

# Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics

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**Abstract:** A chronosequence of three species of logs (*Pinus sylvestris* L., *Picea abies* (L.) Karst, and *Betula pendula* Roth.) from northwestern Russia was resampled to develop a new method to estimate rates of biomass, volume, and density loss. We call this resampling of a chronosequence the decomposition-vector method, and it represents a hybrid between the chronosequence and time-series approaches. The decomposition-vector method with a 3-year resampling interval gave decomposition rates statistically similar to those of the one-time chronosequence method. This indicated that, for most cases, a negative exponential pattern of biomass, volume, and density loss occurred. In the case of biomass loss of *P. sylvestris*, however, polynomial regression indicated decomposition rates were initially low, then increased, and then decreased as biomass was lost. This strongly suggests three distinct phases: the first when decomposers colonized the woody detritus, a second period of rapid exponential mass loss, and a third period of slow decomposition. The consequences for this complex pattern of decomposition were explored at the ecosystem level using a simple model. We found that a single rate constant can be used if inputs vary within a factor of 10, but that this approach is problematical if inputs are more variable.

**Résumé :** Une chronoséquence des billes appartenant à trois espèces (*Pinus sylvestris* L., *Picea abies* (L.) Karst et *Betula pendula* Roth.) et provenant du nord-ouest de la Russie a été rééchantillonnée dans le but de développer une nouvelle méthode pour estimer les taux de perte de biomasse, de volume et de densité. Nous appelons ce rééchantillonnage d'une chronoséquence la méthode de décomposition en vecteur, laquelle constitue une forme hybride entre les approches par chronoséquence et série temporelle. Avec un rééchantillonnage à intervalle de 3 ans, la méthode de décomposition en vecteur a produit des taux de décomposition statistiquement semblables à ceux obtenus par la méthode de la chronoséquence avec un seul échantillonnage. Cela montre que, dans la plupart des cas, la perte de biomasse, de volume et de densité a suivi une courbe exponentielle négative. Cependant, dans le cas de la perte de biomasse chez le *P. sylvestris*, une régression polynomiale montre que le taux de décomposition était initialement faible puis a augmenté et finalement diminué avec la perte de biomasse. Cela suggère fortement qu'il existe trois phases distinctes : la première, lorsque les décomposeurs colonisent les débris ligneux, une deuxième période avec une perte de masse exponentielle rapide et une troisième période de décomposition lente. Les conséquences de ce patron complexe de décomposition ont été explorées à l'échelle de l'écosystème à l'aide d'un modèle simple. Nous avons constaté qu'on peut utiliser une constante de décomposition unique si le taux de décomposition varie par un facteur de 10 ou moins, mais que cette approche est problématique si le taux de décomposition est plus variable.

[Traduit par la Rédaction]

## Introduction

Woody detritus is an important component of forest ecosystems reducing erosion and affecting soil development, storing nutrients and water, providing a major source of energy and nutrients, and serving as a seedbed for plants and as a major habitat for decomposers and heterotrophs (Franklin et al. 1987; Harmon et al. 1986; Kirby and Drake 1993; Samuelsson et al. 1994; McMinn and Crossley 1996). Many of these functions are dependent on the mass of woody detritus present. Tree mortality and decomposition are key pro-

cesses in determining the amount of woody detritus in forested ecosystems. Decomposition rates, however, have proven extremely difficult to measure given the extreme longevity of many dead trees (Franklin et al. 1987). Although there have been some attempts to measure this process using time-series experiments (Edmonds and Eglitis 1989; Alban and Pastor 1993; Harmon et al. 1994; Chueng and Brown 1995; Brown et al. 1996), the majority of studies of woody detritus dynamics have used a chronosequence approach (Lambert et al. 1980; Tritton 1980; Foster and Lang 1982; Graham and Cromack 1982; Sollins et al. 1987; Harmon et al. 1987; MacMillan 1988; Harmon and Chen 1991; Means et al. 1992; Busse 1994). The latter substitutes sampling trees that have died at various times and places for actually observing dynamics over time. Although chronosequences provide rapid estimates of dynamics, they have other features limiting their utility (Harmon et al. 1999). These include uncertainty about the initial condition and size of the

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dead trees and differences in environment associated with different locations.

In this paper we use data from a set of dead trees from northwestern Russia to present a new method to estimate rates of biomass, volume, and density loss. Our past reports on this study have focused on carbon as well as nutrient stores and cycling in connection with forest succession and management practices (Krankina and Harmon 1994, 1995; Krankina et al. 1999). Here we examine data from a resampled chronosequence to explore a new method that we call a decomposition vector. We call it a vector, because it indicates the change in state from one time to the next. This method represents a hybrid between the chronosequence and time-series methods. The chronosequence provides samples of dead trees from various states of decomposition, whereas the time series or resampling provides vectors of change for various parameters that can then be examined as a function of time or extent of decomposition. Our specific objectives are to (i) examine changes in density, volume, and mass of CWD (coarse woody debris) as decomposition proceeds and (ii) compare estimates based on the chronosequence method to our new decomposition-vector method.

## Materials and methods

Experimental data for this study were collected in the St. Petersburg and Novgorod regions of northwestern Russia located at about 59°N and between 31 and 32°E. The climate is cool maritime with cool wet summers and long cold winters (Krankina et al. 1999). Mean temperature of July is 16–17°C and mean temperature of January is –7 to –11°C, with a mean annual surface air temperature of 4°C. Mean annual precipitation is 600–800 mm. The study area is a part of the East-European Plain with elevations between 0 and 250 m above sea level; terrain is gentle and rests on ancient sea sediments covered by a layer of moraine deposits. Soils are mostly of the podzol type on deep loamy to sandy sediments. Natural vegetation of the area belongs to southern taiga types; major dominant conifer species include Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) both growing in pure and mixed stands. After disturbance, these species are often replaced by northern hardwoods including birch (*Betula pendula* Roth.) and aspen (*Populus tremulae* L.).

The sample trees for decomposition rate were taken from 12 permanent experimental plots with long-term records. Dead trees were first sampled in 1993. The same trees were resampled in 1996 using the exact same methods. For each tree the total volume, density, and mass remaining were determined. A total of 69 trees representing the 3 major tree species in northwestern Russia (birch, spruce, and pine) were sampled at both times. In the first sampling there were 44 logs and 25 snags. Since we had to fell the snags for the initial sampling, all trees sampled the second time were logs. An additional 73 trees without dates were sampled to provide data for underrepresented decay classes. Based on plot records, the decomposition period for these trees in 1993 ranged between 1 and 70 years. For pine and birch the full range of decay classes was covered by sampling; however, spruce trees in decay class 5 were not found at either sampling time. A detailed description of the decay-class system and methods has been published (Krankina and Harmon 1994, 1995; Harmon and Sexton 1996). Briefly, samples were taken from four cross sections located systematically along the length of each log or snag examined. For each cross section the density of wood and bark was computed separately as dry mass divided by undried or “green” volume. The mass of each sampled log or snag was calculated based on sample densities and wood and bark volumes in each section (Krankina and Harmon 1995).

One potential problem with past chronosequence studies is that losses of biomass were calculated as the loss of density without accounting for loss of volume (e.g., Sollins et al. 1987). To circumvent this problem, it is necessary to estimate tree biomass at the time of tree death. We estimated the original tree volume based on DBH (diameter at breast height) at the last plot remeasurement before the tree died using volume equations and standard values of wood and bark density for living trees (Moshkalev 1984).

## Statistical analysis

The one-time chronosequence method was contrasted to the decomposition-vector method by calculating the exponential decomposition rates for volume, density, and mass loss for the two sample times. The decomposition rate ( $k$ ) for both methods were calculated as

$$[1] \quad k = -[\ln(\text{Final}) - \ln(\text{Initial})]/t$$

where initial and final are the volume, density, or mass at the start and end of the time ( $t$ ) that the tree has been decomposing. In the case of the vector method, we calculated the difference in a variable in 1996 versus that in 1993 (i.e.,  $t = 3$ ). For the chronosequence studies it is more usual to calculate  $k$  from a regression of the fraction remaining versus the time since a tree died. We did this, but to make the results of the two methods comparable we also calculated the  $k$  for each tree based on the length of time the tree had been dead and the estimated initial volume, density, and mass of each tree. Mean decomposition constants for the two methods were then compared using ANOVA. Our expectation was that, if decomposition followed a simple negative exponential pattern, the two methods should give similar results.

Use of the exponential relationship to estimate decomposition is based on the assumption that the relative rate (as opposed to the absolute rate) of decomposition is constant with time. One might expect that decomposition is initially slow as trees are colonized by decomposers. Moreover, decomposition might also be slow after extensive decomposition has occurred. This suggests that the middle stages of decomposition should be the fastest as neither colonization or substrate quality is limiting. This hypothesis was tested on pine logs by using ANOVA with rate constant as the dependent variable and three classes of decomposition (i.e., <30%, 30–70%, and >70% loss) as the independent variable (SAS Institute Inc. 1985). We also used polynomial regressions to test the effect of time and extent of decomposition on  $k$ .

## Results

Samples were collected from dead trees that represented all the stages of decomposition process including the advanced stages of decay when only 15–22% of the original biomass remained (Table 1). Estimated total volume losses ranged from 17 to 53% and was especially high for the advanced decay classes. Even though volume changes using the chronosequence approach are significant, they may be underestimated because for the advanced stages of decay (classes 4 and 5) there were little good data on the initial tree volume. Density changes largely paralleled those of biomass loss, although they were not as extensive as those for biomass in the advanced decay classes with 20–32% of the class 1 value remaining.

## Chronosequence-based estimates

Regression estimates using all the chronosequence data from 1993 and 1996 indicated that biomass decreased fastest for birch and slowest for spruce and pine (Table 2). This

**Table 1.** Biomass, volume, and density of woody detritus by decay classes and species.

Species and decay class	No. of trees sampled*	Biomass remaining (%) <sup>†</sup>	Volume remaining (%)	Density (g/cm <sup>3</sup> )	Mean age (years)
<b>Birch</b>					
1	5	87.1 (3.5)	93.6 (2.5)	0.480 (0.010)	1.6
2	5	76.2 (5.2)	89.0 (4.0)	0.442 (0.016)	3.3
3	16	40.9 (3.9)	85.8 (5.5)	0.235 (0.023)	14.3
4	11	21.0 (3.8)	82.5 (6.4)	0.125 (0.020)	73.0
5	2	15.1 (1.0)	83.7 (3.3)	0.094 (0.003)	na <sup>‡</sup>
<b>Spruce</b>					
1	9	83.2 (2.1)	90.8 (2.2)	0.347 (0.017)	3.1
2	15	78.3 (3.3)	93.8 (2.1)	0.309 (0.015)	6.5
3	12	50.0 (5.2)	86.9 (4.4)	0.207 (0.018)	12.6
4	6	21.6 (4.5)	46.7 (8.6)	0.110 (0.023)	54.0
<b>Pine</b>					
1	11	95.1 (2.2)	96.8 (2.3)	0.384 (0.018)	2.2
2	15	75.9 (4.6)	91.4 (2.0)	0.311 (0.019)	6.4
3	22	48.7 (2.7)	77.2 (2.6)	0.236 (0.012)	18.8
4	10	22.9 (4.5)	72.2 (5.7)	0.111 (0.018)	28.9
5	3	14.9 (3.1)	54.1 (9.6)	0.108 (0.004)	70.0

Note: Values are means, with SE given in parentheses.

\*Based on first time a tree was sampled.

<sup>†</sup>Accounts for the loss of density and volume.

<sup>‡</sup>Not available.

**Table 2.** Annual decomposition rates for biomass, volume, and density of woody detritus based on one-time regression analysis.

Species	No. of trees sampled	Biomass	Volume	Density
Birch	39	0.046 (0.006)	0.013 (0.001)	0.042 (0.005)
Spruce	38	0.033 (0.002)	0.013 (0.001)	0.027 (0.002)
Pine	48	0.035 (0.003)	0.010 (0.001)	0.024 (0.003)

Note: Values are estimates with SE given in parentheses.

result is similar to our previous analyses using the 1993 data both in terms of values and rankings (Krankina and Harmon 1995). Estimates of annual volume loss using this approach were similar for all three species ranging from 0.01 to 0.013. We expected that these volume-decomposition rates would differ more among the species, especially for birch, which retains its bark and form after extensive decomposition. Decomposition rates for density change were similar to those of biomass, with birch having the fastest and spruce and pine having slower rates of change. Decomposition rates for density loss were lower than for those of biomass loss. This was expected in that biomass loss incorporates both density and volume changes (Lambert et al. 1980).

Estimates of decomposition rates using the initial versus final values from the chronosequence (i.e., eq. 1) were often higher than those estimated using a one-time regression (Tables 2 and 3). The closest match between chronosequence analysis methods was for pine biomass, which was within 3%. However, for spruce and birch biomass loss the comparison of initial versus final values was higher than the one-time regression approach by 45 and 48%, respectively. For density the initial versus final method gave a 79 and 41% higher estimate for birch and spruce, respectively. In contrast, the decomposition rate for pine density for the one-time regres-

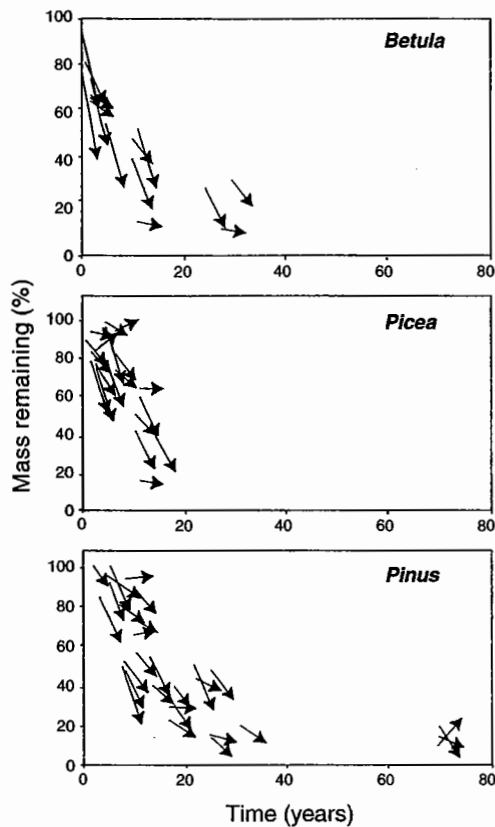
**Table 3.** Annual decomposition rates calculated using chronosequence and decomposition-vector methods for all the remeasured trees.

Species	Chronosequence (1993 only)*	Vector (1993–1996)*	<i>p</i>	No. of observations
<b>Biomass</b>				
Birch	0.068 (0.011)	0.108 (0.022)	0.447	14
Spruce	0.048 (0.004)	0.067 (0.011)	0.265	23
Pine	0.036 (0.003)	0.050 (0.017)	0.473	32
<b>Volume</b>				
Birch	0.036 (0.011)	0.025 (0.011)	0.552	14
Spruce	0.024 (0.007)	0.032 (0.008)	0.467	23
Pine	0.017 (0.003)	0.039 (0.009)	0.024	32
<b>Density</b>				
Birch	0.075 (0.009)	0.083 (0.023)	0.787	14
Spruce	0.038 (0.007)	0.037 (0.010)	0.991	23
Pine	0.015 (0.006)	0.019 (0.016)	0.819	32

\*Values are means, with SE given in parentheses.

sion method was 38% less for the initial versus final method. Decomposition rates for volume differed most, although this was dependent on the species. Volume decomposition rates

**Fig. 1.** Biomass remaining as a percentage of the estimated initial biomass for birch, spruce, and pine (the arrows connect remeasured trees).



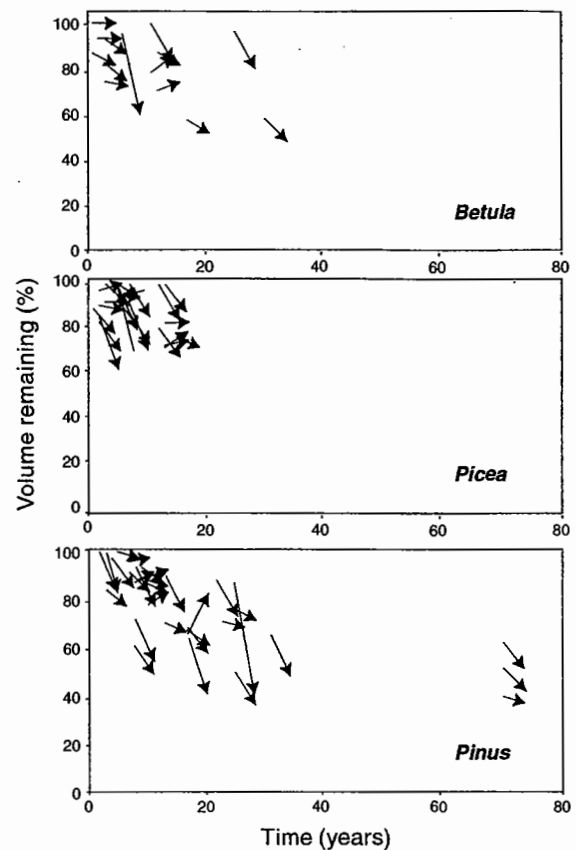
for the initial versus final value method were 177, 85, and 71% greater than the one-time regression method for birch, spruce, and pine, respectively.

#### Decomposition vector estimates

The decomposition vector method with a 3-year resampling period generally gave decomposition rates statistically similar to the chronosequence initial versus final method (Table 3). Thus, the hypothesis that decomposition followed a negative exponential pattern could not be rejected. An exception was for volume loss of pine, in which the chronosequence method gave a significantly lower estimate than the decomposition vector method. Although ANOVA determined the two methods were not significantly different in the other cases, there were consistent variations that should be noted. First, comparisons of density decomposition rates indicate both methods were quite similar and within 3–27% depending on species. Biomass decomposition rates were consistently higher by as much as 69% using the decomposition-vector method. For volume loss the decomposition-vector method was 29% lower for birch, but 129% higher for pine than the chronosequence method.

In addition to statistical analysis a graphical analysis gives indications of cases where the negative exponential model may not be followed. The decreasing trend in biomass and volume with time was evident for all species, although in a few cases, dead tree biomass and volume values increased between measurements (Figs. 1 and 2). This was probably

**Fig. 2.** Volume remaining as a percentage of the estimated initial volume for birch, spruce, and pine (the arrows connect remeasured trees).



caused by measurement imprecision relative to the short remeasurement interval. Pine biomass loss is the clearest example of where decomposition rates may change with time. In this species the decrease in biomass is low for the first 5 years, it is relatively rapid between 5 and 30 years and then appears to decrease after 30 years. The temporal pattern of volume losses also indicated the negative exponential pattern may not be followed. Discounting the few cases where the 3-year loss is excessive or volume increases, it would appear that pine volume has a lag time of approximately 5 years, starts to decrease exponentially, and then reaches an asymptote after 40 years. In contrast, birch and spruce have minimal volume loss with time, although certain logs have high rates of volume loss. Thus, it would appear that volume loss varies more from log to log than biomass loss.

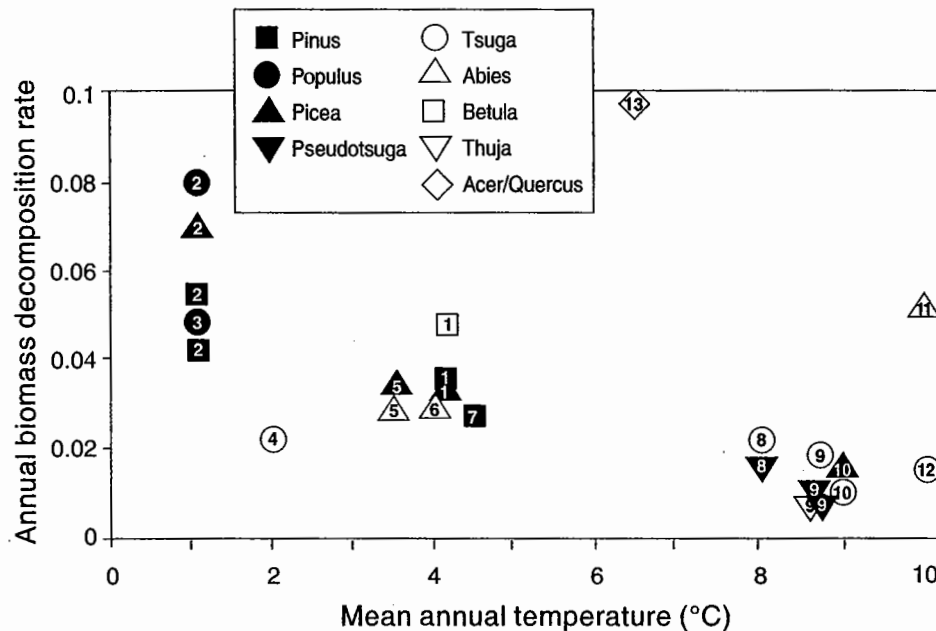
Our comparison of mean decomposition rates may have hidden an underlying time effect. By comparing the decomposition rates for different states of decomposition we found highly significant differences among the early, middle, and later stages in pine (Table 4). For this species, the biomass decomposition rate increases by nearly an order of magnitude between the initial stage (while less than 30% of biomass is lost) and the medium stages when biomass loss is between 30 and 70%. There was a halving of the biomass decomposition rate when >70% of the biomass had decomposed. Polynomial regression also indicated a similar trend with decomposition rates being significantly correlated to

**Table 4.** Mean annual decomposition rates for pine calculated using a one-time chronosequence and decomposition-vector methods for different decomposition states.

Decomposition state	Chronosequence (1993)*	Vector (1993–1996)*	<i>p</i>	No. of observations
Biomass loss <30%	0.014 (0.003)	0.009 (0.008)	0.718	11
Biomass loss 30–70%	0.041 (0.004)	0.099 (0.020)	0.004	13
Biomass loss >70%	0.033 (0.005)	0.055 (0.045)	0.317	8

\*Values are means, with SE given in parentheses.

**Fig. 3.** Relationship of biomass loss rate constant to mean annual temperature. The numbers inside the symbols indicate the source of data: (1) this study; (2) Alban and Pastor (1993); (3) Miller (1983); (4) Tyrrell and Crow (1994); (5) Foster and Lang (1982); (6) Lambert et al. (1980); (7) Busse (1994); (8) Graham (1982); (9) Sollins et al. (1987); (10) Graham and Cromack (1982); (11) Harmon et al. (1987); (12) Grier (1978); (13) Hale and Pastor (1998).



the square of time or the square of cumulative percentage of decomposition that had occurred. This indicates that our initial comparison of decomposition rates did not always distinguish between the negative exponential and other more complicated models.

## Discussion

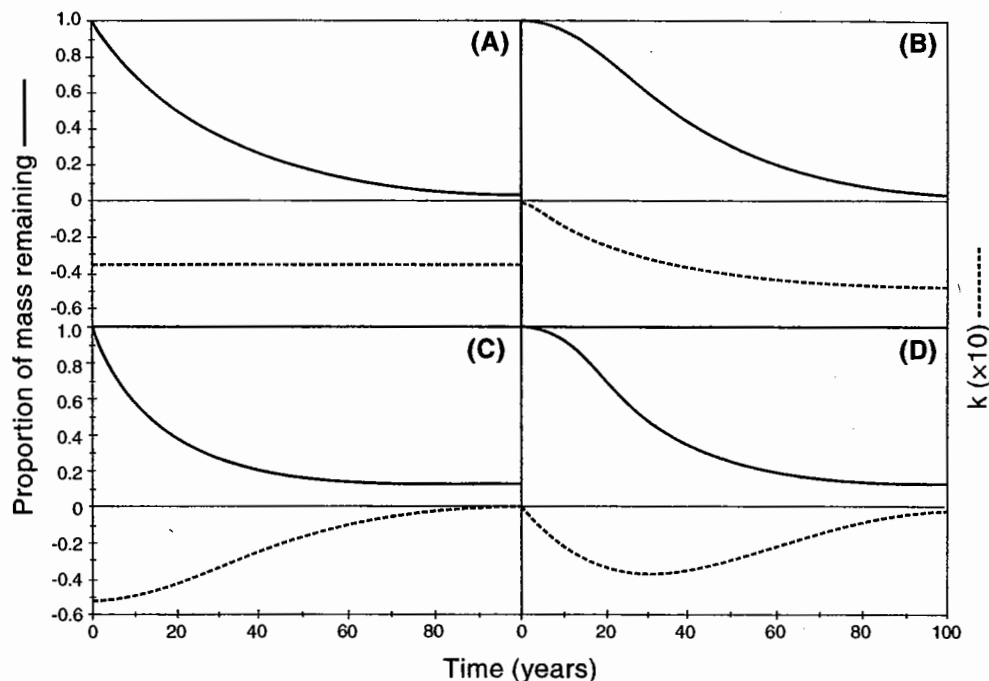
### Comparison with previous studies

A comparison of our biomass decomposition rates to previous studies in northern locations indicates that warmer sites do not necessarily have higher rates of decomposition (Fig. 3). Our one-time, regression-based estimates for annual biomass decomposition rates were 0.046, 0.033, and 0.035 for birch, spruce, and pine, respectively. In a climate colder than our study area, Alban and Pastor (1993) found higher annual biomass decomposition rates for *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss., and *Pinus banksiana* Lamb. of 0.08, 0.071, and 0.042, respectively. These higher rates may have been caused by close contact with the soil since the inception of their study or by the short length of the logs (~1 m). Both factors would speed decomposition. This may be why Miller (1983) who examined whole tree

losses in a similar cold climate in Minnesota reported a lower annual rate constant of 0.05 for *Populus tremuloides*. As mean annual temperature increases for the study site to a range of 2–5°C, annual biomass decomposition rates are between 0.021 and 0.03 (Lambert et al. 1980; Foster and Lang 1982; Busse 1994; Tyrrell and Crow 1994), values that are similar to what we observed at a mean annual temperature of 4°C. Finally, annual decomposition rates from sites with mean annual temperatures between 8 and 10°C have a wider range (0.009–0.05) (Grier 1978; Graham 1982; Graham and Cromack 1982; Harmon et al. 1987; Sollins et al. 1987) than ours.

It is curious that there is not a more consistent increase in decomposition rates with increasing temperature. This may indicate that several other factors, such as moisture, size, and species differences of the trees (e.g., decay resistance) or decomposers (e.g., temperature optima) may be confounded with the temperature gradient. For example, within the genus *Abies* there is an increase in annual biomass rate constant of 0.02 (i.e., 0.03–0.05) as temperature increases 7°C (i.e., 3–10°C). This increase is consistent with a  $Q_{10}$  (quotient 10) of approximately 2. However, over a similar increase in temperature, decomposition rates for the genus

**Fig. 4.** Hypothetical decline in biomass and changes in decomposition rates with time for four different models of decomposition: (A) negative exponential, (B) lag time and negative exponential, (C) negative exponential followed by asymptote, and (D) lag time and negative exponential followed by asymptote. Note that the annual decomposition rate,  $k$ , has been multiplied by 10 for presentation purposes.



*Tsuga* remain the same or in some cases decrease by a factor of two, indicating a  $Q_{10}$  of 0.37–1. The same general pattern is also evident in the genus *Picea*. In these cases, the decomposition decrease with temperature may be caused by high precipitation at the warmer sites, a combination that can cause waterlogging that in turn inhibits decomposers (Harmon et al. 1986). Differences in substrate quality may also account for the general lack of increase with temperature. The fivefold variation in annual decomposition rates in the 8 to 10°C temperature range, for example, is caused by known substrate quality differences, with the genus *Thuja* ( $k = 0.009$ ) having extremely decay-resistant heartwood and *Abies* ( $k = 0.05$ ) having decay-prone heartwood (Harmon et al. 1986).

#### Methodological considerations

Major concerns of using the decomposition-vector approach include the range of decomposition states that are included and the minimum remeasurement interval. Our analysis indicates that it is essential to include as wide a range of decomposition states as possible. If sample trees are biased toward the middle stages of decay it is likely that the decomposition rate will be overestimated with the vector method. In contrast, bias toward the early or later stages of decomposition are likely to underestimate decomposition rates. For such cases the chronosequence method may be a better option.

To calculate the minimum sample interval for the vector method one needs an estimate of the mean decomposition rate and precision of the measurements. The decomposition rate can be determined from the initial chronosequence sampling. For example, our assumption for pine of an annual biomass rate constant of 0.035 and a remeasurement preci-

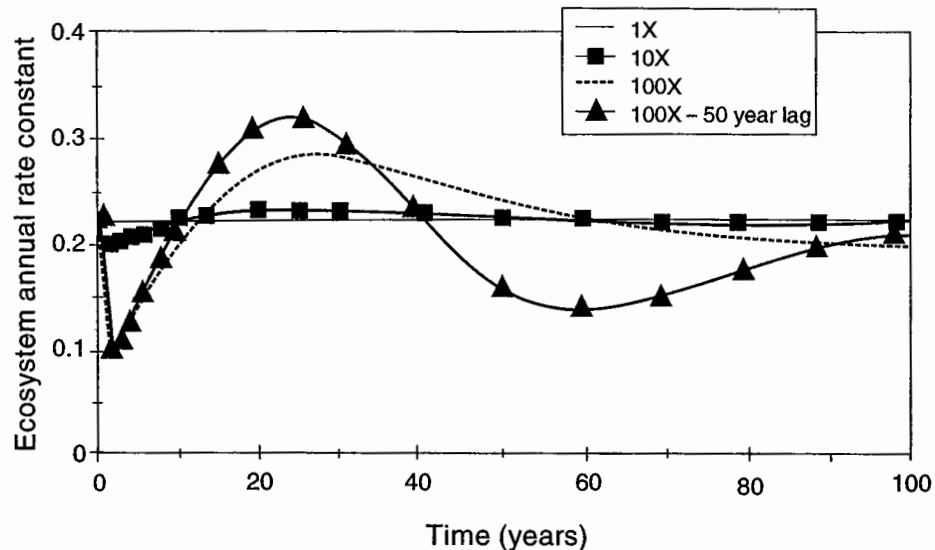
sion of  $\pm 5\%$  appears to have been generally met, although biomass for 3 of the 32 trees sampled increased. A slightly longer resampling interval should have detected declines in all the trees. Based on our experience, an interval of 5 years would be sufficient in boreal and temperate forests, whereas a 2- to 3-year interval should be sufficient for tropical forests.

#### Selection of the “appropriate” decomposition model

For pine biomass and pine and spruce volume losses there seems to be strong evidence the simple negative exponential model is not followed. The changes in decomposition rates for pine biomass over time correspond to several observations we made during the field work. The initial slow rates of biomass decline may have been caused by slow colonization of decomposers we observed, especially in snags. Slow rates of biomass decline for older pine logs corresponded to exceedingly decomposed, brown-rotted logs that retained no sapwood or bark. While pine had the clearest changes, an increase in biomass loss rates after 5 years is also evident in spruce logs, but the decrease in decomposition rate during more decomposed stages is not evident. This may have been caused by the observed presence of white-rot fungi, a functional group that tends to leave little stable residue. Birch decomposition patterns were very different than those of pine in that they did not exhibit either an early or late period with low biomass decomposition rates. The lack of the early slow phase may be associated with rapid colonization by endophytic decomposers that has been observed in several other angiosperm species (Griffith and Boddy 1990). Birch is also prone to white rots, which might explain the lack of an asymptotic phase in this species. The time lag associated with volume loss also is consistent with our observations.



**Fig. 5.** Hypothetical effect of the age-class structure of inputs on stand-level biomass decomposition rates for the lag-time with asymptote model. The four age structures were created by the following inputs: (1x) constant input of 1 Mg-ha<sup>-1</sup> per year; (10x) same as 1x but with one pulse of input of 10 Mg-ha<sup>-1</sup> per year; (100x) same as 1x but with one pulse of 100 Mg-ha<sup>-1</sup> per year; and (100x - 50 year lag) the same as 100x but with a 50-year lag in inputs after the pulse.



Bark loss via fragmentation, for example, did not occur for several years in the two conifer species. Moreover, volume losses caused by the total respiration of parts would take at least a decade based on the biomass loss rates we estimated.

Chronosequence and decomposition-vector methods can both be used to measure decomposition rates; however, they measure different aspects of decomposition. Chronosequences represent cumulative losses averaged over time  $t$  since the tree died (see eq. 1). The vector method measures the short-term rate of change between time  $t$  and  $t + \delta t$ . These methods give the same result only if the relative decomposition rate (or so-called rate constant) does not change during the process of decomposition and, hence, follows a negative exponential decrease. Our data suggests that, at least for pine, decomposition rates do change among the stages of decomposition. A similar conclusion was reached by Busse (1994) for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) by comparing the decomposition rates among decay classes. The decomposition-vector method captures this difference more readily than the chronosequence method (Table 4).

To demonstrate why the two approaches might yield different rate-constant estimates, we compared results for four different models of woody detritus decomposition: (i) the negative exponential, (ii) a time lag followed by a negative exponential, (iii) negative exponential loss followed by an asymptote, and (iv) a time lag with negative exponential loss followed by an asymptote (Fig. 4). For each of these models we used parameters that were consistent with the overall annual decomposition rate for pine biomass loss (i.e., 0.035). For each model we computed the decomposition rate using eq. 1 assuming either a chronosequence or a series of sequential decomposition vectors. As expected, for the negative exponential loss pattern, the mean decomposition rate was the same regardless of the method. For the lag-time model, the decomposition-vector method estimates were 55% higher than the chronosequence method for a mean an-

nual rate constant of 0.033. As the lag time increased we found that the ratio of vector to chronosequence means increased. In contrast, introducing a stable asymptote (e.g., brown rot) had the opposite effect, with the vector method giving a 42% lower estimate than the chronosequence method. We found that as the value of the asymptote increased, the ratio of vector to chronosequence means decreased. Finally, the model combining the lag time with an asymptote had very similar mean decomposition rates for the two methods and could not be distinguished from the negative exponential model.

Although it is common to refer to the exponential decomposition rate as a rate constant, the negative exponential model is the only case where rate constant is a meaningful term. In all the other cases we explored the way decomposition rate varies with time: (i) a monotonic decrease for the asymptotic model, (ii) a monotonic increase for the lag-time model, and (iii) an increase and a decrease for the combined time lag and asymptotic model. Thus, the notion of the rate constant may need to be reexamined as more data on temporal dynamics become available.

The sign and magnitude of the differences between the vector and chronosequence methods may have some potential to indicate the underlying decomposition dynamics. For example, in light of our modeling results, the higher values for the decomposition vector than the chronosequence method may indicate a time lag was present for biomass loss of all three species. Although other tests, such as separating into time or decay classes and testing for differences, would be the most direct way to test if the negative exponential model is being followed, the ratio of the two methods might provide a quick way to identify the most likely alternative model.

#### Application of results to the ecosystem level

Our results indicate that applying decomposition rate estimates to the ecosystem level may be more complicated than

previously thought. If the decomposition rate changes as a function of time, then the average decomposition rate for wood at the ecosystem level is dependent on the age structure of the inputs. This has not been considered an issue in the past, because if the negative exponential decrease is followed, then the age structure of inputs has no effect on the ecosystem-level decomposition rate. To illustrate this point we explored the consequences of age structure for the lag time with asymptote model (see Fig. 4D) using four cases: (i) constant inputs of 1 Mg·ha<sup>-1</sup> per year representing an undisturbed old forest, (ii) same as the first case but with one pulse of input of 10 Mg·ha<sup>-1</sup> per year representing a small disturbance, (iii) same as the first case but with one pulse of 100 Mg·ha<sup>-1</sup> per year representing a large disturbance, and (iv) the same as the third case but with a 50-year lag in inputs after the pulse representing a large disturbance that requires time to restore inputs. In the case of constant inputs through time, the decomposition rate at the ecosystem level was 0.0233 year<sup>-1</sup> regardless of year (Fig. 5). A single high input of 10 Mg·ha<sup>-1</sup> per year lead to some changes in the ecosystem decomposition rate but only within 10% of the constant input case. Variations in the decomposition rate were largest for the case with a large pulse of input and a 50-year time lag. In this case the decomposition rate fluctuated from 50% below to 50% above the constant input case. Interestingly, there was a second period in which the rate constant decreased, a behavior caused by the large pulse of material that entered the asymptotic phase of decomposition. The response to a large input without a time lag for inputs was similar to that with a time lag; however, the decreases and increases over time were dampened. This analysis indicates that the larger the pulse and the longer the time lag to restore inputs is, the larger the temporal deviations in ecosystem level decomposition rate. This suggests that, unless the negative exponential model is followed and (or) the inputs are relatively constant, one needs to address temporal variation in the decomposition rate. This could be achieved several ways but dividing the detrital material into several phases (e.g., time lag, exponential loss, and asymptotic) with different decomposition rates may be the simplest solution.

## Conclusions

The decomposition-vector method can be quite a useful technique to estimate decomposition rates. Not only does it save time over a long-term time-series experiment, but it can also provide evidence for a more refined model of decomposition than the single negative exponential model. These refinements may be important when one is concerned with the temporal dynamics of a pulse of post-disturbance woody detritus. The chronosequence method, however, may be appropriate when one needs to assess decomposition over the long term and (or) for very large areas with unknown temporal patterns of input. In this case it may be quite adequate to assume that the decomposition rate does not vary with time. The interpretation of the decomposition rates estimated using either method must be made with caution as the differences may be greater for trees dying in conditions that increase the initial lag period or those that create stable organic material during the final stages of decomposition.

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