Comparison of decomposition models using wood density of Douglas-fir logs[1]

Joseph E. Means

*Pacific Northwest Research Station, United States Department of Agriculture Forest Service,
Corvallis, OR, U.S.A. 97331*

Kermit Cromack, Jr.

Department of Forest Science, Oregon State University, Corvallis, OR, U.S.A. 97331

AND

Paul C. MacMillan

Department of Biology, Hanover College, Hanover, IN, U.S.A. 47243

Means, J. E., K. Cromack, Jr., and P. C. MacMillan. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. For. Res. 15: 1092–1098.

Logs of *Pseudotsuga menziesii* (Mirb.) Franco that had been on the ground for up to 313 years were grouped into five decay classes that ranged from 1, essentially undecayed, to 5, soft and incorporated into the forest floor but still identifiable. The mean residence times on the forest floor were 7, 17, 33, 82, and 219 years for decay classes 1 through 5, respectively. The single-exponential model of litter decomposition was fitted to the density of these logs. The summation-exponential model was constructed by summing single-exponential models fitted to lignin, cellulose, and the acid detergent soluble fraction. Both models gave virtually identical, statistically significant fits to the data. Wood density of these Douglas-fir logs decreased more slowly than that of most species other researchers have studied. The single-exponential model gave mineralization rates (k) of 0.0063 and 0.0070 year^{-1} when residence time and decay class age (mean residence time of the decay class), respectively, were used as the independent variable. Lignin decayed more slowly than cellulose or the fraction soluble in hot acid detergent, both of which decayed at rates that were not significantly different; thus, the summation-exponential model is recommended when these constituents are of interest.

Means, J. E., K. Cromack, Jr. et P. C. MacMillan. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. For. Res. 15: 1092–1098.

Des billes de *Pseudotsuga menziesii* (Mirb.) Franco qui reposaient sur le sol depuis jusqu'à 313 ans ont été groupées en cinq classes de décomposition allant de 1 (les billes essentiellement non décomposées) à 5 (les billes tendres et incorporées à la couverture morte, mais encore identifiables). Le modèle d'exponentielle unique de décomposition de la litière fut ajusté à la densité de ces billes. Le modèle d'exponentielle sommative fut construit par la somme des modèles d'exponentielle simple ajustés à la lignine, à la cellulose et à la fraction soluble dans un détergent acide chaud. Les deux modèles traduisent fidèlement les valeurs observées. La densité du bois de ces billes de douglas a diminué plus lentement que celle de la plupart des autres espèces étudiées par d'autres chercheurs. Lorsque le temps de résidence et le temps de résidence moyen par classe de décomposition furent utilisés comme variable indépendante, le modèle d'exponentielle unique a fourni les taux de minéralisation (k) de 0,0063 et 0,0070 an^{-1}, respectivement. La lignine s'est décomposée plus lentement que la cellulose ou la fraction soluble dans un détergent acide chaud; les taux de décomposition de ces deux dernières fractions n'étaient pas statistiquement différents. En conséquence, le modèle d'exponentielle sommative est recommandé lorsqu'on porte un intérêt particulier à ces deux dernières fractions.

[Traduit par le journal]

Introduction

Several equations have been proposed for modeling litter decomposition through time. The single-exponential model (Jenny *et al*. 1949; Olson 1963) has been used widely to estimate rates of litter decomposition in many areas of the world. Minderman (1968) suggested that this model is an oversimplification of litter-decay processes, because various carbon constituents decay at different rates as a result of their varying quality as substrate for decomposing organisms. He proposed as a general decomposition model the summation of the exponential decay of individual carbon constituents (e.g., lignin, cellulose) making up given litter components (e.g., leaves, boles). The difference between Minderman's (1968) summation-exponential model and a single-exponential model becomes more evident over long periods during which weight loss is sequentially dominated by increasingly refractory constituents. These models are special cases of the general decomposition model presented by Carpenter (1981).

A version of Minderman's (1968) model, the summation of two exponential decay functions, has been fitted to total weight-loss data by Bunnell and Tait (1974), Lousier and Parkinson (1976), and Jenkinson (1977) when information on different carbon constituents was not available. Bunnell *et al*. (1977) used the sum of single-exponential models fitted to ethanol-soluble and nonethanol-soluble compounds.

We studied a chronosequence of decaying logs of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in a 450-year-old forest in the Oregon Cascade Range. Our first purpose was to estimate mineralization rates (leaching and respiration loss) of wood and of its separate carbon constituents. Our second purpose was to use the data on density and carbon constituents to examine the applicability of the single-exponential and summation-exponential models to decrease of wood density in

these logs. Mass of logs and standing dead boles and changes in log chemistry will be reported elsewhere.

Methods

Study site description

The data were collected on the H. J. Andrews Experimental Forest in the Western Cascades of Oregon. The gently sloping (5−20%) study site was 5 ha of forest dominated by 100−190 cm diameter, 40- to 55-m tall Douglas-firs 350 to 470 years old. Younger western hemlock, *Tsuga heterophylla* (Raf.) Sarg., and Pacific silver fir, *Abies amabilis* Dougl. ex Forbes, were common in the understory. The site was a warm variant of an *Abies amabilis/Tiarella unifoliata* habitat type (Dyrness *et al.* 1974; Zobel *et al.* 1976). Mean January, mean July, and mean annual air temperatures for 1973 to 1982 were −0.4−1.1°C, 13.8−15.5°C, and 5.7−7.3°C, respectively, for three nearby forested sites judged to have generally similar environments. Much of the mean annual precipitation of 220 cm accumulates in a 1.0- to 1.5-m snow pack at this 1070-m elevation. Soils were deep (more than 2 m to bedrock) inceptisols (Anonymous 1975) or silt loam texture, with large amounts of total nitrogen (10 100 kg·ha^{-1}, SE = 400) and total carbon (220 000 kg·ha^{-1}, SE = 2 000) within the top 100 cm of mineral soil. Logs were common on the site (292 ha^{-1}).

Field methods

Douglas-fir logs were grouped into five decay classes by visual criteria previously described by Triska and Cromack (1979) and Sollins (1982). Logs in decay class 1 looked least decayed, had intact bark and branches, and showed no rot. Decay class 3 logs had lost most of their bark and all of their branches and had well-decayed sapwood but generally sound heartwood. Logs in decay class 5 had lost essentially all of their bark, were in an advanced stage of brown cubical rot (Blanchette 1980), and had oval cross sections.

Residence time was determined for each log in the chronosequence, either by dating a wedge cut from a scar on a live tree that was injured when the log fell (Graham and Cromack 1982) or by determining age at the root collar of the one to three largest western hemlocks growing on top of the log and using the greatest age. Twenty-five years were added to hemlock ages to allow time for hemlock establishment on nurse logs (cf. Graham (1981), who added 50 years for hemlocks to become established and grow to 1.4 m height). Only hemlock ages greater than 110 years were used, to minimize the effect of variation in the time between log fall and hemlock establishment.

Each log was also assigned a decay class age equal to the mean residence time for all dated logs in its decay class and this was used as an independent variable. Residence time does not include the time a bole section decays while standing, which can be quite variable (Cline *et al.* 1980). A live tree blown over by the wind will start its residence on the ground as a decay class 1 log, but a bole that died several decades before falling may start as a decay class 3 or 4 log. Decay class age is an index of state of decay on a temporal scale that reflects, in part, differences in initial states of decay of logs and so should be able to explain more variation in the data when models are fitted. This, in turn, would increase the ability to distinguish between models.

Analytical methods

In January 1978, samples were collected from dated logs in the 2.5-ha eastern portion of the stand. Because our objective was to sample all types of fallen, decaying Douglas-fir wood, we used the following guidelines. If the log contained sections of different decay classes, a sample was taken from each section. If end diameters differed by 25% or more, samples were taken near each end; otherwise, samples were taken from the center. Different types of rot (brown rot, white rot) as well as solid wood were collected separately from the heartwood and sapwood (when distinguishable). Thus, 72 samples were collected from 30 Douglas-fir logs. Samples were handled carefully to minimize breakage. Wet volumes were determined in the field by measuring samples as geometric solids or in the laboratory by water displacement of samples enclosed in lightweight plastic bags held closely around the sample by a vacuum. Dry (70°C) volumes

were determined by the latter technique. Thus, sample volume included volume of voids of all sizes as well as volume of chemical constituents of wood. Dried samples were then weighed to determine density after roots had been removed.

Samples collected in July and October 1976 were handled differently, so density estimates of these samples were adjusted using the January 1978 data. These earlier 91 samples were collected from 40 Douglas-fir logs in the adjacent 2.3-ha western portion of the stand. Methods for field sampling and dividing samples in the laboratory were as described above. After drying to constant weight at 70°C, volume was determined three times by submersion of the samples, summing water displaced plus water absorbed, and mean values were used. When fragile samples broke, dry weight and volume were determined on intact subsamples that may have been denser than the total sample. Water probably flowed rapidly in and out of large voids in some highly decayed samples, resulting in underestimates of volume and overestimates of density.

Percent volume loss with drying of the January 1978 samples averaged 10.4% and did not differ significantly among decay classes, so the volumes of the 1976 samples were corrected for this shrinkage. After this correction, average densities of the decay class 3 and 5 samples in the later group were significantly ($p < 0.05$) lower (15 and 39%, respectively) than those of the first group; the decay class 4 densities were 13% lower. Use of intact pieces of broken samples and presence of large pores in more decayed samples apparently resulted in density overestimates in the 1976 samples. These class 3, 4, and 5 densities were decreased by these percentages to correct this error.

To estimate wood-mineralization rate (as decrease in density) when initial sample weights are unknown, initial volumes, present weights, and decomposition times must be known. Present volume was used as initial volume for samples of decay classes 1−4 because there was no indication that the wood structure had changed shape. The oldest logs (class 5), however, had decayed to the extent that they were oval in cross section; thus, the present volume of the sample was less than the initial volume. This volume loss could be caused by vertical shrinkage when compression strength is reduced to a point where compaction can occur or by relatively rapid decomposition near the upper surface of logs mantled with the nutrient-rich forest floor and fine litter that is known to decay rapidly ($k = 0.22-0.31$ year^{-1} for mass loss of needles (Fogel and Cromack 1977)). To estimate this volume loss, we measured cross-section heights and widths of 40 other class 5 Douglas-fir logs and obtained a height:width ratio (0.431, SE = 0.018), which is an estimate of the proportion of the initial sample volume remaining. Multiplying the densities of all class 5 samples by 0.431 provided a correction for this volume loss. We have observed other processes that influence the shape of class 5 Douglas-fir logs and the accuracy of this ratio, although we cannot estimate the importance of these processes. For example, fragmentation of material off the side of logs will tend to make the ratio an underestimate, and fragmentation of the tops or bottoms of logs will tend to make the ratio an overestimate.

To separate the wood into carbon constituents, which we hypothesized would decay at different rates, the 91 samples collected in 1976 were analyzed following the methods of Van Soest (1966; Goering and Van Soest 1970). The hot acid detergent soluble fraction (ADSF) includes lipids, sugars, organic acids, starch, protein, nonprotein nitrogen, pectin, and hemicellulose (Van Soest 1966); it probably also includes uncomplexed phenols. Lignin, cellulose, and lignified nitrogen compounds remained and these were distinguished by digestion of cellulose in 72% H$_2$SO$_4$, leaving the lignin and ash undigested (Van Soest 1966; Goering and Van Soest 1970). The lignin fraction was determined by subtraction of the ash left after oxidation in a muffle furnace. It probably includes recalcitrant, humuslike decomposition products (Martin and Haider 1980). Ash-free density (total density minus ash) was used in the statistical analyses. Carbon constituents were expressed gravimetrically (milligrams per gram) and volumetrically (milligrams per cubic centimetre) after multiplying by wood density (grams per cubic centimetre). Volumetric values were needed for fitting the summation-exponential model.

TABLE 1. Decay class age, sample density, large-end diameter, and surface:volume ratio (mean ± SEM, n in parentheses) of sampled Douglas-fir logs by decay class on the H. J. Andrews study site. The densities of decay classes 3, 4, and 5 are based on the second group of 72 samples

Decay class	Decay class age[a] (years)	Sample density $(mg \cdot cm^{-3})$	Large-end diameter (cm)	Surface:volume ratio $(m^2 \cdot m^{-3})$
1	7.0±2.0(16)	416±18(22)	103±9(13)	4.90±0.55(13)
2	16.7±2.6(16)	317±20(29)	113±6(16)	4.34±0.26(16)
3	32.7±5.1(28)	274±14(22)	74±5(30)	7.34±0.81(30)
4	81.6±9.3(19)	224±23(11)	57±4(25)	8.57±0.40(25)
5	218.7±17.9(15)	80±7(12)[b]	50±4(16)	10.49±0.83(16)

[a] Decay class age is the mean residence time on the forest floor of dated logs in each decay class.
[b] Density of decay class 5 has been multiplied by 0.431 to correct for vertical shrinkage, as explained in the text.

Models

The single-exponential model has the following form:

[1] $Y = Be^{-kt}$

where Y is the density (milligrams per cubic centimetre), e is the base of the natural logarithm, t is the time (years) and B and k are derived coefficients, B is the density at time zero and k is the decay coefficient.

The summation-exponential model (Minderman 1968), which is the summation of a set of single-exponential models for different constituents, has the following form

[2] $Y = B_1e^{-k_1t} + B_2e^{-k_2t} + B_3e^{-k_3t}$

in our study because we partitioned density into three constituents, ADSF, cellulose, and lignin.

Fitting and comparing models

We tested each hypothesis twice, once using residence time and once using decay class age as the independent variable. The first test was for significance of the simplest model, the single exponential. The logarithmic transformation of Eq. 1,

[3] $\ln Y = \ln B - kt$

made the variance more uniform across the range of the independent variable (Draper and Smith 1981). Equation 3 was fitted by linear least squares to all the density data ($n = 163$) and the F-ratio calculated to test the hypothesis that $k = 0$.

The next test was a comparison between the single-exponential model and the summation-exponential model. Using samples for which carbon constituent data were available ($n = 91$), Eq. 3 was fit to the wood density data for the single-exponential model and to volumetric ADSF, cellulose, and lignin data for the summation-exponential model. In both cases, estimates of the dependent variables were calculated as

[4] $\hat{Y}_i = e^{(\ln B - kt_i + s^2/2)}$

where $s^2/2$, half the error mean square when Eq. 3 is fit, is the correction for logarithmic bias found to be adequate by Beauchamp and Olson (1973). For the summation-exponential model, the estimates of ADSF, cellulose, and lignin were summed to obtain an estimated wood density, $\hat{Y}_i$. For each model, the residuals (measured minus estimated wood density) were calculated for each datum and squared:

[5] $E_i^2 = (Y_i - \hat{Y}_i)^2$

We compared the models with a paired t-test (Snedecor and Cochran 1967) of the hypothesis that the mean of the squared residuals of the single-exponential model equaled that of the summation-exponential model. A histogram of the differences between paired residuals appeared approximately normal in each use of this test. This uncommon use of the paired t-test was necessary because standard methods, such as analysis of variance (Draper and Smith 1981), are

not applicable to our method of constructing the summation-exponential model using chemical data on the different carbon constituents.

Comparing independent variables and carbon constituents

We hypothesized that using decay class age instead of residence time as the independent variable would improve model fit because the unknown time a bole decays while standing is not included in its residence time on the forest floor. Therefore, for both models we tested the hypothesis that the mean of the squared residuals using decay class age as the independent variable was greater than or equal to that using residence time, by a paired t-test as described above.

Differences in the rates of decay of the carbon constituents were examined with a conventional t-test.

Significance levels and measures of confidence

The imprecision in the residence times based on hemlock ages affected our methods in two ways. The techniques used to fit the models assume the independent variable (residence time or decay class age) is known precisely (Draper and Smith 1981). We judge that residence times estimated from hemlock ages rarely differ more than 20 years from true residence time; this is 10% of the mean of residence times (about 200 years) from this source. Although dates with a potential discrepancy of 10% are valuable for examining the dynamics of wood decay, they cause the regression error associated with fitting models to be underestimated, so statistical tests that appear to be marginally significant may not be and conventional measures of confidence such as standard errors will be underestimated. For this reason we set $p = 0.001$ as the level for rejecting null hypotheses and do not report standard errors for the coefficients.

The densities of the 1976 decay class 3, 4, and 5 samples were corrected for apparent overestimation using the 1978 samples and so were not independent of the 1978 data. Therefore, the degrees of freedom were reduced by this number of samples (to $n = 96$) in all tests involving both data sets.

The proportion of variation in wood density explained (PVE) by each model was calculated as

[6] $PVE = [\Sigma(\bar{Y} - Y_i)^2 - \Sigma(\hat{Y}_i - Y_i)^2]/\Sigma(\bar{Y} - Y_i)^2$

This statistic is used instead of R^2 because the conventional R^2 for the single-exponential model is for the transformed data and no conventional method for computing R^2 exists for our method of constructing the summation-exponential model.

Results

Characteristics of these logs changed through the decay classes as expected (Table 1). Wood density consistently decreased with decay class. Log diameter was inversely correlated with decay class and decay class age, and surface:volume ratio was positively correlated with these characteristics.

Figures 1 and 2 illustrate the fit of the single-exponential

TABLE 2. Coefficients and the proportion of variation in the untransformed data explained by the single-exponential and summation-exponential models. The single-exponential model was fit to the full data set ($n = 163$) and the summation-exponential model was fit to the samples for which carbon constituents were determined ($n = 91$)

Model	Dependent variable	Coefficients		Proportion of variation explained
		B^a ($mg \cdot cm^{-3}$)	k ($year^{-1}$)	
Using residence time as the independent variable				
Single exponential	Density	350	0.0063	0.503
Summation exponential	ADSF[b]	90	0.0094	0.412
	Cellulose	150	0.0109	0.361
	Lignin	140	0.0039	0.231
	Density	—	—	0.466
Using decay-class age as the independent variable				
Single exponential	Density	370	0.0070	0.613
Summation exponential	ADSF[b]	100	0.0094	0.483
	Cellulose	150	0.0117	0.534
	Lignin	150	0.0045	0.421
	Density	—	—	0.663

NOTE: Measures of variability for the model coefficients are not given because the estimated regression error is inaccurate (see Methods).

[a] The intercepts are corrected for logarithmic bias (Beauchamp and Olson 1973).
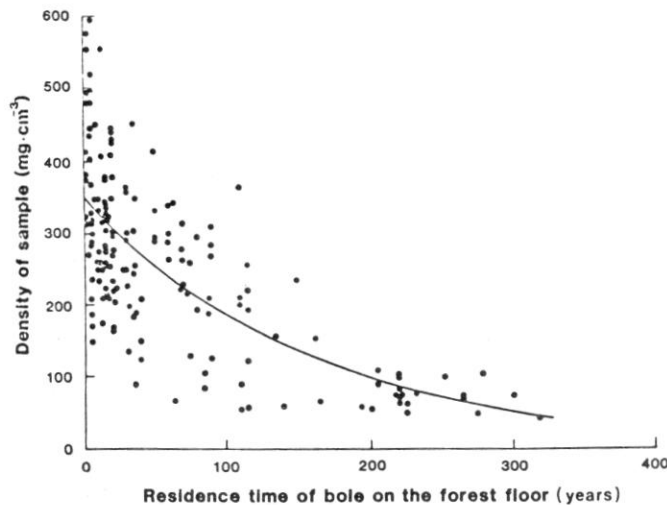
[b] Acid detergent soluble fraction.

FIG. 1. The single-exponential model fit to the data set of 163 density samples with residence time of the log on the forest floor as the independent variable.
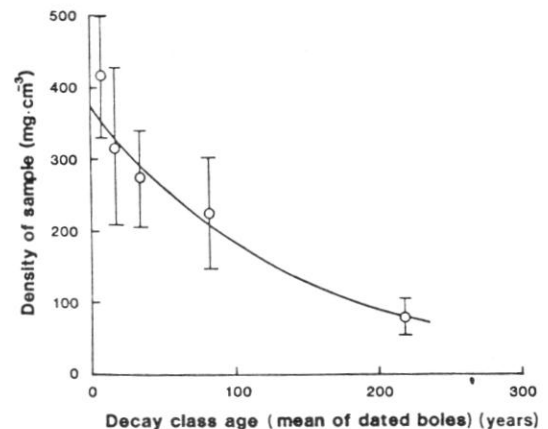

FIG. 2. The single-exponential model fit to the data set of 163 density samples with decay class age as the independent variable. The circles represent decay class means and the bars represent the standard deviations.

model using residence time and decay class age, respectively, as the independent variable and show the influence of these variables on the position of the data on the abscissa. Using these independent variables, the mineralization rates (k) were 0.0063 and 0.0070 $year^{-1}$ and the intercepts were 350 and 370 $mg \cdot cm^{-3}$, respectively. The intercepts were appreciably less than the specific gravity (450 $mg \cdot cm^{-3}$) for undecayed Douglas-fir wood in the Pacific Northwest (Anonymous 1974).

The single-exponential and summation-exponential models were both highly significant ($p < 0.0001$) and explained similar proportions of the variation in wood density regardless of the independent variable used (Table 2). The fit of the summation-exponential model was not significantly different ($p < 0.10$) than that of the single-exponential model. Decay class age explained significantly more variation in the data

($p < 0.0005$) than did residence time for both decomposition models (Table 2).

The single-exponential models of the carbon constituents were all highly significant ($p < 0.0001$) (Table 2). Lignin decayed significantly slower ($p < 0.001$) than cellulose or ADSF when either residence time or decay class age was used as the independent variable (Fig. 3, Table 2). ADSF decayed more slowly than cellulose, the difference between their decay rates being greatest with decay class age as the independent variable ($p < 0.05$). This difference, however, was not judged significant because we chose $p = 0.001$ as the level for rejecting null hypotheses, as described in the methods. This was the only test affected by this choice.

Discussion

Although our data show a large amount of variability (Fig. 1), we judged that the large number of samples and long
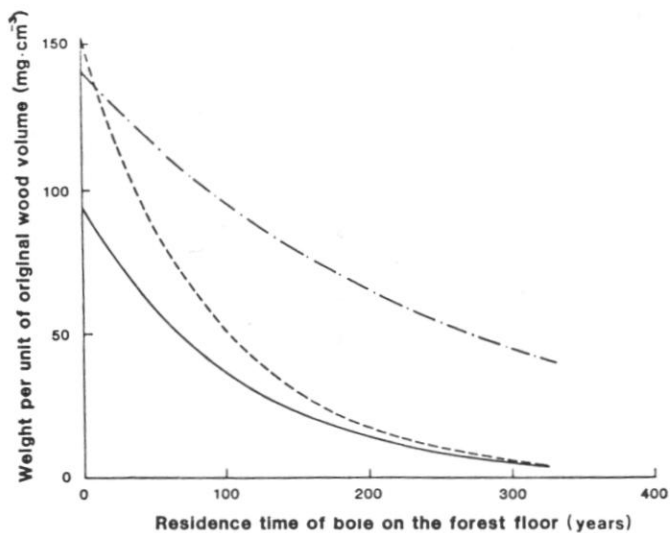
FIG. 3. The single-exponential model fit to volumetric concentration of the acid detergent soluble fraction (——), cellulose (– – – –), and lignin (·–·–·) with residence time as the independent variable.

time span might allow distinguishing among models. Others who have studied wood decay in North American conifers have encountered similar or greater variability in decay, as indicated by similar or smaller R^2 values (range, 0.23−0.67) using the single-exponential model (Lambert et al. 1980; Graham 1981; Foster and Lang 1982; Graham and Cromack 1982). Thus, results of comparisons among models using this data set should be useful. Also, the data on carbon constituents allow the unusual opportunity to compare the summation-exponential model for logs.

Our mineralization coefficients of 0.0063 and 0.0070 year^{-1} (Table 2) are comparable to Graham's (1981) (0.0053 year^{-1}) for Douglas-fir logs at lower altitudes in our area. In contrast, western hemlock (0.0100 year^{-1}), Sitka spruce (Picea sitchensis (Bong.) Carr., 0.0111 year^{-1}; Graham and Cromack 1982), balsam fir (Abies balsamea (L.) Mill., 0.0112 year^{-1}; Lambert et al. 1980), 10 southern Appalachian hardwood and softwood species (0.04−0.20 year^{-1}; Harmon 1982), and white oak (Quercus alba L., 0.0295 year^{-1}; MacMillan 1981) all have greater mineralization coefficients than Douglas-fir. One reason Douglas-fir logs decay more slowly is their decay resistance (Anonymous 1974), caused in large part by up to 1.5% of the polyphenolic dihydroquercetin (Scheffer and Cowling 1966). The generally large size of our logs (Table 1) may also slow their decay, for we noticed the small-diameter ends of logs usually have a higher decay class than the larger ends if the difference in diameters is more than about 50 cm. Graham (1981), however, found decay rates of Douglas-fir logs in three diameter size classes were not significantly different.

The intercepts for both models considered (Table 2) are lower than the generally accepted value for sound Douglas-fir wood of 450 mg·cm^{-3}. This is probably caused in part by the inability of the models to incorporate the rapid initial decay indicated by the relatively large decrease in density between class 1 and class 2 samples. Rapid initial decay of sapwood is probably the most important cause, as indicated by lower sapwood than heartwood densities for decay classes 1 (370 vs. 420 mg·cm^{-3}) and 2 (280 vs. 350 mg·cm^{-3}) (J. E. Means, unpublished data), although the differences were not significant.

The low lignin-mineralization rate is consistent with the predominance of brown cubical rot in class 5 Douglas-fir logs (present in 80% of our class 5 samples) that may persist for centuries.

The models

Both models describe this variable data set equally well, judging by the proportion of variation each explains (Table 2). The summation-exponential model has more terms but provides no better fit than the single-exponential model, thus the latter is preferred on statistical grounds for this data set. The probability that this inference is incorrect (i.e., a type II error occurred) is unknown and we feel the summation-exponential model is the most applicable to these logs for three reasons. First, lignin decayed more slowly than did ADSF and cellulose (Fig. 3). This supports Minderman's (1968) general hypothesis that the true decay curve should be the sum of several exponential curves and not a single-exponential curve. Second, the ADSF constituent lumps a number of substances that probably decay at different rates (compare lipids, sugars, and starch with phenols). This probably explains why ADSF apparently decays more slowly than cellulose. Although the summation-exponential model does not give a significantly better fit, it provides the theoretical framework for incorporating the different mineralization coefficients of the constituents into the decay model and so will be the most applicable when these constituents are of interest. Third, it has greater intercepts (390 and 400 mg·cm^{-3} with residence time and decay class age as independent variables, respectively) that are closer to the density of sound wood (450 mg·cm^{-3}; Anonymous 1974) than does the single-exponential model (350 and 370 mg·cm^{-3} with residence time and decay class age, respectively).

Clark and Paul (1970) point out that the summation-exponential model will overestimate the actual amount of material lost because slowly decomposing constituents are produced by heterotrophs (see also Carpenter 1981), and some constituents (e.g., celluloses) may be masked by more recalcitrant constituents. This overestimation does not occur in our study because decomposition products are included in the lignin, cellulose, and acid detergent soluble fractions as chemically separated (e.g., the acid detergent soluble fraction contains several compounds) so the mineralization coefficients include any effects of masking.

The asymptotic model, a single-exponential model with an asymptote (Howard and Howard 1974), fit no better than the single-exponential model (J. E. Means, unpublished).

The data

This data set has the advantage of covering a long period relative to data sets of most other studies (e.g., Howard and Howard 1974; Swift et al. 1976; Fogel and Cromack 1977; Grier 1978; Graham 1981; Graham and Cromack 1982). The half-lives for the single-exponential model fit to density using residence time and decay class age are 111 and 99 years, respectively, both of which are well within the time spanned by the data set (Figs. 1 and 2).

Our data contains several types of error inherent to a chronosequence study. One problem is that the initial density of each sample is unknown and variation in initial density reduces our ability to distinguish between models. The variation in density of samples from class 1 logs (coefficient of variation (CV), 20%) (Fig. 2) is a result of the variation in the initial density of sound wood (CV, 10%; based on unpublished data from live Douglas-fir trees on drier sites from M. Harmon,

Oregon State University), as well as our efforts to sample all types of rot. Graham (1981) found a coefficient of variation of 10% for decay class 1 Douglas-fir logs, based on samples not separated into different types of rot. Another problem is that long residence times must be estimated using hemlock ages because old scars are difficult to find. The time between stem fall and hemlock establishment on logs is influenced by the decay state of the log when it falls, microclimate, and occurrence of mycorrhizal associates (Christy et al. 1982).

Several sources of error in our data undoubtedly cause the apparent mineralization coefficients given in Table 2 to differ from the true values. First, many stems begin decomposition as standing dead boles, as indicated by the large biomass (134 t·ha^{-1}) and number (30 ha^{-1}) of standing dead Douglas-fir stems over 3.5 m tall (J. E. Means, unpublished data) and the presence of many decay class 3 and 4 logs with short residence times, originating from fallen snags (cf. Cline et al. 1980). Thus, residence time and decay class age are underestimates of decomposition time and more so for higher than for lower decay classes. This would tend to increase the apparent mineralization rates. This is supported by Graham (1981), who found a mineralization rate slightly lower than ours using samples taken only from root-thrown boles (i.e., thought to be alive when they fell).

Second, the residence times estimated from hemlock ages may be underestimated if the understory hemlocks in our stand did not develop growth rings in some years, as has been found in Washington (C. D. Oliver, University of Washington, personal communication). This would also tend to increase the apparent mineralization rates.

Third, surface : volume ratio and decay class age are correlated (Table 1), in part because logs with greater residence times fell when the stand was younger and average diameter was smaller. Smaller logs from younger stands and tree crowns have a higher proportion of sapwood, so they probably decay more rapidly. If this occurs, as indicated by our observation that small-diameter ends of logs generally have higher decay classes than the large-diameter ends, apparent mineralization rates are probably increased for all but the small-diameter pieces.

Fourth, since we studied a chronosequence of logs rather than monitoring a cohort through time, we could only examine what remains. Logs, or portions thereof, which decayed relatively slowly because, for example, of genetically based, more recalcitrant composition or their position would last longer and be more likely to be sampled by us many years after they reached the forest floor than would logs that decayed more rapidly. This source of error would tend to decrease the apparent mineralization rates.

Fifth, the whole log does not start decomposing when a large tree dies. Wood deep within an intact log may not be colonized by microorganisms for decades. This source of error will tend to decrease the apparent mineralization rates.

The first three sources of error have the opposite effect of the last two and the direction of the net effect cannot now be determined. The mineralization rate of 0.0053 year^{-1} (Graham 1981) for Douglas-fir logs at lower elevation near our study area is close to our values (0.0063 and 0.0070 year^{-1}), but it is probably also influenced by the last three of these sources of error. More accurate estimates of mineralization rates of Douglas-fir logs must await long-term studies now being undertaken (M. Harmon, Oregon State University, personal communication).

Factors not considered

When interpreting our results, especially the mineralization rates, the reader should understand that they are influenced by several uncontrolled natural factors, including the following. (i) The environment of a log can change significantly during the hundreds of years it is rotting on the ground. Portions of a log may be suspended above the ground for a few decades after it falls, then settle to the ground, and finally become covered with litter and more or less incorporated into the forest floor. The stand environment changes as succession and disturbances alter stand structure. On the time scale of this study (300+ years), long-term fluctuations in climate may be important (Layser 1980). (ii) Old-growth Douglas-firs commonly contain significant rot in their centers when living (e.g., Phellinus (Fomes) pini (Thore ex Fr.) Pilat.; Boyce and Wagg 1953) and those that do probably decay more rapidly than those that do not. (iii) The decay rate of a constituent as identified by standard chemical and statistical procedures may change. For example, one type of lignin may predominate at the beginning of the decomposition process and another kind may predominate later on. As another example, the C:N ratio in our logs decreased strikingly with time (J. E. Means, unpublished data), so lignin in a decay class 5 log enriched in nitrogen may decay faster than lignin in a decay class 1 log. (iv) Decomposition products (humuslike material) do not decrease exponentially in absolute amount because they are produced by heterotrophs as well as destroyed (Clark and Paul 1970; Swift et al. 1979; Martin and Haider 1980; Carpenter 1981). (v) Carbon-constituent decay rates probably change as microbial succession in logs progresses (Blanchette 1980). We noticed that incidence of brown rots increased and that of white rots decreased in decay class 4 and 5 logs. These last three factors reduce the variation that can be accounted for by the models of carbon-constituent decay (Table 2). (vi) Decay class 4 and 5 logs often contain mycorrhizal western hemlock roots that probably influence decay rates by their physical growth, exudates, and nutrient and water uptake.

Implications for future studies

Grouping Douglas-fir logs into decay classes based on visual criteria produces a useful stratification, even when residence times of the logs are known. This is indicated by the fact that a significantly greater proportion of the variation was explained by decay class age, the mean residence time for each decay class, than by residence time alone (Table 2). Decay of these logs is influenced by other factors in addition to residence time and the visual decay classification scheme we used was able to explain a significant amount of this additional variation.

Clearly, the long-term process of Douglas-fir log decomposition is complex. The variability in our data (Fig. 1) and that of Graham (1981) is evidence of this complexity; some reasons for it have been proposed in the preceding discussion. In part because of this complexity, we suggest using the single-exponential model for mineralization of Douglas-fir logs unless the dynamics of the carbon constituents are of interest.

provided helpful statistical guidance. J. F. Franklin, R. L. Graham, M. E. Harmon, G. E. Lang, J. S. Olson, and P. Sollins, among others, provided valuable reviews.

ANONYMOUS. 1974. Wood handbook: wood as an engineering material. Rev. ed. Agric. Handb. (U.S. Dep. Agric., Sci. Educ. Adm.), No. 72.

ANONYMOUS. 1975. Soil classification. Agric. Handb. (U.S. Dep. Agric., Sci. Educ. Adm.), No. 436.

BEAUCHAMP, J. J., and J. S. OLSON. 1973. Correction for bias in regression estimates after logarithmic transformation. Ecology, 54: 1403–1407.

BLANCHETTE, R. A. 1980. Wood decay: a submicroscopic view. J. For. 78: 734–737.

BOYCE, J. S., and J. W. B. WAGG. 1953. Conk rot of old-growth Douglas-fir in western Oregon. Bull. Oreg. For. Prod. Lab. No. 4.

BUNNELL, F. L., and D. E. N. TAIT. 1974. Mathematical simulation models of decomposition process. *In* Soil organisms and decomposition in tundra. *Edited by* A. J. Holding, O. W. Heal, S. F. MacLean, Jr., and P. W. Flanagan. Tundra Biome Steering Committee, Stockholm, Sweden. pp. 207–225.

BUNNELL, F. L., D. E. N. TAIT, and P. W. FLANAGAN. 1977. Microbial respiration and substrate weight loss. II. A model of the influences of chemical composition. Soil Biol. Biochem. 9: 41–47.

CARPENTER, S. R. 1981. Decay of heterogenous detritus: a general model. J. Theor. Biol. 89: 539–547.

CHRISTY, E. J., P. SOLLINS, and J. M. TRAPPE. 1982. First-year survival of *Tsuga heterophylla* without mycorrhizae and subsequent ectomycorrhizal development on decaying logs and mineral soil. Can. J. Bot. 60: 1601–1605.

CLARK, F. E., and E. A. PAUL. 1970. The microflora of grassland. Adv. Agron. 22: 375–435.

CLINE, S. P., A. B. BERG, and H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44: 773–786.

DRAPER, N. R., and H. SMITH. 1981. Applied regression analysis. 2nd ed. John Wiley & Sons, New York.

DYRNESS, C. T., J. F. FRANKLIN, and W. H. MOIR. 1974. A preliminary classification of forest communities in the central portion of the Western Cascades in Oregon. U.S. Int. Biol. Programme, Coniferous For. Biome, Bull. No. 4.

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

FOSTER, F. R., and G. E. LANG. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. 12: 617–626.

GOERING, H. K., and P. J. VAN SOEST. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agric. Handb. (U.S. Dep. Agric., Sci. Educ. Adm.), No. 379.

GRAHAM, R. L. L. 1981. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. thesis, Oregon State University, Corvallis, OR.

GRAHAM, R. L., and K. CROMACK, JR. 1982. Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 511–521.

GRIER, C. C. 1978. A *Tsuga heterophylla – Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can. J. For. Res. 8: 198–206.

HARMON, M. E. 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. Oecologia, 52: 214–215.

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

JENKINSON, D. S. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from ^{14}C labelled rye grass decomposing under field conditions. J. Soil Sci. 28: 424–434.

JENNY, H., S. P. GESSEL, and F. T. BINGHAM. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68: 419–432.

LAMBERT, R. L., G. E. LANG, and W. A. REINERS. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology, 61: 1460–1473.

LAYSER, E. F. 1980. Forestry and climatic change. J. For. 78: 678–682.

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

MACMILLAN, P. C. 1981. Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. Am. Midl. Nat. 106: 335–344.

MARTIN, J. P., and K. HAIDER. 1980. Biodegradation and stabilization after two years of specific crop, lignin and polysaccharide carbons in soils. Soil Sci. Soc. Am. J. 44: 1250–1255.

MASER, C., R. G. ANDERSON, K. CROMACK, JR., J. T. WILLIAMS, and R. E. MARTIN. 1979. Dead and down woody material. *In* Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. *Edited by* J. W. Thomas. Agric. Handb. (U.S. Dep. Agric., Sci. Educ. Adm.), No. 553.

MINDERMAN, G. 1968. Addition, decomposition and accumulation of organic matter in forests. J. Ecol. 56: 355–362.

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

SCHEFFER, T. C., and E. B. COWLING. 1966. Natural resistance of wood to microbial deterioration. Annu. Rev. Phytopathol. 4: 147–170.

SNEDECOR, G. W., and W. G. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State University Press, Ames, IA.

SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can. J. For. Res. 12: 18–28.

SWIFT, M. J., O. W. HEAL, and J. M. ANDERSON. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley, CA.

SWIFT, M. J., I. N. HEALEY, J. K. HIBBERD, J. M. SYKES, V. BAMPOE, and M. E. NESBITT. 1976. The decomposition of branch-wood in the canopy and floor of a mixed-deciduous woodland. Oecologia, 26: 139–149.

TRISKA, F. J., and K. CROMACK, JR. 1979. The role of wood debris in forests and streams. *In* Proceedings of the 40th Annual Biology Colloquium. Forests: fresh perspectives from ecosystem analysis. *Edited by* R. H. Waring. Oregon State University Press, Corvallis, OR. pp. 117–190.

VAN SOEST, P. J. 1966. Nonnutritive residues: a system of analysis for replacement of crude fiber. J. Assoc. Off. Anal. Chem. 49: 546–551.

ZOBEL, D. B., A. MCKEE, G. M. HAWK, and C. T. DYRNESS. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the Central Western Cascades of Oregon. Ecol. Monogr. 46: 135–156.