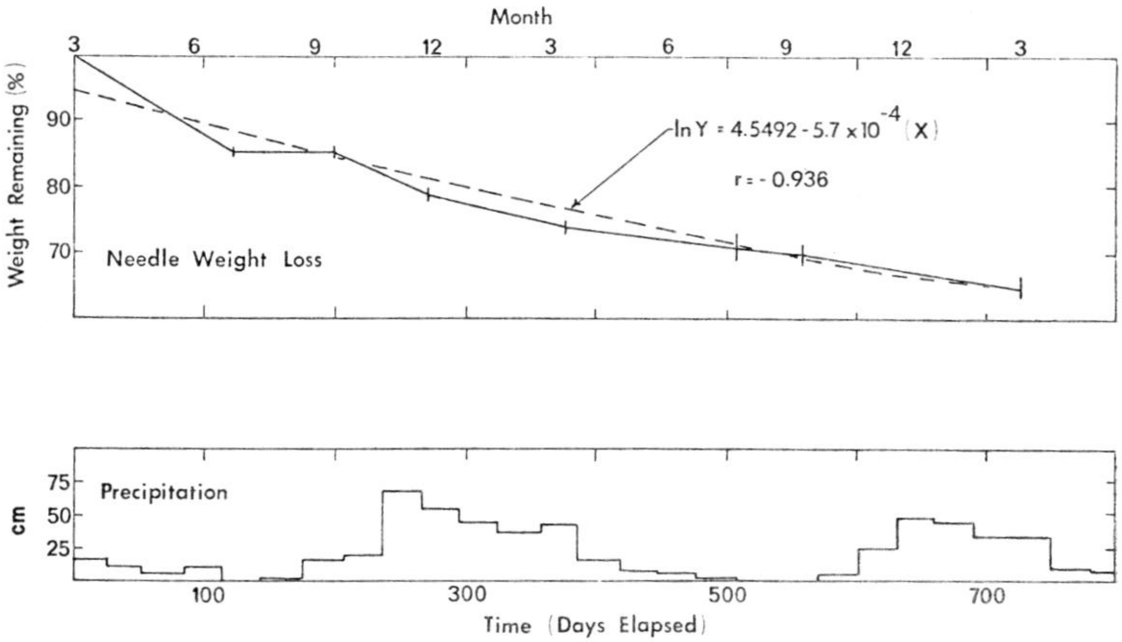

FIG. 1. Douglas fir needle litter decomposition and monthly precipitation from March 1973 to March 1975 on site 2 (Tshe–Rhma–Bene association), H. J. Andrews Experimental Forest, Oregon. Bars indicate 95% confidence interval; solid line indicates cumulative weight loss; and broken line, transformed predicted weight loss plotted on untransformed axes.

decomposition, and then by the effect of substrate quality on the rate of weight loss. The rates of decomposition between sites for the same substrate are very similar. Consequently, the data for the Tshe–Rhma–Bene association (site 2), the most commonly occurring habitat type in the central Western Cascades, have been presented in Figs. 1 and 2 to avoid the visual confusion of a large number of similar curves on the same graph.

Needles

Needle weight decreased exponentially with time while variance in weight loss increased with time (Fig. 1). No weight loss occurred during the first summer and no significant loss the second summer. After 1 year, negative linear correlations ($P < 0.01$) existed between weight loss and time for the wetter habitat types (Tshe–Pomu–Oxor and Tshe–Rhma–Bene) and less significant correlations ($P < 0.05$) for the drier habitat types (Tshe–Cach and Psme–Hodi). After 2 years (Table 2), all correlations were highly significant ($P < 0.01$) and the slopes of the regression lines for the wetter and drier habitats were significantly different ($P < 0.01$) using the Student's t-test.

The annual decomposition constant (k) ranged from 0.22 for site 1 to 0.31 year^{-1} for site 17 (Table 2). Half time (H)[1], or time required for a 50% weight reduction to occur, ranged from 2.5 to 3.5 years for sites 17 and 1, respectively. The decomposition constant for needles had a negative linear correlation ($P <$ 0.01) with the maximum index of *PMS* (Table 3), excluding site 17 and assuming the same value for sites 6 and 7. Positive linear correlations ($P < 0.05$) existed with percentage cover of mature trees, minimum litter moisture, and minimum soil moisture (0–5 cm deep). The stand variables providing the best multiple regression estimates of k were maximum *PMS* and *TGI*.

Site 17 was excluded from the linear regressions because it had an abnormally high decomposition rate that may reflect the high spatial variability in moisture stress patterns on this site. In part, this may represent microsite differences associated with slope and bank topography. In addition, the hemlock saplings selected for moisture-stress measurements were shallow rooted and may have received unusual

[1]Half time is not synonymous with half-life which is $0.69/k$ as derived from the exponential equation.

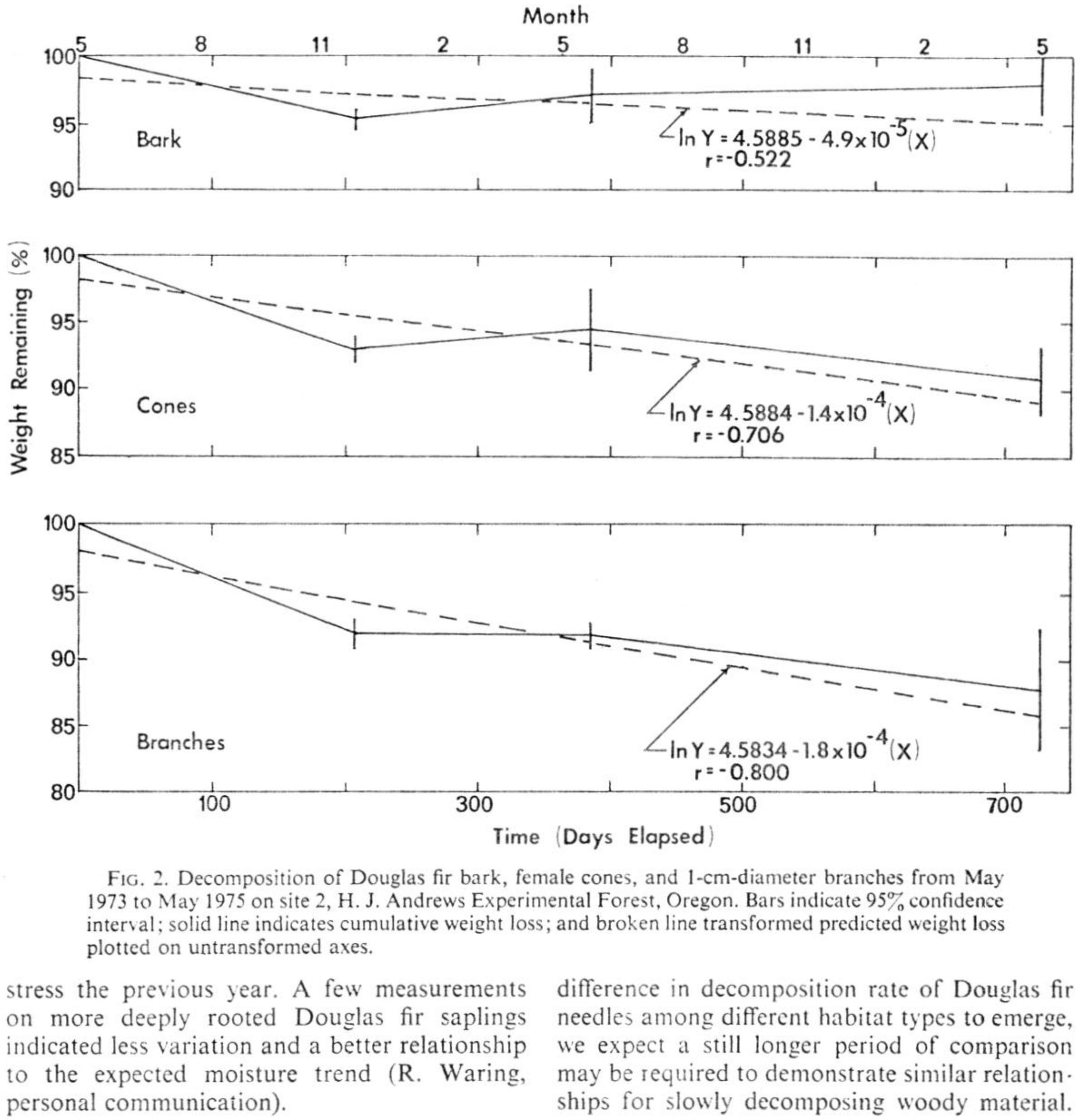

FIG. 2. Decomposition of Douglas fir bark, female cones, and 1-cm-diameter branches from May 1973 to May 1975 on site 2, H. J. Andrews Experimental Forest, Oregon. Bars indicate 95% confidence interval; solid line indicates cumulative weight loss; and broken line transformed predicted weight loss plotted on untransformed axes.

stress the previous year. A few measurements on more deeply rooted Douglas fir saplings indicated less variation and a better relationship to the expected moisture trend (R. Waring, personal communication).

Branches

Branch weight loss was also exponential with time (Fig. 2) but occurred at a slower rate than needle decomposition. After 2 years, negative linear correlations ($P < 0.01$) existed between weight loss and time for all sites (Table 3). Decomposition constants for branches ranged from 0.059 (site 6) to 0.089 year^{-1} (sites 2 and 7). Corresponding half times ranged from 10.0 to 20.1 years. No apparent correlation existed between k and any stand variable although decomposition appeared to be greater on the wetter sites. Since it required 2 years for a clear difference in decomposition rate of Douglas fir needles among different habitat types to emerge, we expect a still longer period of comparison may be required to demonstrate similar relationships for slowly decomposing woody material.

Cones

Cone decomposition after 2 years (Table 3) was similar to branch decay, with k ranging from 0.047 to 0.083 year^{-1} for sites 4 and 16 and half times from 9.7 to 24.8 years for sites 1 and 4 respectively. Negative linear correlations ($P < 0.01$) existed between weight loss and time for all sites. Because of the slow decomposition of cones, no correlation was apparent between k and any stand variable after 2 years.

Bark

Bark decomposition was extremely slow with

TABLE 2. Weight loss rates for Douglas fir needles, branches, cones, and bark on the H. J. Andrews Experimental Forest, Oregon. Regression of ln percentage weight remaining (Y) against days elapsed (X). H, half time (days); k, annual weight loss rate. Based upon 2 years of cumulative weight loss data

	Site	r	H	k	n
Needles	6	−0.89**	980	0.29	100
	7	−0.89**	1007	0.28	92
	2	−0.94**	1139	0.26	99
	17	−0.56**	910	0.31	97
	4	−0.95**	1167	0.25	94
	16	−0.94**	1253	0.24	99
	1	−0.92**	1261	0.22	53
Branches	6	−0.618**	7333	0.059	49
	7	−0.686**	4067	0.089	49
	2	−0.800**	3651	0.089	49
	17	−0.740**	4219	0.085	49
	4	−0.738**	5492	0.064	49
	16	−0.686**	5799	0.064	49
	1	−0.748**	4037	0.084	49
Cones	6	−0.809**	5222	0.064	47
	7	−0.863**	4844	0.063	49
	2	−0.706**	4923	0.067	47
	17	−0.879**	4401	0.074	49
	4	−0.658**	9058	0.047	49
	16	−0.791**	5742	0.083	49
	1	−0.908**	3530	0.080	49
Bark	6	−0.297*	19909	0.030	47
	7	−0.541**	14944	0.031	46
	2	−0.522**	13781	0.035	45
	17	−0.564**	11061	0.040	49
	4	−0.512**	13231	0.033	49
	16	−0.423**	14652	0.033	48
	1	−0.212	2785	0.005	45

*Significant at the 5% level.
**Significant at the 1% level.

TABLE 3. Needle decomposition. Correlation of rate of annual weight loss (k) with stand variables. CO, % cover of mature trees; PMS, maximum plant moisture stress; TGI, temperature growth index; SM, minimum soil moisture (0–5 cm deep); LM, minimum litter moisture

Stand variable	Regression equation	r	SE of slope $\times 10^{-4}$	n
CO	$k = 0.1778 + 9.25 \times 10^{-4}(CO)$	0.87*	2.1	6
PMS	$k = 0.3102 - 5.30 \times 10^{-3}(PMS)$	−0.92**	11.7	6
TGI	$k = 0.4350 - 1.99 \times 10^{-3}(TGI)$	−0.33	28.6	6
SM	$k = 0.2045 + 2.80 \times 10^{-3}(SM)$	0.91*	6.3	6
LM	$k = 0.2087 + 2.30 \times 10^{-3}(LM)$	0.89*	5.7	6
$PMS + TGI$	$k = 0.0599 - 7.1981 \times 10^{-3}(PMS) + 0.003(TGI)$	0.987**	8.6 = B_1 8.5 = B_2	6

*Significant at the 5% level.
**Significant at the 1% level.
[a] x_1 and x_2 are independent variables where $y = a + B_1x_1 + B_2x_2$, and B_1 and B_2 are slopes of triangles.

negative linear correlations ($P < 0.01$) existing between weight loss and time for all sites except 6 and 1 (Table 3). Weight loss with time for the Psme–Hodi habitat type (site 1) was not significantly different from zero and only significant at the 5% level for site 6. The decomposition constants, disregarding site 1, ranged from 0.030 to 0.040 year^{-1} for sites 6 and 17 respectively and half times from 30.3 to 54.6 years for sites 17 and 6. Again, no apparent correlation existed between k and any stand variable after 2 years although k was substantially higher on the modal sites (2 and 17).

Substrate Quality

The differences observed in decomposition rate of needles, cones, branches, and bark can be explained by substrate quality. The traditional index (Table 4) of substrate quality, C:N ratio, was not significantly linearly correlated with k for any of the individual sites, but did give a significant negative linear correlation ($r = -0.877$, $P < 0.01$) with k when individual substrate k values from all sites were combined. Lignin content was significantly correlated with k for a given substrate for all sites except site 4 ($P < 0.01$ for site 1, $P < 0.05$ for sites 2, 6, 7, 16, and 17). For all sites combined, lignin gave a better negative linear correlation ($r = -0.947$, $P < 0.01$) with substrate k than did the C:N ratio.

Discussion

Confining leaves of various tree species in litter bags has become a standard technique for estimating the decomposition rate of leaves, comparing the decomposition of various species, and characterizing different geographic areas (Ando 1970; Gosz *et al.* 1973; Macauley 1975; Mikola 1960; Witkamp 1966). To our knowledge, no one has previously reported significant differences in rate of leaf decomposition among stands in the same locality. Mikola (1960), for instance, found no clear differences in decomposition of pine needle litter in pine and spruce stands in the same locality but did find a difference between stands in southern and northern Finland (Table 5). Jenny *et al.* (1949) reported annual k values (calculated by dividing total litter input by forest floor standing crop) ranging from 0.63 in tropical forests to 0.015 year^{-1} in ponderosa pine forests of California. Our values

TABLE 4. Substrate quality and nutrient content of Douglas fir needles, cones, branches, and bark

Substrate	% C	% N	C:N ratio	% lignin
Needles	50.8	0.82	62	21.8
Female cones	49.3	0.24	205	44.2
Bark	56.4	0.19	297	58.6
Branches, 1 cm diam.	49.3	0.15	329	43.4

for Douglas fir needle litter ($k = 0.22$–0.31 year^{-1}) are intermediate to their forest floor values and lower than those reported for coniferous litter in the southeastern United States ($k = 0.42$–0.58 year^{-1}) and for coniferous litter covered by snow ($k = 0.31$–0.56 year^{-1}) for most of the year in the Pacific Northwest and Finland (Table 5). Our values are substantially higher than that reported ($k = 0.11$ year^{-1}) for Jeffrey pine litter in Nevada (Table 5).

Decomposition of more resistant woody materials has received very little attention compared with foliage litter decomposition. Gosz *et al.* (1973) report dry weight losses, after 1 year, of 21% for branches (0.5 cm × 30–45 cm long) of *Picea rubens* and 10% for *Abies balsamea* branches. Stark (1973) estimates weight loss after 1 year to be 5.69% for *Pinus jeffreyi* cones and 6.82% for branches 1.5 to 2 cm in diameter; after 2 years, weight losses were 11.3% for cones and 10.7% for branches. Our values are similar to Stark's; after 1 year weight loss was 4.4–8.6% (mean = 5.4%) for cones and 4.1–9.6% (mean = 6.2%) for branches about 1 cm in diameter; after 2 years the weight loss ranges from 6.0 to 10.8% (mean = 9.7%) for cones and 6.2 to 12.4% (mean = 9.1%) for branches.

Litter decomposition is the result of complex interactions between biotic factors such as microorganisms, soil fauna, nutrient and carbon components of litter, and abiotic factors (e.g. temperature and moisture) (Witkamp 1971). Our finding that the rate of annual weight loss is more influenced by lignin content than by C:N ratio supports the contention by Bollen (1953) that the structural complexity of material containing lignin and cellulose may exert more control over the rate of decomposition than the quantity of total nitrogen *per se.* Peevy and Norman (1948) found the decomposition of various carbon-containing fractions prepared from oat straw to be directly related to the lignin content of the fractions. Lignin retards overall decomposition because of its own even more resistant decomposition products and its physical interference with cellulase (EC 3.2.1.4) activity owing to lignin encrustation of cellulose fibers (Bailey 1973; Russell 1973).

Unlike the needle decomposition data, the wood decomposition data show no clear habitat relationship, indicating that more than 2 years may be needed to establish any definite differ-

TABLE 5. Comparison of annual decomposition rate (k) for a variety of coniferous leaf litter

Site	Tree species	k	Reference
Oak Ridge, TN	*Pinus virginiana* Mill.	0.45→0.46	Sollins *et al.* 1973
	Pinus taeda L.	0.51→0.58	Sollins *et al.* 1973
Coweeta Hydrologic Sta., NC	*P. strobus* L.	0.42→0.52	Cromack 1973
Little Valley, NV	*P. jeffreyi* Grev.	0.11[a]	Stark 1973[b]
Findley Lake, WA	*Abies amabilis* (Dougl.) Forbes	0.56[a]	Turner and Singer 1976[b]
Pallas järvi, Finland (north)	*Pinus* spp.	0.31[a]	Mikola 1960[b]
Vippula, Finland (south)	*Pinus* spp.	0.43[a]	Mikola 1960[b]
Blue River, OR	*Pseudotsuga menziesii*	0.22→0.31	This study
Wildcat Mt., OR	*Pseudotsuga menziesii*	0.38	Fogel and Cromack, unpublished[b]
	Abies procera Rehd.	0.31	Fogel and Cromack, unpublished[b]

[a]Calculated from published weight loss data using the exponential decay model.
[b]Sites having winter snow pack of several months' duration.

ences between habitats. Despite the uncertainty about habitat differences, the correlation between substrate k and lignin content indicates initial quality and nutrient content of litter are important variables controlling the decomposition rate of fine Douglas fir litter. Fogel and Ogawa (unpublished data) have estimated that decomposition of Douglas fir logs greater than 50 cm in diameter may require 180–200 years, considerably longer than for small-branch litter. Their data indicate that other variables, i.e. surface-to-volume ratio, become important in wood decay as particle size increases. Consequently, relationships established in this study should not be applied directly to material other than foliage and fine woody material.

The forest floor is heterogeneous and frequently subject to fluctuations in temperature and moisture. Among the factors influencing the forest floor environment are the complex mixture of materials in the floor, depth of the litter layer, annual precipitation pattern, vegetation cover, and insolation. On the Andrews Experimental Forest, Douglas fir needle litter shows almost no weight change during the summer (Julian days 124–200) of the 1st year, probably because of the low precipitation during this period (Fig. 1). Turner and Singer (1976) report a similar pattern in a western Washington subalpine *Abies amabilis* forest. At the stand level, needle decomposition on the Andrews Experimental Forest is highly correlated ($r = 0.987$) with temperature and moisture (Table 3) and reflects the ordination of plant communities along temperature–moisture gradients proposed by Dyrness *et al.* (1974). The deviation of one modal stand (site 17) from the ordination emphasizes the necessity of selecting uniform stands and adequate sampling procedures.

Conclusions

Several conclusions for decomposition research result from this study. First is the need to use cumulative data for more than 1 year in calculating decomposition rate constants (k) of slowly decomposing materials. Constants for Douglas fir needle litter, for example, were consistently higher when calculated after 1 year than after 2 years. A second problem is the increasing variance in weight loss with time, probably because of microsite effects becoming more pronounced. The number of observations required per site to limit the variance to 1% of mean weight loss after 1 year, calculated using Stein's two-stage estimate of sample size (Steel and Torrie 1960), is 22 needle litter bags; after 2 years 246 litter bags have to be collected per site.

It is possible to detect subtle differences in decomposition rate between stands in the same locality by using an adequate statistically designed experiment. However, a simplified model for each substrate can be used for all low elevation sites on the H. J. Andrews Experimental Forest in the construction of a generalized nutrient cycling or decomposition model since the regression models for each substrate were very similar.

Acknowledgments

This research was supported by National Science Foundation grant No. BMS 76-02656 to the Coniferous Forest Biome (contribution No. 237) and done in cooperation with the Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Corvallis, Oregon, under supplement 147 to the master memorandum of understanding between the Forest Service and Oregon State University. The assistance of R. L. Fredriksen in site selection and precipitation data, E. Holcombe for nutrient analysis, and W. H. Emmingham for plant moisture stress and temperature growth index data is acknowledged. This is contribution No. 1097 from the Forest Research Laboratory, Oregon State University.

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