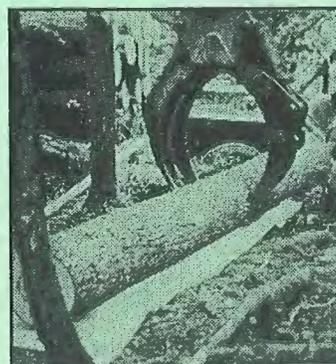

GUIDELINES

for

MEASUREMENTS *of* WOODY DETRITUS

in

FOREST ECOSYSTEMS



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&

Jay Sexton

U.S. LTER Publication No. 20

LTERR



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Mark E. Harmon & Jay Sexton

April 1996

PREFACE

This publication describes some of the most common methods used to quantify the amount and dynamics of woody detritus in forest ecosystems. A hierarchical scheme is presented that will help assure data comparability for intersite studies. For each type of measurement several methods are described and compared. Detailed guidelines are presented for measuring mass, nutrient stores, production, and decomposition processes. Additionally, references are included for more detailed process studies including nitrogen fixation, leaching, respiration, sporocarp production, and insect production.

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INTRODUCTION

Dead trees serve many key functions in ecosystems (Franklin et al. 1987). Since dead trees may persist for centuries (McFee and Stone 1966, Triska and Cromack 1980), they can influence ecosystems as long as living trees. Woody detritus reduces erosion and affects soil development; stores nutrients and water; is a major source of energy and nutrients; serves as a seedbed for plants; and is a major habitat for microbes, invertebrates and vertebrates (Lutz 1940, Anderson et al. 1978, Swanson and Lienkaemper 1978, Franklin et al. 1981, Frankland et al. 1982, Davis et al. 1983, Harmon et al. 1986). Despite these many functions, the importance of this material in forest ecosystems has, until recently, been overlooked by ecologists (Harmon and Chen 1991) and forest managers alike (Kirby and Drake 1993, Samuelsson et al. 1994).

The importance of woody detritus in forest ecosystems has, until recently, been overlooked by ecologists and forest managers alike

The recognition of the role of dead trees and woody detritus in forests has led to an increasing demand for appropriate methods for field studies. Given the relative youth of this field, however, there are only a few scattered published sources for methods. Moreover, the specific information and practical experience needed by newcomers to establish a sampling program are often lacking in these publications. This is unfortunate, because woody detritus studies require considerable effort (although no more than live tree studies), and it would be highly advantageous for intersite comparisons to collect such data in a comparable way.

We have prepared these guidelines as a step toward collecting comparable data and providing a logical starting point for intersite collaboration (Table 1). In addition to describing the basic methods involved, we have attempted to compare alternative methods and to indicate their relative precision and accuracy. This approach recognizes that the level of detail used in examining woody detritus at a given site depends upon the study objectives. Therefore, rather than suggest a single method, we have developed a series of methods that will yield comparable results at the most general level. Our emphasis is not on setting absolute standards, but on achieving data standardization and comparability.

Finally, we offer a word of caution concerning our recommendations. Although our primary experience has been in the Pacific Northwest, it would be a mistake to assume that the described methods and recommendations will only work in that region. During the past 20 years, we have used these methods successfully in boreal forests (Russia), tropical forests (Mexico), temperate deciduous forests (Tennessee), and temperate conifer forests (California, Colorado, Montana, Oregon, and Washington); however, there are undoubtedly areas or situations in which they will not apply. We can only encourage the reader to use common sense and to avoid reinventing the wheel whenever possible.

Table 1. Sites with ongoing or planned studies on woody detritus.

Site	Location	Biome
Andrews	Oregon	cool conifer
Bonanza Creek	Alaska	boreal conifer/deciduous
Changbai	China	cold deciduous
Chapel Hill	N. Carolina	warm deciduous/conifer
Coweeta	N. Carolina	warm deciduous
Fraser	Colorado	cold conifer
Harvard Forest	Massachusetts	cool deciduous
Hubbard Brook	New Hampshire	cool deciduous
Juneau	Alaska	temperate rainforest
Luquillo	Puerto Rico	moist tropical
Olympics	Washington	temperate rainforest
Puerto Morelos	Mexico	dry tropical
SERC	Maryland	warm deciduous
Sevilleta	New Mexico	cold conifer
St. Petersburg	Russia	boreal conifer/deciduous

INSTALLATION LEVELS

Before describing methodological details, we will consider the overall problem of developing comparable data. A typical approach is to try to match data for a given variable, regardless of the temporal, spatial, or process resolution. For example, all sites to be compared might measure nitrogen fixation rates in the same fashion, producing data that is comparable but only in a limited way. That is, the rates of nitrogen fixation could be compared, but the implications of these rates to overall ecosystem nitrogen cycling may not be evident. This is because the latter depends not only on the rate of nitrogen fixation, but also on the mass and state of decay of the woody detritus present at a site. So, to maximize comparability one needs to consider not only the variable itself, but also how it relates to other variables.

The greatest opportunities for intersite comparison will occur if one proceeds from less to more detail

With this in mind, we have followed the hierarchical system used by the U.S. Long-Term Ecological Research (LTER) Meteorology Committee, defining a number of levels of detail depending upon the resources and objectives (Greenland et al. 1987). A key point to remember is that the data at more detailed levels can be made comparable to those at less detailed levels by reducing the temporal, spatial, or process resolution. While it is certainly possible to start with the greatest detail or resolution and work toward less detail or resolution, we feel the greatest opportunities for intersite comparison will occur if one proceeds in the opposite direction. Moving from less to more detail also will help put the detailed process studies in context (see nitrogen fixation example above).

We have ordered the following installation levels by increasing detail and expense:

- ◆ **Level One** includes sites with inventories of logs and snags within forest plots. “Generic” density and nutrient content values from the literature are used to estimate mass and nutrient stores.
- ◆ **Level Two** includes sites that have inventories of stores in forest plots, estimates of mortality rates from permanent plots, and estimates of decomposition rates from chronosequences. Inventory estimates would be based on site-specific density and nutrient contents.
- ◆ **Level Three** includes sites with a Level Two installation and one or more time series to estimate decay rates of dominant species.
- ◆ **Level Four** includes sites with a Level Three installation and detailed process studies such as seasonal respiration patterns, leaching, insect utilization, and nitrogen fixation.

DEFINITION *of* TYPES *of* WOODY DETRITUS

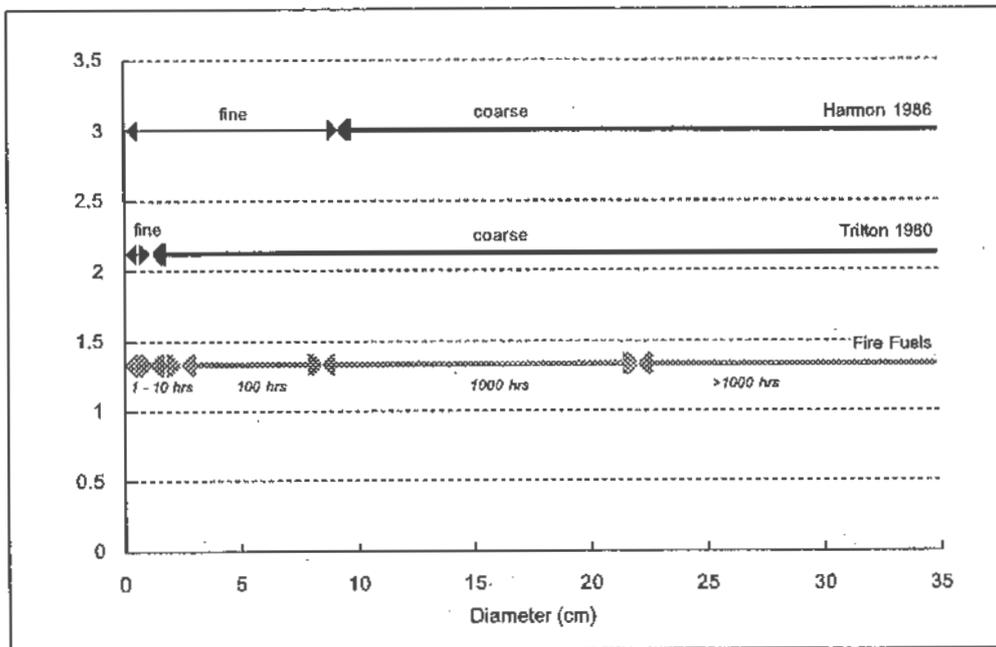
Woody detritus or debris takes many forms in forested ecosystems. For ecologists, the most useful distinctions are based on the size (length and diameter) and position (standing, downed, buried in soil) of the detritus. Other classification systems, such as those used for fire fuels, depend upon the moisture time lag, but are operationally divided by diameter (Fosburg 1971). Unfortunately, common terms have not been used to describe woody detritus, and this has led to confusion and the creation of major barriers to comparisons.

For most forests, we recommend that the fine-coarse woody detritus breakpoint be made at 10 cm at the large end of a piece

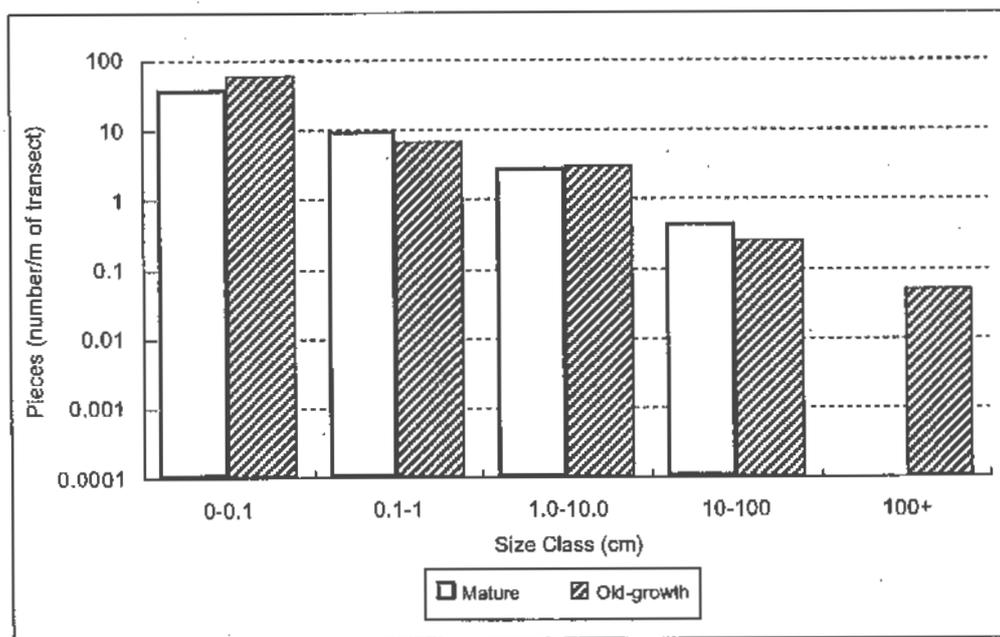
The most important size distinction is between coarse and fine woody detritus fractions. This distinction often depends upon the ecosystem being examined (Figure 1), but we have used size "break points" at 1 and 10 cm diameter in a wide range of forest systems. The use of this order of magnitude division of classes does not preclude the use of finer divisions that may be appropriate for other objectives; however, if these divisions match our suggested break points at some level of aggregation, we believe the opportunity for comparability is greatly increased. For most forests, we recommend that the fine-coarse woody detritus breakpoint be made at 10 cm at the large end of a piece. This is roughly comparable to the 7.5 cm diameter (i.e., the 100-hour fuel size limit) break point commonly used in fuel inventories and avoids the problem of measuring an excessive number of pieces in large plots or long transects (Figure 2). As

most fuel sampling methods record the diameter of each piece exceeding 7.5 cm, one can create a 10 cm breakpoint in these data (Brown 1974).

Given that the number of pieces of woody detritus increases as diameter decreases, another useful size breakpoint is at 1 cm diameter (Figure 2). Woody branches, twigs, and bark pieces less than this diameter can be exceedingly numerous and are best treated as a special case of fine litter (in fact, they usually are included in litterfall studies). In the case of dead roots, however, we would strongly recommend against using 10 cm as the cut-off between fine and coarse woody detritus because most live roots do not exceed this diameter. We therefore recommend that dead fine roots be separated from dead coarse roots at a diameter of 1 cm.



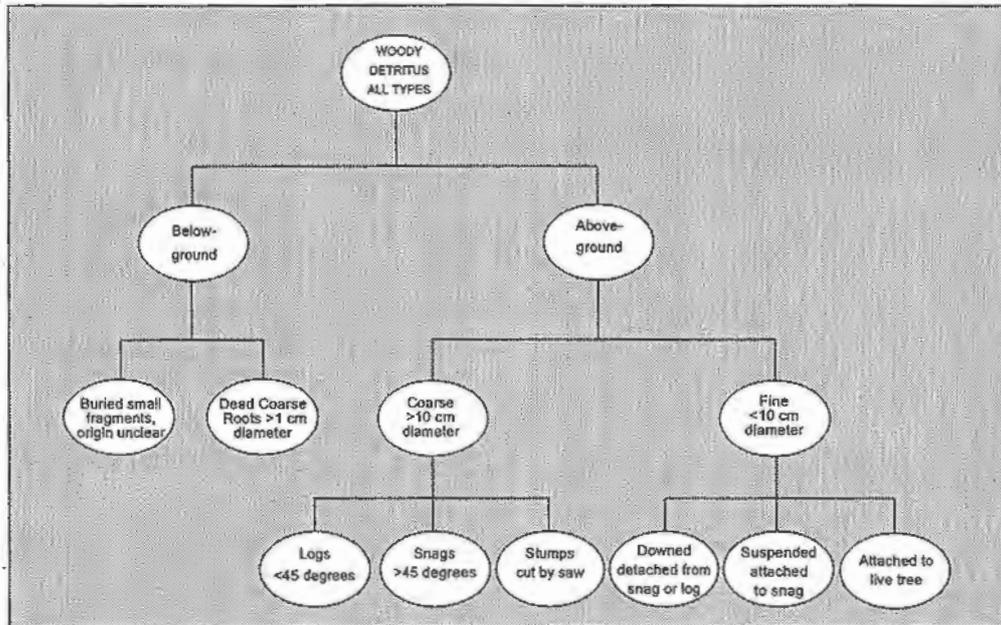
◆ *Figure 1.*
Diameter classes
commonly used to
define sizes of woody
detritus.



◆ *Figure 2.* Size
class distribution of
downed woody
detritus for an 80-
year-old mature and
an old-growth
Douglas-fir forest.

In addition to variable terminology and size definitions, we have found that the lack of consistency in the types of woody detritus inventoried has made it difficult to compare data. Figure 3 is an attempt to present how we divide the types of woody detritus. To avoid confusion, we strongly recommend that researchers be consistent in selecting types to inventory. We have avoided to the greatest extent possible using the names of living parts to define or divide types of woody detritus. For operational definitions, we have found that it is clearer to use position and size. The terms *woody detritus* or *woody debris* should be used to include all the forms of dead woody material above- and below-ground. Above-ground woody detritus can be divided into coarse or fine fractions. The minimum dimensions for coarse woody detritus are usually 10 cm diameter at the large end and 1.5 m in length. Smaller pieces than these are usually considered fine woody detritus. Coarse fractions can in turn be divided into snags (or standing dead) and logs (or dead and downed). The separation of snags from logs is usually at a 45-degree angle. In addition to snags, we recognize stumps in managed settings. We recommend that short, vertical pieces resulting from natural processes always be called *snags*, and that the term *stump* be reserved for short, vertical pieces created by cutting. Fine fractions can also be divided into suspended or downed fractions. In the case of suspended fine wood, one must distinguish between that attached to living woody plants and that attached to dead woody plants. Below-ground woody detritus has rarely been studied, but we recommend that it be divided into buried wood (very decayed material in the mineral soil or forest floor) and dead coarse roots. The distinction between these two types of below-ground material is primarily based on whether one can tell its origin (similar to the distinction between O₁ and O₂ layers in organic soil layers).

When conducting inventories, it is important to bear in mind that some forms of woody detritus are highly correlated, while others are not. This means that some forms are easy to estimate from others, while others are impossible. For example, we have found that size classes of woody detritus often are highly correlated. This is probably because, as trees die, the proportions of dead tree size classes reflect the proportions of size classes of living tree parts (Leopold 1971). Thus, it is not unusual to find that fine downed wood comprises <20% of the total downed woody detritus (Harmon et al. 1986), just as it makes up < 20% of the live biomass. Similar proportions might be



◆ *Figure 3. Classification of woody detritus based on position, size and degree of decomposition.*

expected for suspended fine wood versus snags. A good correlation probably also exists between above-ground woody detritus and dead coarse roots, as their relationship is largely controlled by the structure of living trees. Perhaps the worst correlation between forms of woody detritus is for standing or suspended and downed material. Even within a single forest type, it is not unusual to find that this proportion varies widely; snags can make up as little as 2% or as much as 98% of the dead wood biomass (Harmon et al. 1986). The ratio of standing to downed woody detritus depends upon many variables, including the dominant form of mortality (e.g., wind versus insects), the age of the forest, and the tree species.

INVENTORIES *of* MASS *and* NUTRIENT STORES

One of the most fundamental things to know about woody detritus is how much of the ecosystem mass and nutrient capital is stored in this pool. This data also places much of the process data in an ecosystem context. Therefore, we consider it the major criterion for a Level One installation.

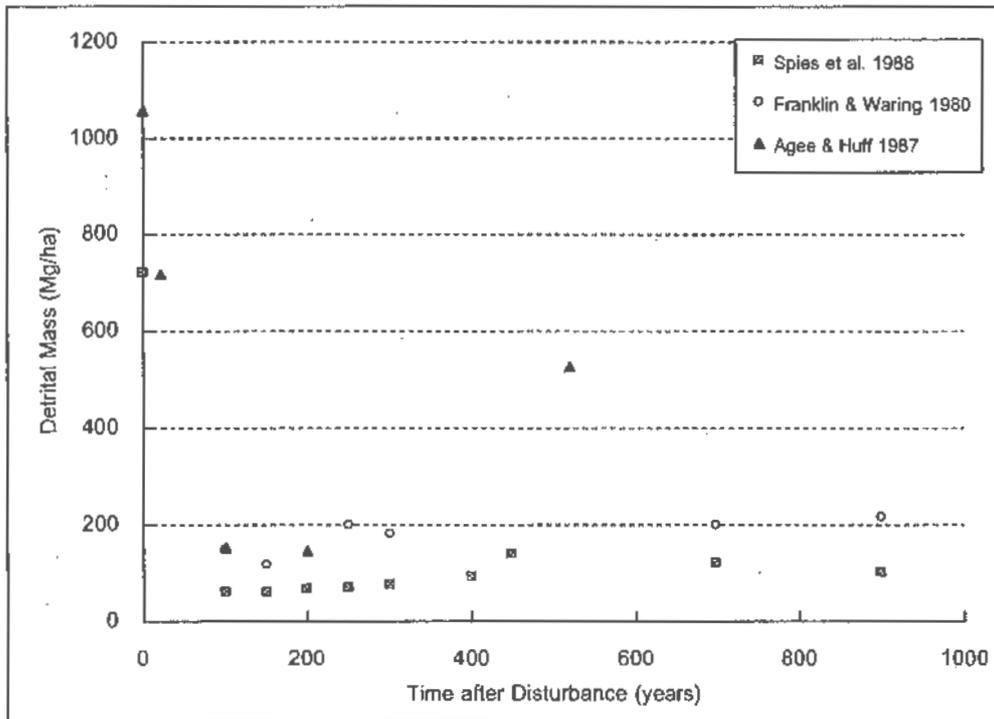
Woody detritus is highly variable in space and time. Given limited resources, one must decide how to balance the long-term goal of intersite comparisons with shorter-term study objectives. Although each investigator must determine this balance, we offer several ideas to consider. If only one type of ecosystem is to be sampled, then it is best to select one that is typical of the study area or the region. However, given the variation found in any region, this is not as simple as it sounds. If resources permit, the extremes of edaphic or climate conditions should be sampled as well. As these extremes

are often easier to define, their inclusion may make some intersite comparisons clearer. For example, knowing that the range of two regions does or does not overlap may be more insightful than simply knowing that the typical ecosystems differ.

*We recommend sampling
in three key stages of
forest succession: recently
disturbed forests, mature
forests, and old-growth
forests*

One must also consider the fact that woody detritus mass changes greatly during succession. This means that unless the successional stages sampled are comparable, an intersite comparison may be misleading. Although sampling woody detritus in all stages of succession would be ideal, it may not be possible. We recommend sampling in three key stages of forest succession: 1) recently disturbed forests, 2) mature forests, and 3) old-growth forests. This allows one to establish a temporal range in woody detritus levels. The highest levels are typically

found following disturbance. Given that it is relatively easy to calculate the amount of coarse woody detritus (CWD) following disturbance (Snell and Brown 1980, Harmon et al. in press), we suggest that initial inventories should concentrate on mature to old-growth forests. The mature phase is important to include because the minimum woody detritus stores are often reached in the middle stages of succession (Figure 4). The old-growth or climax stage is also important because it represents a condition where inputs and outputs are, theoretically, in balance.



◆ *Figure 4.*
Temporal pattern of
woody detritus
following a major
disturbance in
Douglas-fir/western
hemlock forests of the
Pacific Northwest.

To be most useful for comparison, woody detritus should be measured in plots or stands that have inventories of living biomass and other detrital pools. Not only will this provide a more complete inventory of the ecosystem, it will allow one to couple process rates such as mortality to these “static” measurements. Moreover, it will allow one to estimate expansion factors that relate one form of biomass to another. For example, we have found that the ratio of old-growth CWD to bole mass ranges between 0.20 to 0.30 in the Pacific Northwest (Harmon and Chen 1991). This ratio can then be applied to live tree biomass to estimate regional CWD stores within old-growth forests (Harmon et al. 1993).

Finally, woody detritus takes many forms, and the optimal method used to inventory each form differs. For example, downed coarse wood can be estimated using either plots or line intercepts, while attached dead wood and suspended fine dead wood

are usually estimated from allometric relationships from tree diameters gathered in fixed or variable radius plots. Below, we describe inventory methods that we commonly use in fixed area plots, line intercepts, and variable radius plots. In cases where suitable methods do not already exist, we suggest some to try based on our own field experience.

Fixed Area Plot Sampling

By *fixed area plot sampling* we refer to the quadrat sampling method widely used in other ecological fields. In this form of sampling, the shape and size of the plot is constant and has two dimensions, length and width. This is in contrast to line intercept samples, which have length but no width, and variable radius plots, which are two dimensional but change in size depending upon the plot.

Coarse Woody Detritus. The mass and nutrient stores in coarse woody detritus can be estimated by measuring the diameters and lengths of pieces in fixed area plots. One can also use line transects for measuring logs (see below) but, since it can not be used for snags, this option can result in a methodological mismatch between standing

Table 2. Coefficient of Variation in Coarse Woody Detritus Mass as a Function of Sample Size and Area.

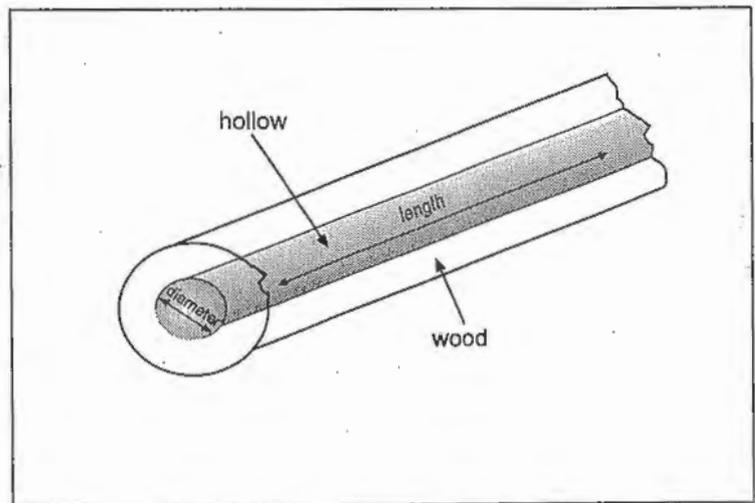
Ecosystem	Plot Area (ha)	Coefficient of Variation (%)				
		Number of plots	3	6	9	12
Lodgepole pine	0.04	48	49	48	43	46
	0.08	42	36	34	—	—
	0.12	35	30	—	—	—
	0.16	24	24	—	—	—
	0.20	26	—	—	—	—
Sitka Spruce	0.06	50	55	—	—	—
	0.12	43	47	—	—	—
	0.18	25	29	—	—	—
	0.24	17	—	—	—	—

dead and downed inventories. If the tree species being examined have many large branches with bases exceeding 10 cm diameter (likely to occur in trees with a decurrent habit), these should be included in the coarse wood inventory.

Plot size is a crucial consideration when inventorying coarse woody detritus. To couple with living biomass estimates, the size of the coarse woody detritus plots may have to correspond to that of preexisting tree plots. If new plots are being established, one should consider a cumulative area of at least 0.1 ha to represent a normally stocked stand. In western coniferous forests, it is not unusual for the coefficient of variation to drop dramatically with increasing plot size (Table 2). For situations where tree stocking is very low (e.g., savannas), plots may have to be quite large (i.e., 1 ha or larger) to include any large pieces of woody detritus.

Coarse woody detritus assumes at least four forms: 1) snags, 2) stumps, 3) logs and 4) *blobs*. The latter is a somewhat whimsical term that refers to the piles of decomposed bark and wood that accumulate around the base of large conifer snags. The variables recorded for each log inventoried include: diameters at both ends and at the midpoint (this allows one to avoid assuming any particular form such as a cone or neiloid), length, species, position, decay class, and whether the piece is hollow or solid. In many forests it is very important to subtract out the volume associated with hollows (Figure 5). This can easily be done by noting the exterior diameter and the diameter and length of the hollow. The variables required for all other forms of coarse woody detritus are similar to those used for logs, with the exception of diameter. For snags, the diameter at breast height is recorded for intact boles and the diameters at the base and top for boles that have broken. The base and top diameters can also be recorded for stumps (cut by saw) or one can use a midpoint measurement. Finally, the diameter at the base is the only diameter required for blobs.

◆ Figure 5, below. Measurements needed to correct for "missing" volume in hollow logs.



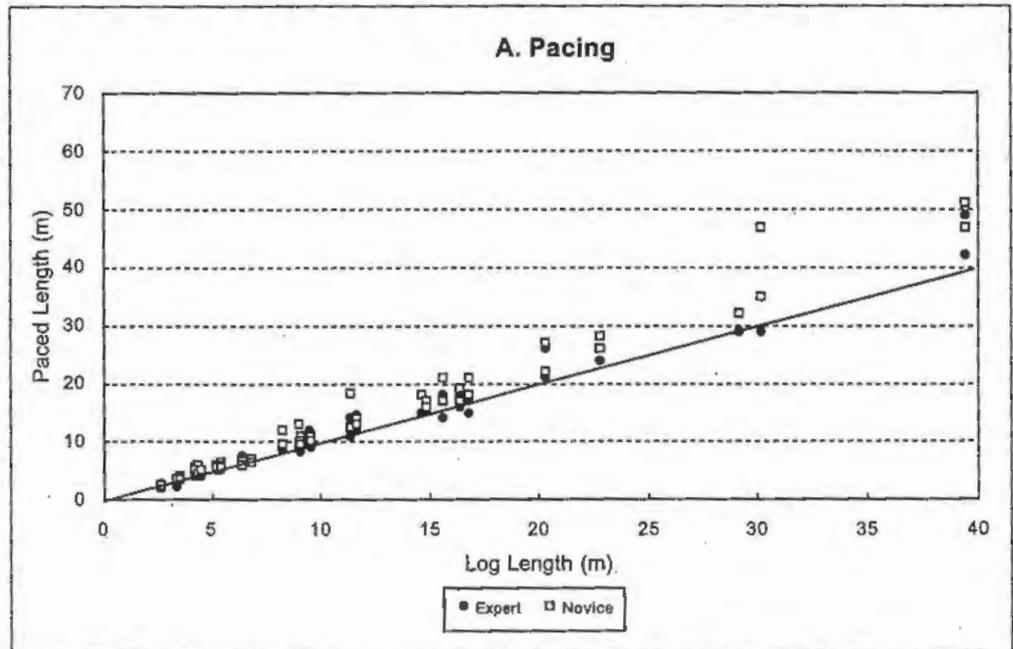
Diameters are best measured using 100 cm calipers, as it is often impossible to wrap a tape around logs and parallax errors may be significant if a meter stick is used. When pieces are elliptical in shape, we have found it impractical to estimate the "round" diameter in the field. In contrast, the maximum and minimum diameters are easily measured and can be converted to a round equivalent diameter using a modified version of the formula for the area of an ellipse (formulas 1 through 8 are numbered in brackets below):

$$A = D_{\max} * D_{\min} \quad [1]$$

$$D_{\text{round}} = \text{Sqrt}(A) \quad [2]$$

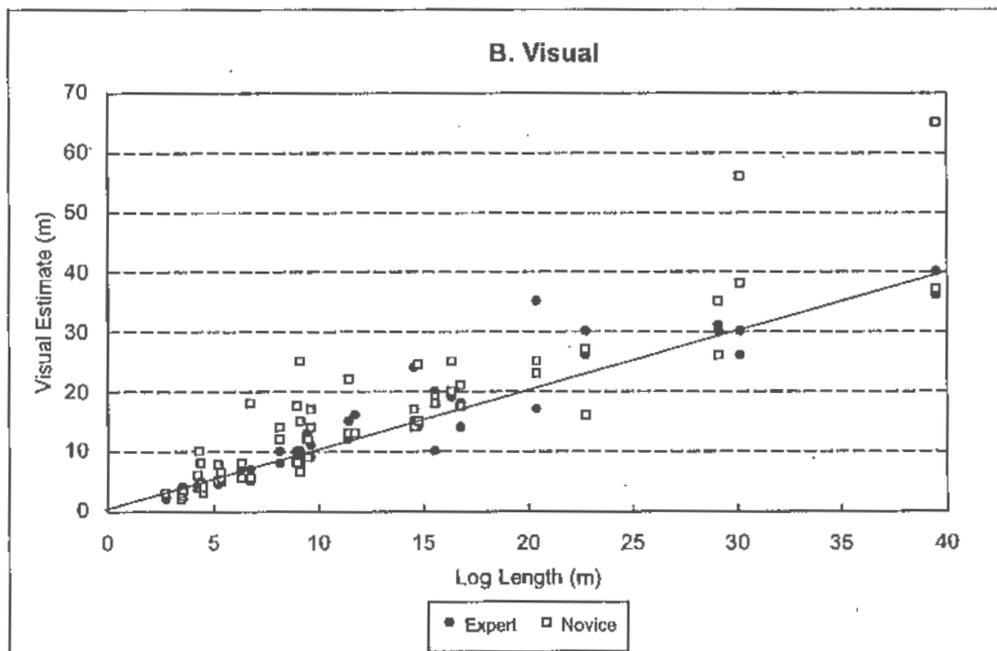
where D_{\max} , D_{\min} , and D_{round} are the maximum, minimum, and round equivalent diameters, respectively.

◆ *Figure 6. Comparison of two length estimation methods: A. pacing and B. visual (figure at right). Two "experts" and two novices independently estimated the length of 30 logs. These estimates were plotted against the length measured by tape.*



The top diameter of tall snags can usually be accurately measured by finding the top. If the top cannot be located, a visual estimate will usually suffice. However, our experience indicates that there is a tendency to visually underestimate the top diameter; we recommend calibrating the eye with snag tops that can be located.

The length of logs can be measured with a tape, or can be paced out or visually estimated. The most accurate method is to use a tape measure. Recently, we have been exploring the use of sonic tape measures. For lengths < 40 m, they are faster and nearly as accurate as tapes. Our methodological studies indicate that pace estimates are generally accurate for logs up to 20 m long, provided that the paces are calibrated carefully (Figure 6). Visual estimates can also be used, but are not accurate above a length of 10 m. A key finding for either estimation method is that experience and training is crucial. Experienced workers generally overestimated lengths by 5 to 7% regardless of the method used, while novice workers overestimated lengths by 20 to 26%. It is also possible to estimate log length from stand maps, although the accuracy of this method has not been tested (Harmon et al. 1987).



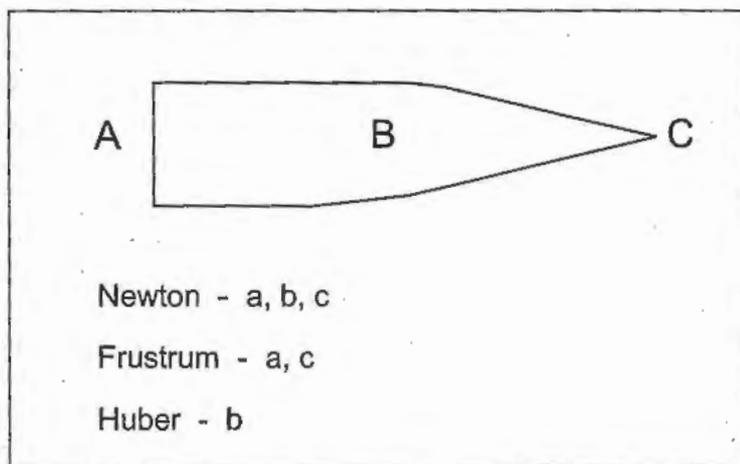
The height of snags is often difficult to measure or estimate. If a snag is not broken, one can estimate its volume or height from the breast height diameter by using allometric relationships developed for living trees (Garman et al. 1995). If a snag is not intact, one must estimate the length or height. For snags less than 4 m, it is possible to use a 100 cm caliper or meter stick to estimate height to the nearest 0.1 m. For taller snags, a clinometer and tape can be used. Although one can record the distance and slope angles and calculate the height, we have found the fastest method is to move across the slope until the clinometer indicates that the angle to the top of the snag is 45 degrees or a 100% slope. This distance, usually measured with a sonic tape measure, is the snag height minus the height to the eye.

Although we recommend measuring diameter at three points along the downed stem, other systems can be used (Figure 7, previous page). The most flexible of these is Newton's formula, which requires three diameter measurements:

$$V = L (A_b + 4 A_m + A_t)/6 \quad [3]$$

where V is the volume, L is the length, and A_b , A_m , and A_t are the areas of the base, middle, and top, respectively.

◆ *Figure 7.*
Diameter
measurements
required by the
Newton, Frustum,
and Huber methods
of volume
estimation.



One can also use the formula for a frustum of a cone, paraboloid, or neiloid if only the end diameters are measured. This would be most appropriate for snags or stumps. The formula for a frustum of a cone is:

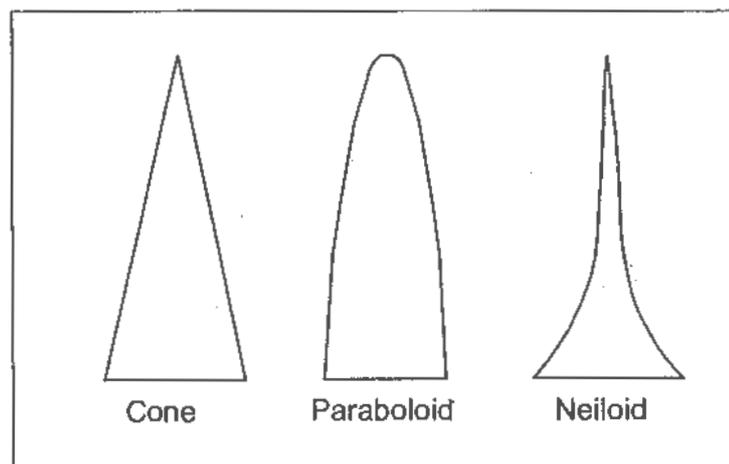
$$V = L (A_b + (A_b A_t)^{0.5} + A_t) / 3 \quad [4]$$

where V is the volume, L is the length, and A_b and A_t are the areas of the base and top, respectively. The formula for a frustum of a paraboloid is:

$$V = L (A_b + A_t) / 2 \quad [5]$$

where V is the volume, L is the length, and A_b and A_t are the areas of the base and top, respectively. For blobs, we have used a modification of equation 5 assuming that A_t is 0.

The limitation of using the formula for a frustum is that one must select a form factor. Unfortunately this can vary even within a species, depending upon the portion of the stem being measured (Figure 8). The most common form assumed is a cone.



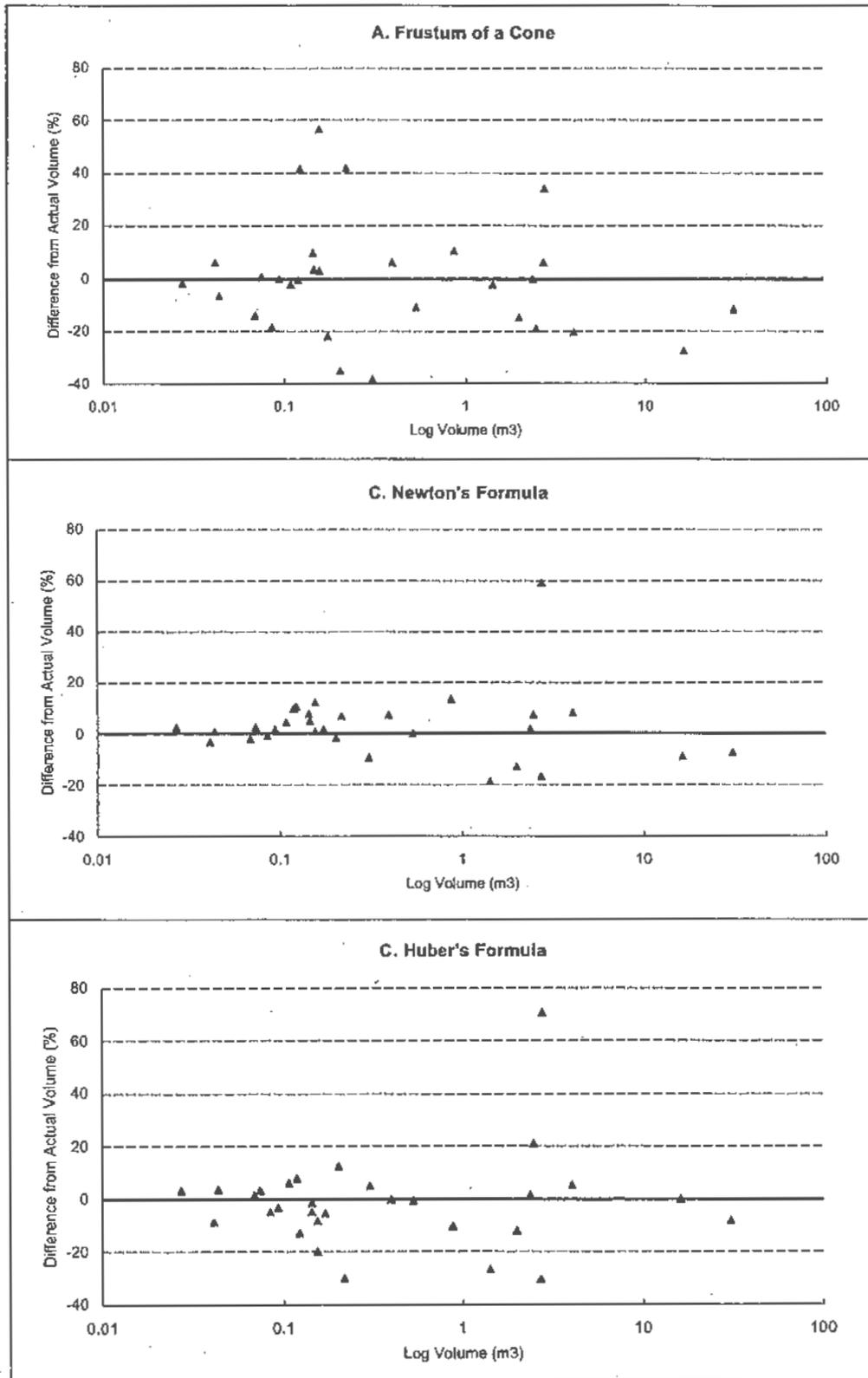
◆ *Figure 8.*
Volumetric forms
common in dead
trees (see formulae
above).

Finally, one can use the Huber formula (Wenger 1984) to estimate volume if one diameter at the midpoint is measured:

$$V = A_m L \quad [6]$$

where V is the volume, A_m is the area at the midpoint, and L is the length. We find the latter method does not really save time for logs (to determine length one must walk to the ends, anyway) and is impossible to use for snags above a few meters in height. It does save time for stumps if one only records the midpoint diameter of the stumps during an inventory. It also might prove a timesaver for short logs that have little taper along their length.

There have been numerous discussions concerning the ideal formula to estimate bole or log volume (Wenger 1984). One must bear in mind that coarse wood pieces are often quite irregular in shape, and that major errors can result unless one measures diameters at many points along the length. For example, when volumes estimated from seven diameters were compared to calculations using the formulae presented above, none of the formulae were biased (Figure 9). This means that, on average, all the formulae should give satisfactory results. For individual logs, Newton's formula had the smallest average deviation from the "true" volume (+/- 13%) and the formula for a frustum of a cone had the greatest average deviation from the true volume (+/- 22%). The worst fit between the true volume and all the formulae results when the smallest diameter along the log occurs at a place other than the ends or the center of the length.

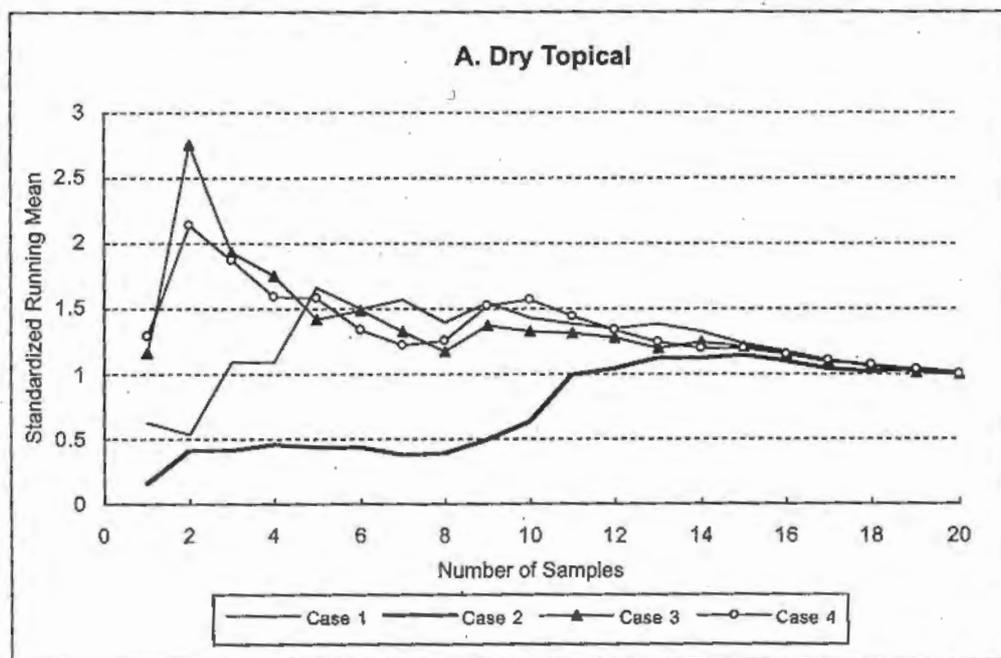


◆ *Figure 9.* Comparison of volume estimation methods: A. frustum of a cone (top left), B. Newton's formula (middle left), and C. Huber's formula (bottom left). The "actual" volume was based on seven diameter measurements spaced equidistantly along the length. The y axis indicates the percent deviation from the actual volume.

Fine Woody Detritus. Downed fine wood may also be estimated in small fixed area plots. Rather than estimate volume, we find it easier to harvest all the fine downed wood in the plots and weigh it using a portable electronic scale. Subsamples of this wood are then taken to estimate the moisture content, and the total field weight is adjusted using the estimated field moisture content. We find that 1 m² plots are adequate for sampling woody detritus <10 cm in diameter. As the distribution of fine downed wood is highly variable, we recommend that at least 10 plots be used for each stand sampled (Figure 10).

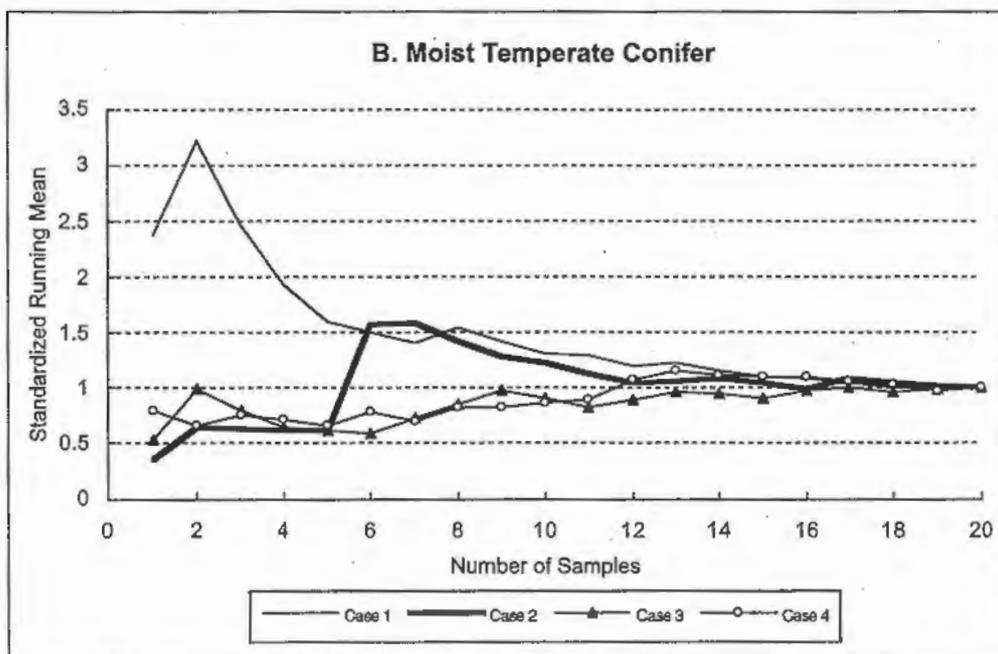
It is extremely difficult to estimate suspended fine wood directly unless it is close to the ground. We recommend that an indirect estimate be used, based on the inventory of coarse standing woody detritus. For standing dead trees that are not too decomposed (usually classes 1 and 2), one could estimate the volume of branches from allometric equations. For boles that have broken, this volume could be prorated

◆ Figure 10. Running mean of downed fine woody detritus mass as a function of sample size for two ecosystems: A. (right) dry tropical and B. (far right) moist temperate conifer. Each sample plot was 1- by 1 meter and was placed systematically along line transects. The values are standardized so that the mean of the 20 samples is set equal to 1.



according to snag height so that only snags with the entire length have the entire branch volume and those that have broken off below the crown do not have any volume. The mass of suspended fine wood could then be estimated from the branch volume by multiplying the branch density for the appropriate snag decay class. Unfortunately, we know of no estimates of branch density as a function of snag decay class. Lacking this data, one might assume that the decline in bole and branch density are proportionally equal; that is, if bole density declines 50%, then branch density declines 50%.

Attached Dead Wood. Allometric relationships to predict attached dead wood from tree diameter exist for many species. Unless one has ready access to tree crowns, we suggest that these equations be used with live tree diameter measurements from plots to give a crude approximation of stores in this pool. More detailed descriptions of potential methods can be found in Swift et al. (1976), Christensen (1977), and Chojnacky (1994).



Buried Wood. A significant fraction of the forest floor in some forests can be in the form of buried, highly decomposed wood (McFee and Stone 1966, Little and Ohmann 1988). Rotten wood that is fully incorporated into the forest floor or buried under thick moss mats is usually not included in coarse woody detritus inventories unless the shape of the log is obvious. This buried material is best measured with the forest floor. The color of the forest floor can usually be used to separate wood and non-wood fractions. Material derived from leaves and fine roots is usually black-brown in color, whereas that derived from wood is reddish-brown. We have used stainless steel corers, 2.5 cm in diameter, to sample wood buried in the forest floor. Our preliminary work indicates that at least 20 cores, spaced out along a transect >20 m long, are required to even detect the presence of rotten wood buried in the forest floor. A similar system was used by Harvey et al. (1979 and 1981), but they used a larger diameter corer (10 cm) and took orders of magnitude more samples (in one stand they sampled 1,050 cores!). Little and Ohmann (1988) used 12 to 15 samples per stand and reported reasonable results. One may also excavate along transects to record the depth of buried wood (McFee and Stone 1966) and then convert this depth into mass by multiplying by the density of class 5 wood ($<0.15 \text{ g cm}^{-3}$). This will give results in g cm^{-2} , however, so one must multiply by 10^4 to report values in g m^{-2} .

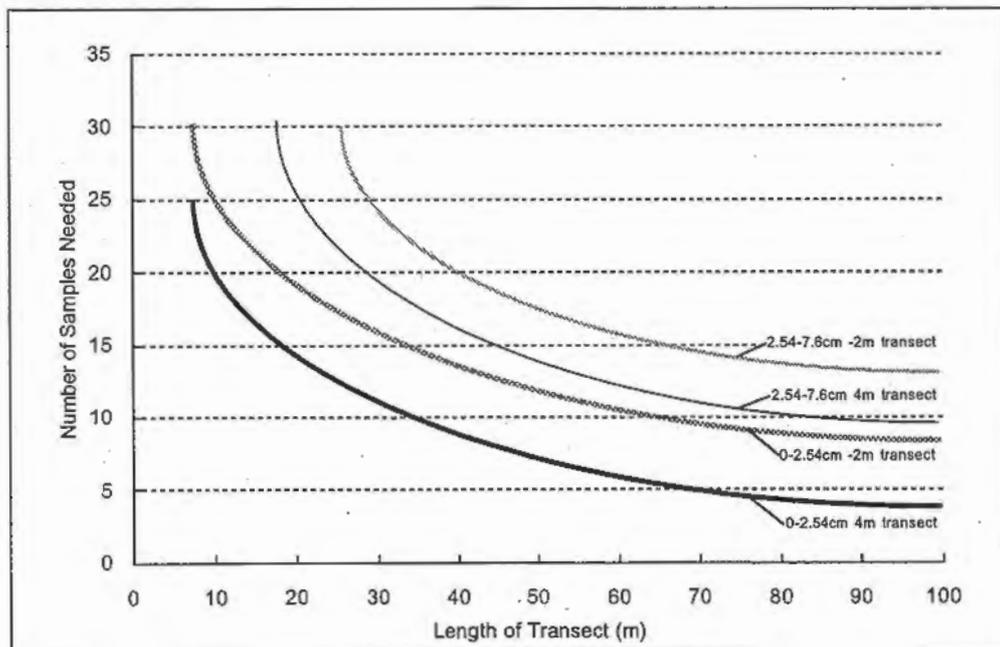
To our knowledge, decayed wood buried in the mineral soil has rarely been sampled. During most soil sampling, this material is sieved out prior to analysis; nevertheless, it would be interesting to know the size of this pool. Our observations indicate that coarse woody roots are often decomposed by white-rot fungi, suggesting that little woody residue except for that derived from bark would be found below-ground.

Dead Coarse Roots. We know of no one who has tried to directly inventory dead coarse roots. One possible indirect method would be to use allometric relationships based on tree diameter to predict the volume of dead roots for each dead tree in a fixed area plot. Each dead tree inventoried would then have a predicted dead root volume, and one could adjust the density based on the decay class of the dead tree. Unfortunately, we know of no estimates of dead root density as a function of snag decay class. Lacking this data, one might assume that the decline in bole and root density is proportionally equal; that is, if bole density declines 25%, then root density declines 25%

Line Intercepts for Downed Wood

The line intercept method is relatively fast, but one needs to use a suitable transect length. The past tendency of ecologists has been to use a transect length that is too short (<100 m), especially for coarse wood sampling. The length needed for an adequate sample is inversely related to particle density (Brown 1974, Pickford and Hazard 1978). Therefore, smaller wood pieces require less transect length than larger wood because their frequency is higher (Figure 11).

Although the line intercept method is fast and accurate, there are several problems with it. First, the traditional fire fuels sampling method has only two decay classes: sound and decayed wood, which are probably adequate for sampling woody detritus after recent disturbance such as clear cut harvest. However, for most ecosystems, this method lacks sufficient resolution. This problem is easily overcome by employing a decay class system similar to that used in the fixed area plots described above. The second problem with the fire fuels sampling method involves its use for long-term monitoring of change. Because lines are used and pieces may move, an inaccurate



◆ *Figure 11.*
Percent errors as a
function of the
number of pieces
encountered on a
transect (after
Brown 1974).

measure of the rate at which pieces are input or decomposed may result. This error also occurs in fixed area plots, but decreases as the plot size increases. For line intercepts, a possible solution is to tag or mark logs so that one can determine whether pieces actually decomposed or were input during the measurement interval. The third problem lies in the fact that line intercepts exclude snags, making a total woody detritus inventory impossible. This is especially problematic when trying to relate snags to logs over time. One must be aware that snags could fragment and be added to the log pool, yet not be detected with the line intercept system.

Coarse Woody Detritus. To estimate the volume of downed coarse woody detritus, one need only record the species, decay class and diameter. Contrary to popular belief, length is not used to estimate the volume when using line intercepts. Recording length still may be desirable when using this method, however, because the line intercept method yields better length estimates than fixed plots, which may truncate many log lengths at plot boundaries.

The formula to calculate V , the volume per unit area ($m^3 m^{-2}$), from line intercepts is:

$$V = 9.869 * \sum (d^2/8 L) \quad [7]$$

where d is the piece diameter (m), and L is the transect length (m) (Warren and Olsen 1964, Van Wagner 1968). For coarse woody fractions it is best to record the actual diameter of each piece. As with fixed radius plots, the maximum and minimum diameters of elliptical pieces on line intercepts should be recorded. These can later be converted to the round diameter equivalent (see equations 1 and 2 above).

Fine Woody Detritus. Line intercepts can also be used to estimate the volume of downed fine woody detritus. In this approach, one tallies pieces by size class and then converts to volume using size-class averages of particle diameter and secants of incidence angle (Table 3, next page). The formula used is similar to that of coarse detritus:

$$V = 9.869 * N * a * (d_q^2/8 L) \quad [8]$$

where V is the volume per unit area ($\text{m}^3 \text{m}^{-2}$), d_q is the quadratic mean piece diameter for a size class (m^2), L is the transect length (m), N is the number of pieces intercepted along the transect, and a is the average secant pieces along the transect. The latter term (a) is used to correct bias introduced by the non-horizontal orientation of the pieces (Brown and Roussopolos 1974). This correction is not required for downed coarse woody detritus, as this bias decreases with piece diameter (Pickford and Hazard 1978).

Variable Radius Plots for Suspended Woody Detritus

When using the line intercept method for inventorying downed wood, one must use an alternative method to estimate snags or suspended detritus. This could be either fixed area plots as described above or variable radius plots, often used for living trees (Grosenbaugh 1958, Ordwald 1981). We have not tested the latter approach, but it may prove useful. In the variable radius plot system, a prism with a certain basal area factor (BAF) is used to determine if snags are to be included or excluded from the tally. Each snag tallied is equivalent to the basal area of the BAF. For example, using a BAF of 5 means each snag adds a basal area of $5 \text{ m}^2/\text{ha}$ (assuming a metric prism is used). In this case, three snags tallied at a sample point would give a basal area of $15 \text{ m}^2/\text{ha}$.

To estimate volume, mass, and nutrient stores from variable radius plots, the species, decay class, diameter at breast height and top, and the height should all be recorded for each snag that is included in the tally. The density per unit area of snags for each size class can be computed by dividing the BAF by the actual basal area of the snag measured. Using a BAF of 5, for example, a snag with a diameter at breast height (DBH) of 50 cm would have a basal area of 0.19 m^2 and, therefore, would represent 25.6 snags/ha. The estimated volume or mass of each snag would then be multiplied by the number of snags it represents per unit area. For example, if the 50 cm DBH snag used in the example above had a mass of 0.25 Mg, it would represent a mass of 6.4 Mg/ha ($25.6 \text{ snags ha}^{-1} * 0.25 \text{ Mg snag}^{-1}$). One could estimate the fine suspended woody detritus associated with each snag using the approach outlined above for fixed area plots.

INVENTORIES of MASS and NUTRIENT STORES

Table 3. Mean bulk density (D), squared average quadratic mean diameter (d_q^2), and average secant (a) for correcting orientation bias used in planar or line intercept methods (see equation 8).

Species	Diameter Class (cm)	d_q^2 (cm ²)	a	D (g/cm ³)	Source
conifers					
<i>Larix occidentalis</i>	0-0.63	0.096	1.15	—	1
	0.63-2.54	1.535	1.13	—	1
	2.54-7.62	13.999	1.10	—	1
<i>Picea rubens/Abies fraseri</i>	0-0.63	0.066	1.15	—	3
	0.63-2.54	1.540	1.13	—	3
	2.54-7.62	18.900	1.10	—	3
<i>Pinus contorta</i>	0-0.63	0.129	1.15	—	1
	0.63-2.54	1.535	1.13	—	1
	2.54-7.62	18.516	1.10	—	1
<i>Pinus ponderosa</i>	0-0.63	0.221	1.25	—	1
	0.63-2.54	1.535	1.25	—	1
	2.54-7.62	20.128	1.22	—	1
<i>Pinus rigida/Pinus virginiana</i>	0-0.63	0.129	1.15	0.421	3
	0.63-2.54	1.870	1.13	0.395	3
	2.54-7.62	16.560	1.13	0.397	3
<i>Pseudotsuga menziesii</i>	0-0.63	0.079	1.15	—	1
	0.63-2.54	1.961	1.13	—	1
	2.54-7.62	18.516	1.10	—	1
<i>Tsuga canadensis</i>	0-0.63	0.058	1.15	0.451	3
	0.63-2.54	1.540	1.13	0.387	3
	2.54-7.62	18.900	1.13	0.389	3

Table 3. continued

Species	Diameter Class (cm)	d_q^2 (cm^2)	a	D (g/cm^3)	Source
conifers					
<i>Conifer composite</i>					
	0-0.63	0.097	1.15	0.480	1
	0.63-2.54	1.864	1.13	0.480	1
	2.54-7.62	17.806	1.10	0.400	1
hardwoods					
<i>Acer/Betula/Tilia</i>					
	0-0.63	0.185	1.24	0.540	3
	0.63-2.54	1.720	1.11	0.390	3
	2.54-7.62	17.580	1.03	0.342	3
<i>Quercus prinus</i>					
	0-0.63	0.136	1.24	0.558	3
	0.63-2.54	1.890	1.11	0.454	3
	2.54-7.62	17.350	1.03	0.471	3
<i>Quercus spp.</i>					
	0-0.63	0.137	1.24	—	2
	0.63-2.54	1.562	1.11	—	2
	2.54-7.62	—	1.03	—	2
<i>Quercus spp.</i>					
	0-0.63	0.156	1.24	0.559	3
	0.63-2.54	1.750	1.11	0.427	3
	2.54-7.62	17.350	1.03	0.444	3

Sources: 1) Brown (1974), 2) Brown and Roussopolos (1974), 3) Harmon et al. (1980).

A serious drawback of using variable radius plots to estimate snag basal area is that snag density is usually quite low relative to trees. In order to sample an adequate number of snags for volume and density estimates, one must use a prism with a relatively small BAF. This creates another problem, however, in that a small BAF leads to an underestimate of basal area (as more trees become hidden and are missed). We currently do not know the optimal trade-off between these two considerations.

Conversion of Volume to Mass and Nutrient Stores

Regardless of the method used to estimate volume (fixed radius plots, variable radius plots, or line intercepts), one can use the data generated to estimate mass and/or nutrient stores. To convert these dimensional data to mass or nutrient values, however, one must know the density and/or nutrient content of wood and bark in various stages of decay. In a Level One installation, these values would be taken from the literature (Table 4). Although not using site-specific values (especially for nutrient stores) increases the potential for error, the literature values of density and nutrient contents will provide a first approximation.

In a Level Two installation, the decay class information would be specific to a site, although this need not include each and every forest for which dimensional data is gathered. To establish an objective decay class system, it is necessary to correlate the external characteristics to variables of interest such as density, bark cover, and nutrient content (see also the chronosequence description below). Physical characteristics that have proven useful in the past to distinguish decay classes include the presence of leaves, twigs, branches, bark cover on branches and boles, sloughing of wood, collapsing and spreading of log (indicating the transition from round to elliptic form), degree of soil contact, friability or crushability of wood, color of wood, and whether the branch stubs can be moved (Table 5, page 33). Biological indicators such as moss cover, fungal fruiting bodies, or presence of insect galleries seem to be of very little value in separating decay classes, as they vary widely even within a limited area.

Table 4. Mean density and nutrient concentration of wood for decay classes of coarse woody detritus.

Species	Location	Decay Class	Density (g cm ⁻³)	Nitrogen	Phosphorus	Potassium	Calcium	Source
				-----ppm-----				
Mexico-Tropical								
<i>Beaucarnea pliabillis</i>								
		1	0.248	2950	167	5125	5500	1
		2	0.195	2950	167	5125	5500	1
		3	0.061	2900	83	17117	29833	1
		4	0.061	4520	120	24100	44340	1
		5	0.061	6960	126	26180	47580	1
<i>Blomia cupanioides</i>								
		1	0.794	2870	106	11333	18233	1
		2	0.794	2870	106	11333	18233	1
		3	0.794	2900	83	17117	29833	1
		4	0.538	4520	120	24100	44340	1
		5	0.226	6960	126	26180	47580	1
<i>Brosimum alicestrum</i>								
		1	0.619	2150	102	9350	16100	1
		2	0.441	2150	102	9350	16100	1
		3	0.300	2900	83	17117	29833	1
		4	0.200	4520	120	24100	44340	1
		5	0.200	6960	126	26180	47580	1
<i>Bursera simaruba</i>								
		1	0.327	4200	411	17300	21280	1
		2	0.227	4200	411	17300	21280	1
		3	0.131	2900	83	17117	29833	1
		4	0.131	4520	120	24100	44340	1
		5	0.166	6960	126	26180	47580	1
<i>Manilkara zapota</i>								
		1	0.806	2100	105	10750	18950	1
		2	0.814	2100	105	10750	18950	1
		3	0.807	2900	83	17117	29833	1
		4	0.538	4520	120	24100	44340	1
		5	0.226	6960	126	26180	47580	1
<i>Myrcianthes fragrans</i>								
		1	0.726	2870	106	11333	18233	1
		2	0.726	2870	106	11333	18233	1
		3	0.505	2900	83	17117	29833	1
		4	0.300	4520	120	24100	44340	1
		5	0.228	6960	126	26180	47580	1

Table 4. continued

Species	Location					
Decay Class	Density (g cm ⁻³)	Nitrogen	Phosphorus	Potassium	Calcium	Source
		-----ppm-----				
Mexico-Tropical						
<i>Talisia olivaeformis</i>						
1	0.794	2870	106	11333	18233	1
2	0.600	2870	106	11333	18233	1
3	0.567	2900	83	17117	29833	1
4	0.300	4520	120	24100	44340	1
5	0.226	6960	126	26180	47580	1
<i>Unknown decay resistant species</i>						
1	0.775	2870	106	11333	18233	1
2	0.696	2870	106	11333	18233	1
3	0.671	2900	83	17117	29833	1
4	0.639	4520	120	24100	44340	1
5	0.220	6960	126	26180	47580	1
<i>Unknown non-decay resistant species</i>						
1	0.619	2150	102	9350	16100	1
2	0.441	2150	102	9350	16100	1
3	0.300	2900	83	17117	29833	1
4	0.200	4520	120	24100	44340	1
5	0.200	6960	126	26180	47580	1
Sierra Nevada-Temperate						
<i>Abies concolor</i>						
1	0.340	976	70	1336	2656	2,3
2	0.333	1194	80	1337	2670	2,3
3	0.202	1917	112	2432	5158	2,3
4	0.185	2140	100	2313	5781	2,3
<i>Libocedrus decurrens</i>						
1	0.426	1423	90	819	2053	2,3
2	0.345	1423	90	819	2053	2,3
3	0.328	2070	104	494	1690	2,3
4	0.157	1450	37	2019	2578	2,3
<i>Pinus jefferyi</i>						
1	0.387	1050	53	707	1175	2,3
2	0.349	1056	55	490	1142	2,3
3	0.340	1150	47	195	1255	2,3
4	0.222	2866	114	261	1984	2,3

Table 4. continued

Species	Location	Decay Class	Density (g cm ⁻³)	Nitrogen	Phosphorus	Potassium	Calcium	Source
				-----ppm-----				
Sierra Nevada-Temperate								
<i>Pinus lambertiana</i>								
	1	0.366	1125	37	757	1339	1339	2,3
	2	0.352	1550	51	620	1329	1329	2,3
	3	0.230	1962	85	281	1292	1292	2,3
	4	0.173	2700	89	2987	2409	2409	2,3
Olympics-Temperate								
<i>Picea sitchensis</i>								
	1	0.434	760	100	160	970	970	4
	2	0.301	800	80	220	840	840	4
	3	0.284	1020	83	90	1090	1090	4
	4	0.160	2280	161	320	1430	1430	4
	5	0.148	4467	267	310	3000	3000	4
<i>Tsuga heterophylla</i>								
	1	0.374	980	274	1130	1460	1460	4
	2	0.321	1360	170	900	1440	1440	4
	3	0.320	1130	310	420	1360	1360	4
	4	0.197	2640	270	420	1330	1330	4
	5	0.195	2640	270	420	1330	1330	4
Cascades-Temperate								
<i>Pseudotsuga menziesii</i>								
	1	0.450	900	40	155	1400	1400	5
	2	0.341	1000	39	148	1200	1200	5
	3	0.277	1000	41	141	1100	1100	5
	4	0.137	2400	111	171	1700	1700	5
	5	0.148	4467	267	310	3000	3000	5
<i>Thuja plicata</i>								
	1	0.318	1100	48	279	1600	1600	5
	2	0.259	1400	51	313	1700	1700	5
	3	0.248	1700	78	178	1600	1600	5
	4	0.154	2100	107	283	3100	3100	5
	5	0.143	4467	267	310	3000	3000	5

Table 4. continued

Species	Location					
Decay Class	Density (g cm ⁻³)	Nitrogen	Phosphorus	Potassium	Calcium	Source
		-----ppm-----				
Cascades-Temperate						
<i>Tsuga heterophylla</i>						
1	0.376	800	93	760	1400	5
2	0.295	1100	59	203	1300	5
3	0.242	1200	88	355	1700	5
4	0.146	2500	135	208	2100	5
5	0.142	4467	267	310	3000	5
Rocky Mountains-Temperate						
<i>Abies lasiocarpa</i>						
1	0.414	510	15	1499	1312	3
2	0.238	1270	101	1871	2554	3
3	0.250	1192	100	869	2324	3
4	0.177	2747	183	766	2661	3
5	0.139	3600	313	557	3437	3
<i>Pinus contorta</i>						
1	0.405	465	25	395	787	3
2	0.405	230	18	316	625	3
3	0.370	620	31	248	965	3
4	0.176	2825	204	444	2492	3
5	0.175	2866	212	380	2412	3

Sources: 1) Harmon et al. 1995, 2) Harmon et al. (1987), 3) Harmon unpublished, 4) Graham and Cromack (1982), 5) Sollins et al. (1987) and Graham (1982).

In areas with high species diversity, it may be impossible to measure decay classes for each species. One way to get around this problem would be to group species within a genus or within some larger functional class. In diverse tropical forests, for example, we have established two groups—decay resistant and non-decay resistant species—to cover the many rare species that exist (Harmon et al. 1995). This grouping is based on the fact that species with a thin sapwood and decay resistant heartwood tend to decay very differently from those with thick sapwood or nonresistant heartwood.

Table 5. Example of data form used to characterize decay classes at H.J. Andrews LTER.

Date _____	Location _____	Forest Type _____	Log Number _____
Species _____	Position Log/Snag _____	Decay class _____	
Age _____ years	Method _____	Cause of Death _____	
DBH _____ cm	Diameter (Base) _____ cm	Diameter (Top) _____ cm	
Total Length _____ m		Bark Cover _____ %	
Volume Missing From Rot _____ cubic meters			
Diameter 1st Sample	cm	Height	m
Diameter 2nd Sample	cm	Height	m
Diameter 3rd Sample	cm	Height	m
Diameter 4th Sample	cm	Height	m
Diameter 5th Sample	cm	Height	m
FRAGMENTATION INDICATORS (Circle answer)			
leaves present	Y/N	color _____	
twigs present	Y/N		
branches present	Y/N		
bark on branches	Y/N		
bark on bole	Y/N		
sapwood sloughing	Y/N		
log collapsing	Y/N	can not support own weight	
log scattered	Y/N	log x-section elliptical	
sapwood friable	Y/N	can crush with hand	
heartwood friable	Y/N	can crush with hand	
branch stubs move	Y/N		
BIOTIC INDICATORS			
conks present	Y/N		
moss covering log	Y/N	percent cover _____ %	
lichens covering	Y/N	percent cover _____ %	
carpenter ants	Y/N		
termites	Y/N		
bark beetle Gal.	Y/N		
bear damage	Y/N		
brown rot	Y/N	where? _____	
white rot	Y/N	where? _____	
Notes:			

INPUT RATES

To understand woody detritus dynamics, it is very important to measure input rates as well as the standing crop. For example, in old-growth forests this information will allow a first approximation of coarse woody debris turnover rates. If independent data that include fragmentation exist on decomposition rates, one can also estimate whether woody detritus is accumulating or declining during succession (Krankina and Harmon 1994). The addition of input and decomposition data is therefore a crucial factor in separating Level One and Level Two installations.

The addition of input and decomposition data is a crucial factor in separating Level One and Level Two installations

We consider inputs of woody detritus in several forms. The first is that associated with tree mortality. The second is from branchfall. We do not consider the inputs of detritus associated with attached dead wood, although others have investigated this problem (Swift et al. 1976).

Coarse Woody Detritus Inputs

The majority of coarse wood inputs are associated with tree mortality. We do not consider the fragmentation of standing dead trees or snags to be an input to the coarse woody detritus pool. If interested in this flux, one may wish to measure this input to the log or downed coarse wood pool in fixed area plots or by tracking the fate of selected snags.

Tree mortality rates are best measured using permanent plots, although various reconstruction methods have also been used to estimate long-term rates (McCune et al. 1988). The only parameters required to estimate woody detrital inputs are the diameter and species of the dead tree at the time of plot remeasurement. Biomass equations and fresh nutrient contents are then used to compute the amount added. It is also easy to note which fraction of the tree died standing or fell over. Other variables such as cause of death and associated symptoms can also be recorded with little increase in expense (Table 6).

Table 6. Example of data collected during mortality surveys at H.J. Andrews LTER.

DIRECTIONS FOR TREE MORTALITY SHEET (890601)

Header

1. *Location:* e.g., HJA, Olympic NP, Wildcat Mt. RNA
2. *Personnel:* PLEASE USE SURNAMES
3. *Date:* YYMMDD (Year, Month, Day)
4. *Study ID:* copy from reference stand data sheet
5. *Stand ID:* copy from reference stand data sheet

Mortality Data

1. *Plot ID and tree tag number.*
2. *Species Code:* Four- or five-character acronym (PSME, PICO, CADE3)
3. *DBH (cm):* Most recent diameter measurement
4. *Canopy Class:* Canopy class at time of death.
5. *Standing:* Entry indicates tree is still rooted.
 - a. *% Crown:* Estimate percent of crown standing intact. Do not enter values of less than 100% for sparse crowns or gradual dieback.
 - b. *% Tree:* Estimate percent of the entire main stem length that is standing unbroken. Maximum in this category is 100%.

NOTE: % Crown and % Tree standing may sum to > or < 100%.

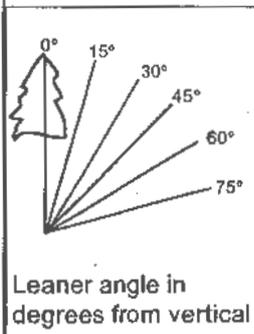
6. *Leaner Angle:* If tree is still rooted and is leaning, estimate the angle of lean in degrees from vertical. (See figure at right.) Use this category for trees.

7. *Down:* Entry indicates that part or all of the dead tree is down. Use this category only if %Tree standing is less than 100% and only when part of the tree is down. A tree that is crushed but still rooted is not considered to be down. Consider ONLY the down part of the tree stem. % On ground and % Supported MUST sum to 100%.

- a. *% On Ground:* Estimate the percent of the down portion of the stem that is in DIRECT contact with the ground.
- b. *% Supported:* Estimate the percent of the down portion of the stem that is supported ABOVE the ground.

Special Cases:

- a. Record missing data as -1. E.g., if the top of a broken tree cannot be found, record data about the standing portion of the tree under STANDING and a -1 in both columns of DOWN.
 - b. Broken tops hung up in the canopy are considered down but supported.
8. *Tree Position:* Record one Tree Position Code from the front of the mortality sheet that describes the position of the dead tree. THIS INFORMATION MUST BE ENTERED.
 9. *Tree Condition Codes:* Use these codes ONLY if condition is visible. Write the appropriate code(s), one code per box, under the tree condition category.
 10. *Mortality Cause*
 - a. *Primary Cause:* If possible, enter primary cause of death. Use one code ONLY. If "unknown" is selected as primary cause make brief notes and/or diagrams where applicable.
 - b. *Secondary Cause:* Optional. Enter only if a contributing cause can be identified.
 - c. *Confidence:* Enter a "1" if confident of the primary cause; otherwise, leave blank.



There are various methods for identifying trees that have died during a measurement interval. The least ambiguous is to uniquely tag all the trees in a plot. When trees are checked it is important to examine every tree; just cruising for obvious dead trees can underestimate mortality by a factor of two! It is also possible to locate trees using maps, although tree identification questions may crop up using this method. The least reliable method would be to search plots for "new" dead trees. In cases where tagging of trees is not allowed, we suggest making a cut or blaze into the wood with a hatchet or ax to mark dead trees that have been inventoried.

Coarse woody detritus inputs are highly variable in both time and space. Although working on an existing permanent plot has benefits, most plot systems are designed to estimate biomass and production, but not mortality. The following guidelines may assist in determining whether existing plot systems are adequate. In Pacific Northwest and Rocky Mountain forests, we have found that a remeasurement interval of five to six years is suitable to measure input rates and position at the time of death. In other regions, such as the tropics, a shorter time interval may be required as decomposition rates are much higher. If the cause of mortality is to be determined, annual checks should be made (Franklin et al. 1987). For periods exceeding 10 years, one can only estimate the size of the tree at the time of death (if the bark has sloughed, even that is questionable). Moreover, saplings may have entered the tree size class and died during intervals exceeding 10 years. So, while long intervals can provide some useful information, the data must be carefully interpreted (Volk and Fahey 1994).

Tree mortality rates are also highly variable and there are few quantitative guidelines for the area or time required to obtain good estimates. A review of the literature indicates that there are numerous short-term or small-area mortality estimates that are extremely misleading (i.e., removing one tree can halve the reported rate). As a first approximation, data should not be dependent upon the inclusion or exclusion of a single tree. To be within 10% of the live stem mortality rate (defined here as the percentage of tree stems dying each year), at least 10 trees have to die within some combination of area and time. For woody detritus input rates (defined here as the mass input each year), perhaps twice this number would be adequate because inputs are highly dependent upon the number of large trees that die. On the basis of observed

rates of mortality (Table 7), 5 hectare-years would appear to be the minimum sample required to generate reliable data for temperate and tropical hardwood forests. In contrast, the minimum sample for temperate conifer forests would appear to be 10 hectare-years. Although one can substitute time for space and vice versa, single year estimates over a large area will rarely equal the long-term average of a smaller area.

Fine Woody Detritus Inputs

Although one could measure the input of fine woody detritus directly, this can be a difficult task because many trees die standing. We recommend that inputs of fine woody detritus be indirectly estimated using allometric equations. These estimates can be based on the diameters of the trees that died in the mortality surveys (Sollins 1982). We have found that a relatively small fraction of the downed fine woody detritus is input from branches that have snapped off in windstorms or from ice and snow damage. These inputs can be measured on fixed area plots (generally, 4 m^2 has been used), as long as one separates freshly killed branches from decayed branches that have fallen from snags or from dead branches attached to live trees (Swift et al. 1976). Neither of the latter forms actually represents new inputs of woody detritus. Finally, it is also possible to use the allometric approach to estimate the mass input of dead coarse roots, although no one has tested the accuracy of this method.

Table 7. Expected number of trees dying for various biomes during periods of background mortality.

Biome	Number of Trees	
	per hectare/year	per 5 hectare years
western conifer	1-3	5-9
eastern deciduous	2-6	10-30
moist tropical	4-18	20-90

DECAY RATES *and* NUTRIENT MINERALIZATION

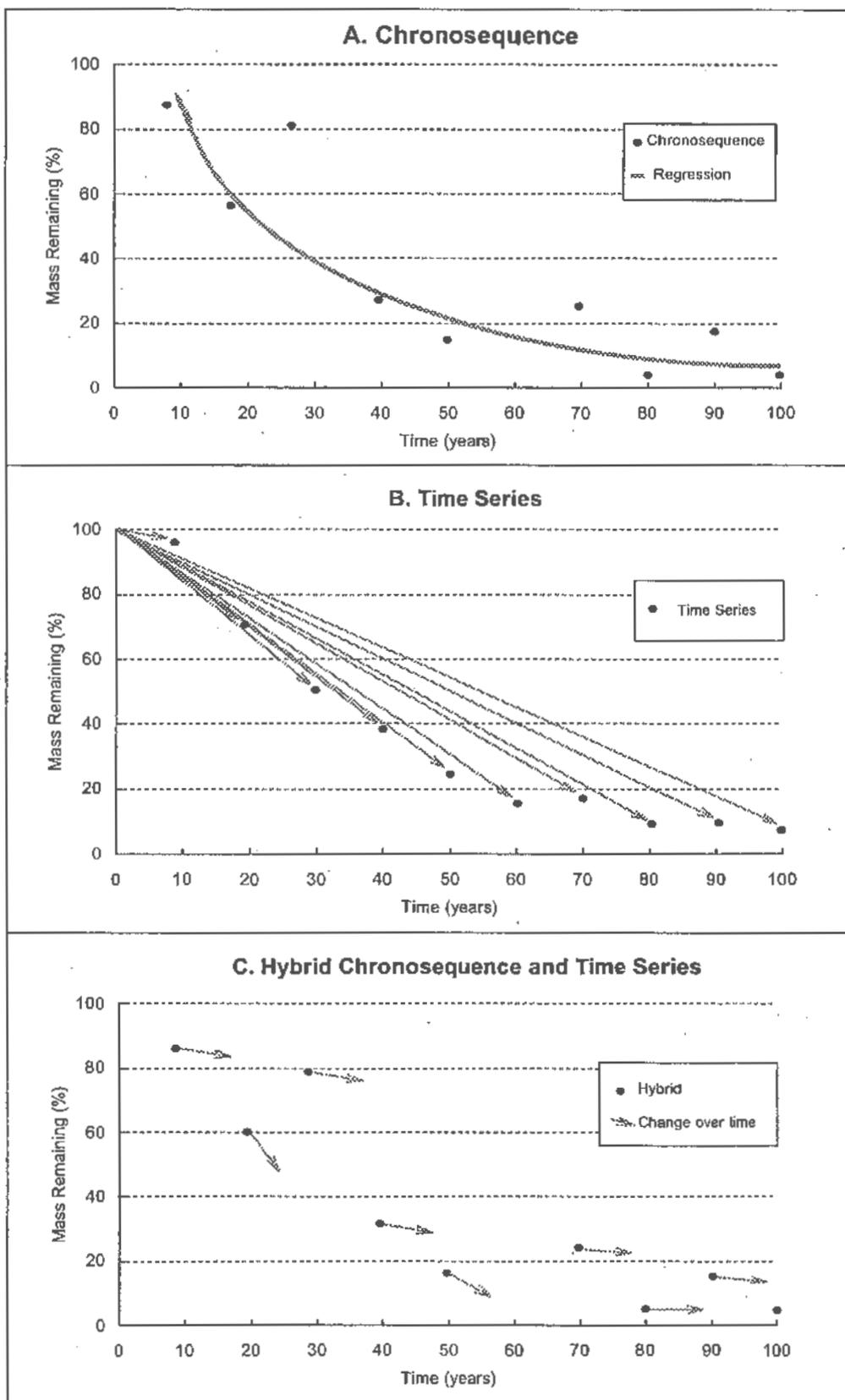
While inventories of woody detritus stores are valuable, they have limited value for understanding dynamics and the role this pool plays in the larger ecosystem context. Coupling stores information with a knowledge of the rate at which this material decomposes and releases nutrients, however, provides an excellent foundation for answering these questions. The addition of variables that allow a dynamic analysis is the major criterion separating a Level One from the higher levels of installation.

There are two complementary approaches to understanding the decomposition dynamics of coarse woody detritus: 1) chronosequences, which give a short-term snapshot of the process and 2) the time series, which is a long-term effort yielding excellent resolution of temporal patterns and processes (Figure 12). One may combine these two approaches to form a hybrid method by resampling a chronosequence. Although the hybrid method has not been published, our preliminary studies indicate it combines the advantages of both approaches. Given the greater precision, site specificity, and cost (at least in terms of time!) of the time series approach, we have separated Level Two from Level Three installations based on the use of this method. This is not to say that the chronosequence method is any less valuable; for example, the decay class data used to convert volumes to mass or nutrient stores are best measured in a chronosequence.

Below, we describe the general characteristics of and trade-off between chronosequence versus time series sampling. This is followed by a section on common considerations in sampling using either method (e.g., species selection). We then conclude with specific methods to measure mass loss and nutrient change.

Chronosequence/Decay Classes

In a *chronosequence*, one ages as many pieces as possible in various states of decay and examines how a parameter such as density changes over time. This is the classic substitution of space for time. Dates can be taken from fall scars, seedlings, living stumps, and records of disturbance (e.g., fire, insect outbreak, wind storm, thinning). This approach has been used extensively for coarse woody detritus (Grier 1978,



◆ *Figure 12.* Contrast of the A. chronosequence (top left), B. time series (middle left), and C. hybrid (bottom left) methods of estimating decomposition rates. The lines with arrows indicate a direct estimate of time effects; and the open circles indicate the samples.

Graham 1982, Harmon et al. 1987, Means et al. 1987, Sollins et al. 1987), but also can be used for downed fine woody detritus (Erickson et al. 1985) and dead coarse roots (Fahey et al. 1988).

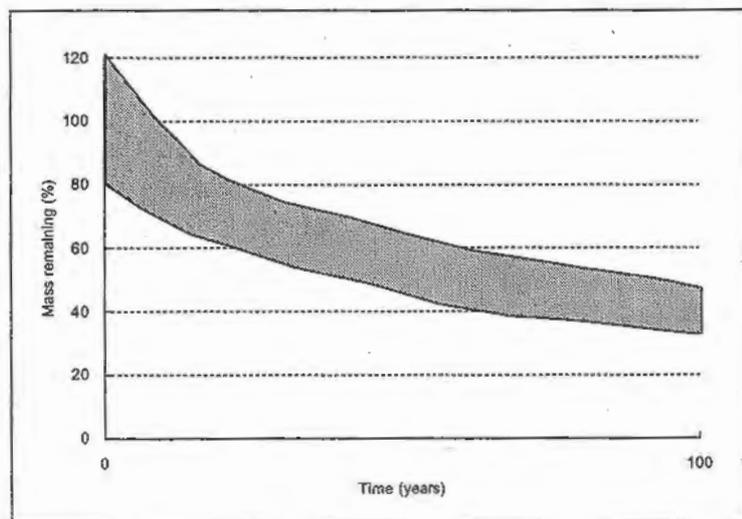
The interpretation of chronosequence data varies depending upon its use. This is equally true if one is using the approach for coarse or fine woody debris, or for coarse roots. There are two uses of chronosequence data: 1) to convert volume measurements into mass or nutrient stores (see above) and 2) to determine the rate mass is lost or nutrients are absorbed or released. In the case of using decay classes to estimate density or nutrient concentration, one needs to know the current values so no adjustment for fragmentation is required. In contrast, if the aim is to use the decay chronosequence data to estimate rates of mass loss or nutrient release, then the data must be adjusted for past fragmentation losses to estimate these rates correctly. Unless these losses are accounted for, the rates of mass loss and nutrient release may be substantially under-estimated. There are numerous cases in the literature where this step has not been completed; as a result, about one-third of current published studies are of questionable value.

To correct for fragmentation losses, one must compare the present store to the initial store of mass or nutrients. The original mass and nutrient content can often be approximated from the original diameter at breast height using allometric equations. In cases where the log has fragmented at the point that was breast height, one may try several methods to reconstruct the diameter. First, one can add back the radial thickness of parts that have fragmented. For example, if the bark has sloughed off, then adding the bark thickness to the existing wood diameter will approximate the original DBH. A similar approach can be used when sapwood has fragmented. Sapwood thickness does not vary greatly along the bole (Bamber and Fukazawa 1985), so it is possible to use thickness measurements from elsewhere along the bole for these corrections. In cases where there is no sapwood remaining, one can often use the "wings" of sapwood attached to branch stubs as an indicator of the original thickness. These wings of sapwood are quite common at the point where a branch emerges from a conifer bole. We have also observed these wings on *Alnus* and *Quercus* logs, so it is possible the method is of use for other taxa as well. Finally, if all else fails, one may estimate the DBH from the diameter at the base of the tree. In many regions, tables and equations exist to estimate DBH from stump diameters (Hann 1976, Alemdag and Honer 1977, McClure 1968, Raile 1977, Kozak and Omule 1992). By setting the stump height to zero, one can estimate the DBH using these equations.

Time Series

Although chronosequences are fast, there are serious temporal resolution problems caused by errors in dating and estimates of initial conditions (Figure 13). A *time series* circumvents these problems by examining how a cohort of pieces progresses through time. Hence, there is no substitution of space for time when using the time series approach. Although the method requires substantial investments in effort and time, it lends itself nicely to process studies. To take full advantage of the approach, one should: 1) place out more material than a typical short-term study requires and 2) fully document the original condition of the material.

As with the chronosequence method, one must adjust results for losses due to fragmentation or for parts that have decomposed completely. This is less of a problem in time series studies, however, because one should know or be able to estimate closely the initial mass and nutrient stores of each piece being examined.



◆ *Figure 13.* Theoretical errors introduced by poor estimates of initial conditions. The shaded area represents the uncertainty of mass remaining, assuming that the coefficient of variation of the initial density is 10%.

Selection of Dependent Variables

While a large number of potential variables can be measured in either a time series or a chronosequence study, the specific variables that are the most desirable to measure will vary with the study objectives. For larger pieces, we recommend that at a minimum the density and radial thickness of the major tissue types (i.e., outer bark, inner bark, sapwood, and heartwood), the total volume of the piece, bark cover, and the depth and type of decay (white rot versus brown rot) be measured. The position of the pith is also a very useful to measure, as it can serve as a reference point to estimate fragmentation losses in either time series or chronosequence studies. If cross-sections are removed, it is best to photograph them as soon as possible after harvesting to document the areas of decay and the extent of insect galleries, and to aid in determining the volume of each of the tissue types. Since bark, sapwood, and heartwood decay at different rates, it is crucial to know their relative proportions if one intends to model the decay of different-sized pieces by adjusting proportions of the tissues. These parameters should be measured both before (not possible for chronosequences, of course!) and after decay has started. There are many features one cannot detect once decay starts, so these initial records are essential. Moreover, one cannot fully exploit the power of a time series without obtaining information on initial conditions for each and every log. Lack of such information is the major shortcoming of chronosequence studies.

Species Selection

Species selection for a chronosequence will depend upon the degree of species richness and the number of functional classes present in a location. Except for large, diverse genera with resistant heartwood, such as *Pinus* or *Quercus*, there is probably no precision to be gained by sampling below the genus level. That is, most species within a genus such as *Acer* or *Picea* will probably be fairly similar, so there is no need to sample each species present at a site. In highly diverse ecosystems such as tropical forests, one may wish to avoid the genus level altogether and simply sample functional groups such as palms, resistant hardwoods and nonresistant hardwoods.

Table 8. Decay resistance of North American genera (partially based on USDA Forest Products Laboratory ratings)

Very Resistant	Resistant	Moderate	Non-resistant
<i>Maclura</i>	<i>Calocedrus</i>	<i>Gleditsia</i>	<i>Abies</i>
<i>Morus</i>	<i>Castanea</i>	<i>Larix</i>	<i>Acer</i>
<i>Robinea</i>	<i>Catalpa</i>	<i>Lithocarpus</i>	<i>Alnus</i>
<i>Taxus</i>	<i>Chamaecyparis</i>	<i>Pinus</i> (old yellow)	<i>Betula</i>
	<i>Juglans</i>	<i>Pinus</i> (white)	<i>Carya</i>
	<i>Juniperus</i>	<i>Pseudotsuga</i>	<i>Celtis</i>
	<i>Quercus</i> (white)	<i>Quercus</i> (white)	<i>Fagus</i>
	<i>Prunus</i>		<i>Fraxinus</i>
	<i>Sassafras</i>		<i>Liquidambar</i>
	<i>Sequoia</i>		<i>Liriodendron</i>
	<i>Sequoiadendron</i>		<i>Magnolia</i>
	<i>Taxodium</i>		<i>Nyssa</i>
	<i>Thuja</i>		<i>Picea</i>
			<i>Plantanus</i>
			<i>Populus</i>
			<i>Pinus</i> (young)
			<i>Quercus</i> (black)
			<i>Quercus</i> (white)
			<i>Salix</i>
			<i>Tilia</i>
			<i>Tsuga</i>
			<i>Ulmus</i>

Similar considerations apply to choosing species for a time series. However, given the greater cost and investment in establishing a time series study, one may have to be even more selective. The suggested minimal design for establishing a time series at a site is to select common species that represent both the fast and slow ends of the decay resistance spectrum. This has the advantage of allowing one to compare the range of decomposition rates among biomes (Table 8). In the past, single species have been described as typical of a region but, the problem is, this may or may not be true. As with stores, the extremes are far easier to compare than the putative "representative"

case. If additional resources exist, species with intermediate or extremely high decay resistance should be included. Another advantage of this scheme is that it allows one to rank unsampled species along a decay continuum.

At present, there are no plans to include a common reference species in intersite studies; in fact, it may be impossible to have a common species at all sites because no species grows at all sites and transporting large logs would introduce a whole set of problems. We suggest that a reasonable alternative would be to choose for comparison a common genus or group of species from genera with wide distributions, or narrowly dispersed genera that have low heartwood extractive contents and decay resistance. We recommend the latter, based on the assumption that the primary controlling factors for nonresistant species are decomposers and climate.

Time Resolution

Given the fact that in a chronosequence one must find pieces to age, it can be difficult to establish a fixed time interval (e.g., every five years) between pieces. Therefore, in chronosequences it may be more workable to consider time resolution in a relative, rather than an absolute, sense by first establishing decay classes or states and then attempting to find a given number of pieces within each decay class. This approach has several advantages; primarily, it insures that the entire time period of decomposition is considered, offsetting the natural tendency to sample the pieces that are the easiest to age (those most recently added to the woody detritus pool).

Various methods have been used to distinguish decay class systems, but most are keyed to physical changes rather than biological indicators. In terms of temporal resolution, the key issue is the number of classes that should be distinguished. We recommend that five classes be used, although as few as two (Brown 1974) and as many as eight (McCullough 1948) have been used in the past. We find that using five classes offers several advantages over other methods; most significantly, there are enough classes to resolve the many changes during decomposition, but not so many that one loses sight of the criteria separating classes.

In a time series study, one can actually determine the sampling interval. The number of times samples are collected may depend upon the resources available at a site. While we recommend eight to 10 sample times as a minimum, even two would allow some intersite comparisons of long-term decomposition rates. A greater number of samples allows one to test whether coarse woody decomposition curves are linear, or non-linear as work at the H.J. Andrews LTER suggests (Carpenter et al. 1988). Carpenter et al. found that there is an initial lag with little change, followed by a period of rapid decomposition, which is then followed by a long period with a relatively slow rate of decomposition.

Standardization of intervals between time series sampling is almost pointless, given the dependence of decomposition rates on site conditions. For example, in tropical sites some species could completely disappear in 10 years. In eastern hardwood forests, 50 years might be required and, in the Pacific Northwest, >200 years. Moreover, since regression analysis is used to calculate decomposition rates, standardization of the time interval is not necessary. Therefore, as with chronosequences, it makes more sense to use relative sampling intervals. We recommend that the sample interval should be approximately 10% of the expected maximum life span; however, our recommendations do not preclude the use of shorter time intervals for a finer time resolution (Harmon 1992).

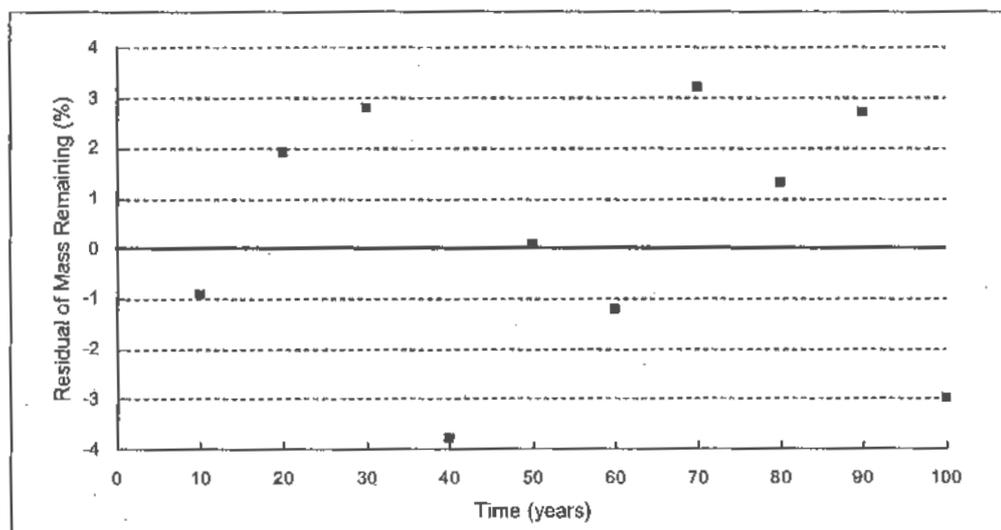
A relative sampling interval also has the advantage of ensuring that decomposition exceeds the errors introduced by variation in initial conditions and measurements. To some degree, the sampling interval for a time series study is limited by the accuracy of initial condition measurements. For example, if the decay rate is approximately 2% per year and the initial values are known within 10%, then it makes little sense to sample any more frequently than every five years. On the other hand, if initial conditions are known within 1%, then annual sampling would be reasonable.

Sample Replication

Replicates of samples for both chronosequences and times series studies need to be considered on at least three levels of variation. The first level is between sites. At least three sites should be sampled each time (decay class in the case of chronosequences) to avoid pseudo-replication problems. In chronosequences this between-site replication may be difficult to achieve; nevertheless, it is just as crucial to avoid pseudo-replication with this method as in time series studies.

The second level is between logs. Wood decomposition is highly dependent upon microtopography and small differences in initial conditions. To some degree, uncertainty caused by differences in density, nutrient content, sapwood and bark thickness can be eliminated if one knows the initial values of these parameters. If the density of log A, for example, is initially 10% higher than the density of log B, then the losses after decay can be adjusted mathematically to reflect these differences. Variations caused by microtopography are harder to eliminate, but noting whether a cross-section is removed from a suspended section or is in close contact with the forest floor could help control for these effects. Even if only one log is sampled each time at a site, it is still possible to estimate the between-log variance from the residual of the time regression (Figure 14); therefore, variation among logs at a site is the easiest to estimate without having actual replicates each time. This runs counter to the traditional approach, but it suggests that sampling at more sites is a better strategy than sampling more logs at a single site.

The third level of variation is within logs. Our experience indicates there is probably just as much variation within logs as among logs at a single site. We recommend that if the entire log or branch is not harvested and weighed, then at least three cross-sections should be taken for moisture content and/or density measurements. If there is extreme variation within a cross-section, it may also be desirable to have replicates within a cross-section. In our experience, the top and bottom of a log can have decomposition rates that differ by a factor of two!



◆ Figure 14.
Estimating the
variation among
logs at a site from an
analysis of residuals
of mass lost.

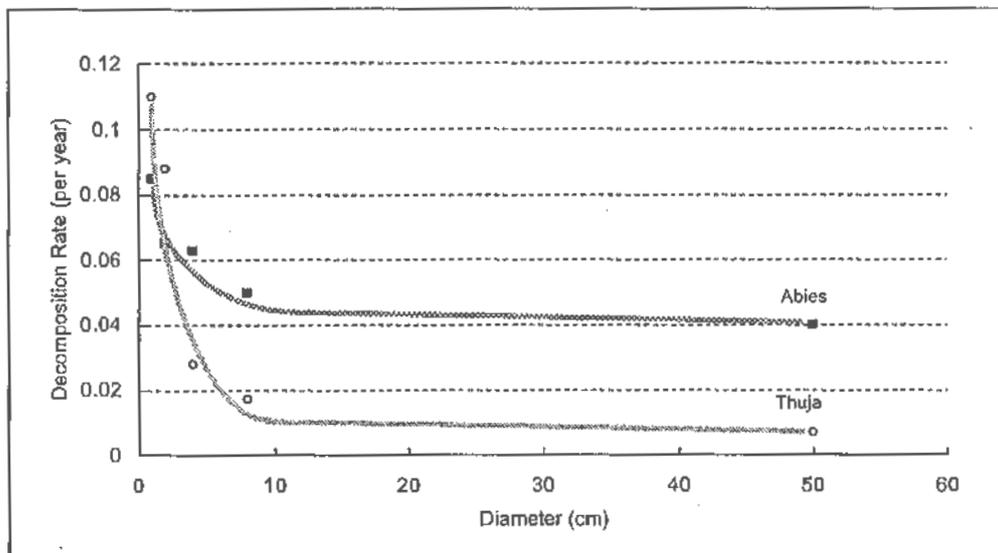
Size Effects

Since the decomposition of wood is primarily a function of size, it is important to consider size differences during intersite comparisons. Although most discussions on piece size are centered on diameter, length can also influence decomposition rates.

In a chronosequence study one can examine the effect of diameter in several ways. The most straightforward approach is to separate the pieces sampled into diameter classes, but it can be difficult to find enough pieces to gain sufficient replication to statistically separate more than two diameter classes (Graham and Cromack 1982). Sampling pieces along their lengths to examine diameter effects (Harmon et al. 1987) has the advantage of increasing the sample size for diameters (each piece results in three to five diameters). It also controls for microclimatic

differences within pieces. The latter results in an autocorrelation within pieces, but this effect can be factored into the experimental design. Regardless of approach, when examining diameter effects one must consider the effect of the parts that have already decomposed and are no longer present to be sampled. This problem is somewhat analogous to the fragmentation "problem" in chronosequences described above. For example, suppose that the smaller, upper portions of downed tree boles decompose faster than the larger, lower portions. If these differences in decomposition rates are large enough, the upper sections may have disappeared before the lower sections. However, since the upper sections no longer exist, one can not sample them or include them in a regression analysis. One is therefore left with a smaller and smaller range in diameters as decomposition progresses, and a reduced ability to statistically estimate the effect of diameter. And this is when one can plainly observe that the smaller diameter pieces have decomposed completely!

In a time series study the most straightforward approach is to use a standard diameter; however, as forests vary in stature, this may not always work in practice. For example, a relevant diameter in the Pacific Northwest might be 50 to 100 cm whereas, in New England, 20 to 40 cm might be more characteristic. A more flexible method would be to place a range of diameters out at each site and then statistically adjust for size effects when comparing species or environment. A geometric series of diameters is probably most useful, since the effect of diameter tends to decrease with size. At the H.J. Andrews LTER, pieces that have diameters of 1, 2, 4, 8, 25, 50, and 100 cm have been placed at the same sites (Harmon 1992). In our Yucatan work, we have placed out 1, 4, 8, 15, and 30 cm pieces (Harmon et al. 1995). Although it would be ideal to have identical diameters for a class, one must allow for variability. As a rough guideline, a tolerance of 20% should be allowed for variation in diameter (otherwise too many pieces will be rejected). For example, 1 cm pieces could range from 0.8 to 1.2 cm, and 100 cm pieces could be allowed to range from 80 to 120 cm, etc. Although we assign pieces to size classes, we also record the diameter of each piece to use as an independent variable. For intersite comparisons, species or sites could be compared directly where classes overlap, or indirectly by comparing regression slopes of decomposition rate on size, or by adjusting for size effects (Figure 15).



◆ *Figure 15.*
Interaction between
piece diameter and
decay resistance.
Based on Harmon
(unpublished data)
from the H.J.
Andrews LTER site.

The length of pieces used in time series decomposition studies is probably far more crucial than the diameter in terms of methodology, because decomposers will colonize from the ends and when pieces are too short the decomposition rate is elevated. Several previous studies have remained unpublished because the piece lengths sampled were unrealistically short. As a preliminary guideline, we recommend making the piece length 10 times longer than the mean diameter. This would mean a 1 cm diameter piece would be 10 cm long, a 2 cm diameter piece would be 20 cm long, and so on. The rationale is that if the radial colonization rate is 10% of the longitudinal colonization rate, then a 10:1 length:diameter ratio would result in nearly equal effects. Longitudinal colonization is unlikely to occur that fast (for *Abies* logs in the Andrews study, radial and longitudinal penetrations for the first 10 years were equal at 10 cm per year).

To some extent, the length problem can be avoided by using an end sealer when short lengths have to be used because of shortage of material or extreme taper of pieces (e.g., coarse roots). Paraffin or an epoxy sealer have been used in the past, but we have had excellent luck using a neoprene paint. We have tested the effects of all three

types of sealers on fungal growth in culture and found that none inhibits growth chemically, indicating their main effect is as a physical barrier. The end surfaces must be clean and dry before the sealer is applied, or most sealants will not adhere to the ends properly and the physical barrier will be incomplete. However, given that these conditions are rarely met in the field, end sealing may not solve the underlying problem. We recommend that pieces selected as samples be as close to the 10:1 length:diameter ratio as possible, given diameter class and material availability constraints.

Position Effects

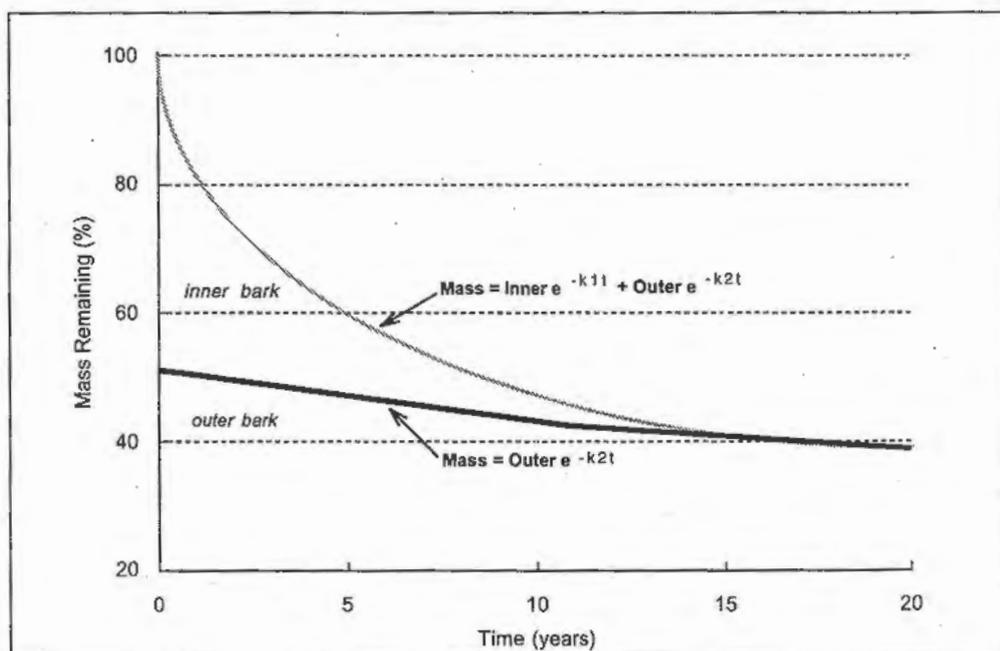
A final consideration that is especially important when interpreting results in either a time series or chronosequence study is the position of the pieces with respect to the soil. Pieces could be suspended above, resting on, or buried within the soil. In our experience, pieces of the same size rarely decompose at the same rate for these three positions. This phenomenon is further complicated by the fact that the relative rankings for these positions may shift with changes in macroclimate or edaphic conditions. For example, in extremely dry environments suspended wood decomposes the slowest and buried wood the fastest. In a humid, hydric environment the ordering is the opposite. A final complication is that pieces above ground steadily progress from being suspended above the soil to resting on the soil to being partially buried within the soil over the natural course of decomposition.

Unlike chronosequence studies, in a time series study one can partially control the effect of position. For example, one can place pieces upon the forest floor, suspend them or bury them to examine the effect of position on the decomposition rate. While it is desirable to study all these situations, just one should be selected for each site as a reference case for intersite comparisons. We recommend using logs or branches in contact with the forest floor as the reference case for each site because this approach is safest (snags are very dangerous to fell) and easiest (creating artificial snags or burying roots is time consuming and costly), and a substantial fraction of woody detritus is found in this category.

In addition to considering the position with respect to the soil, one needs to consider the layers within pieces that will be sampled. This depends largely on the piece size and objectives of the specific study. We have tended to examine more layers as the size of pieces increases. At a minimum, bark and wood layers should be examined on logs exceeding 10 cm diameter. Past studies have assumed that wood forms the bulk of woody detritus and that, therefore, bark can be excluded (Harmon et al. 1987). However, this assumption may ignore the fact that the nutrient content and decomposition rates of wood and bark are very different. For example, in *Abies amabilis* logs, 60% of the log K is initially stored in bark and most of this is lost within four years (Harmon, unpublished data). If the intent is to understand the overall dynamics, focusing solely upon the wood may yield misleading results. It is also very useful to separate the sapwood from the heartwood because, even in species without decay resistant heartwood, this layer decays slower than the sapwood due to the time required to colonize the inner layers. In slowly decomposing species, such as *Thuja plicata*, it is the heartwood that controls long-term decay and nutrient dynamics. Although it is interesting to separate the inner and outer bark (the fastest and slowest decaying layers, respectively), these two layers can be very difficult to separate with any degree of accuracy or safety.

Instead, we suggest that bark be treated as one tissue, separating the dynamics of the individual layers using non-linear regression analysis (Figure 16). An example would be a two-component exponential equation:

$$\text{Mass}_t = \text{Inner } e^{-k_1 t} + \text{Outer } e^{-k_2 t}$$



◆ Figure 16, below. Use of non-linear regression to estimate rates of decay for two tissues.

where *Mass* is the total mass at time *t*, *Inner* and *Outer* are the initial masses of inner and outer bark, and κ_1 and κ_2 are the decomposition rate constants of these two layers, respectively.

Measurement of Mass Loss

Mass loss can be calculated in a number of ways for either chronosequences or time series. Commonly used methods are to 1) harvest and dry the entire piece, 2) weigh the entire piece in the field and subsample for moisture and nutrient content, or 3) estimate the total piece volume and subsample for density. To some degree, the favored method depends on the remoteness of the sample site and the size of the pieces to be examined.

Harvesting and oven drying the entire piece of woody debris being studied is obviously the most direct and accurate methodology. Harvesting the entire piece is also the most useful for fine woody detritus (<10 cm diameter), where the pieces are small enough to fit on an accurate electronic scale. This method avoids the very challenging problem of subsampling layers in small pieces, and it can also be used for entire roots, branches or twigs. Although it is usually not used in chronosequence studies, one could use this method as long as the initial mass could be determined using the third method identified above. Even for time series studies, a major limitation of the entire harvest method is determining the initial dry mass of pieces. Since one should not oven dry pieces before they are placed in the field, it is necessary to estimate the initial moisture content. This parameter is highly variable, and should be determined for each piece by taking samples from the ends. A less accurate alternative is to estimate the initial dry weight from the mean moisture, but, given the typical coefficient of variation of 10 to 20%, this method can create a high degree of uncertainty about the initial dry mass. Another alternative is to develop a regression between piece end diameters and length (Abbott and Crossely 1982). This method is slow, but given the potential for error in using mean moisture content, it may be worth the extra initial effort.

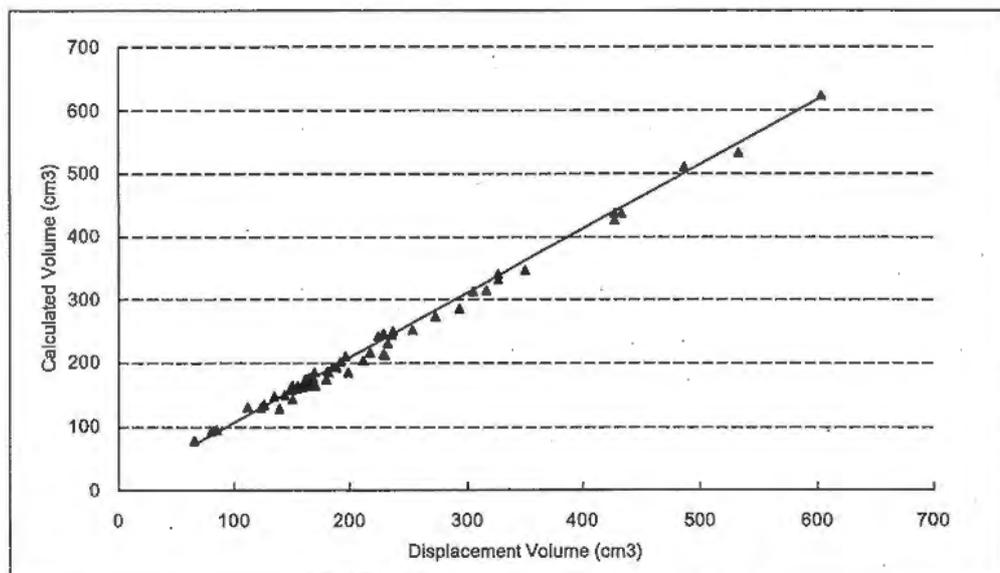
The second method involves weighing the entire piece in the field and then subsampling to determine the moisture content that is then used to estimate the dry mass. We recommend using this method for coarse fraction pieces (e.g., logs) that are too heavy to move large distances, or when sampling very remote sites where transportation is limited. There are, however, several problems with this method: 1) large field spring scales used for this method are not very accurate (an error rate of +/- 5% is not uncommon), 2) electronic scales have a relatively small capacity (<10 kg), 3) moisture content is highly variable, and 4) one can not examine how the various layers of large diameter pieces contribute to the overall mass or nutrient loss. Despite these shortcomings, this method may be the only practical option in some cases.

The third method is to measure the external dimensions of pieces to estimate the volume and then remove cross-sections to determine density and nutrient and moisture contents. At a minimum, the middle and end diameters should be measured for volume determinations (see equation 3, page 16). The maximum and minimum diameter at each point should be measured with a caliper or diameter tape if one can actually reach around the piece. Regardless of the type of material being sampled (i.e., boles, branches, or roots), one should always compare the current volume with the estimated original volume (see above for tips on estimating initial volumes for chronosequences). To determine the density, moisture and nutrient content of a piece, we recommend removing a minimum of three cross-sections per piece spaced systematically along the length.

Density Measurements

In many cases, one uses density as a key variable to estimate mass loss in woody detritus decomposition studies. Density estimates, however, can be highly variable unless one pays attention to sample volume estimates. Unlike volume, mass can be measured with high accuracy and precision. If samples are regularly shaped, then volume estimates based on external measurements correlate exceedingly well with water

◆ *Figure 17.*
Comparison of
volumes estimated
from external
dimensions and
those based on water
displacement. The
diagonal line
indicates one-to-one
match of the
methods.



displacement estimates (Figure 17). This is especially true if the samples are cut using a saw and sufficient replicates of measurements are made (three to four per dimension should suffice). Unless the bark is extremely smooth, the volume of that tissue is best measured using water displacement. It is not unusual to have 10% error in bark volume using external measurements (Harmon 1992), which severely limits the detail one can see.

Nutrient Analysis

Since there are already a number of guidelines for the actual measurement of nutrient concentrations, we will limit our discussion here to the preparation of the samples themselves. First, samples should be saved for nutrient and carbon analysis even if money for processing is not currently available. One must keep in mind that the main limiting factor in the study of woody detritus dynamics is not money, but time! Next, if water displacement is used for volume determination, then separate density and chemical samples should be taken. The nutrient content of wood is an order of

magnitude lower than that of leaves; this represents a real problem for microKjeldahl N analysis. We have found that doubling the sample from 0.5 to 1.0 g yields consistent results for wood standards. ICAP (Inductively Coupled Argon Plasma) will provide good data for most cations using sample amounts similar to leaf tissue (i.e., 0.5 g). Standard wood samples should be run with all analyses. This will also allow one to adjust for different types of analysis (it is unlikely everyone will use the same instruments). We have been using standards developed by Sollins et al. (1987), and can make them available upon request.

One can err by preparing only a small sample for analysis. While we recognize that space and time are limited, removing a toothpick-sized sample for the sake of saving time and effort can result in a questionable sample. Since the chemical composition of woody detritus is highly variable, we advise pooling 100-200 g samples from several cross-sections, coarse grinding and mixing this amount thoroughly, and then removing a smaller subsample (5 to 10 g) for fine (40 mesh) grinding. This approach physically mixes as much material as possible to derive the small sample that is actually used for analysis.

DETAILED PROCESS STUDIES

To explain changes that occur during the course of decomposition, it is often necessary to examine subprocesses such as respiration or leaching. Because they are the most diverse and intensive types of measurements, we have designated detailed process studies as constituting a Level Four installation. While it is certainly possible to start examinations at this level, we have found that without the data provided from the other less refined levels, it is more difficult to scale up and place these measurements in a larger context.

A great deal of interpretive power can be gained by linking measurements of detailed processes to a time series or a chronosequence

Rather than give specific guidelines for each type of detailed process study possible, we highlight studies that best illustrate these measurements. Some examples below represent the only time a process has been measured; others simply are the examples with which we are most familiar. We have found that although there is obvious value in measuring detailed processes in separate studies, a great deal of interpretive power can be gained by linking these measurements to a time series or a chronosequence (Harmon 1992). This allows one to link detailed processes (e.g., leaching) to long-term changes in state variables (e.g., nutrient content).

Respiration Rates

Understanding the factors that control seasonal patterns of respiration are very important in predicting response to climate change. This is also critical information for comparing the effect of micro- or macroclimate on decomposition. One may choose to measure respiration rates in the field (Carpenter et al. 1988) or under standard laboratory conditions (Griffiths et al. 1993). Both static traps using soda lime and gas chromatography have been used to measure these fluxes.

Leaching

Leaching is one of the major ways that woody detritus adds nutrients to the forest floor and influences the mineral soil, yet we know little about this process. The usual method for measuring leaching fluxes involves placing tension-free lysimeters beneath pieces. Short-term leaching studies were conducted by Yavitt and Fahey (1985) and water balance studies by Harmon and Sexton (1995). A key finding of these studies was that much of the nitrogen leaching from logs was not in a mineral form (NO_3^- or NH_4^+), so we know that if only mineralized forms are measured, total leaching fluxes of N will be underestimated. We have had limited success in using exchange resins as a mechanism to collect and concentrate nutrient exports. Besides the fact that much of the N may be leaving in forms that are not bound by the resins, we found that many inorganic elements such as Ca and K were not retained by the exchange resins. Tests made using log leachates indicated that a smaller fraction of inorganic elements was retained in comparison to laboratory stock solutions. Until this interesting phenomenon is more fully explained, we advise against placing too much reliance on exchange resins when measuring absolute nutrient flux.

Nitrogen Fixation

Most of the studies on nitrogen-fixation in woody detritus indicate this process is occurring at very low levels compared to symbiotic fixation. The majority have involved removing samples and measuring acetylene reduction within the laboratory (Griffiths et al. 1993). We know of no one yet who has convincingly shown how seasonal variations in temperature and moisture control rates in the field. There are two problems with past studies: 1) removing a small piece from a larger piece changes the diffusion characteristics, and 2) the lack of temporal resolution over the seasons makes estimates of annual rates highly uncertain.

Fungal Imports/Exports

We have found that fungal fruiting bodies or sporocarps account for as much as 75% of the gross N losses from logs in the early stages of decomposition (Harmon et al. 1994). The method used in this study involved simply tallying sporocarps by species or size and subsampling to determine average mass and nutrient concentrations. For woody sporocarps that continue to grow, we predicted their biomass from allometric equations using the product of the long and short horizontal dimensions.

In addition to providing an understanding of nutrient dynamics, the examination of sporocarps can reveal interesting insights into the biodiversity of ecosystems and carbon sequestration. An excellent example of this type of work is presented in Renvall (1995), who found that a total of 166 basidiomycete species on two species of conifers in Finland. Of the sporocarps observed, the majority (>60%) were white-rot fungi, indicating that the accumulation of buried, brown-rotted wood in the forest floor of these ecosystems may be limited.

Insect Activity

Insects are largely responsible for initiating the decay process in dead trees. Determining the roles of the major functional groups (i.e., bark beetles, ambrosia beetles, wood borers, termites, and ants) in initiating this process is relatively simple and involves counting galleries by taxa or functional group. One can then use average mass and nutrient content to estimate exports from logs (Zhong and Schowalter 1989). An alternative is to place litter traps beneath logs to capture insect frass (Edmonds and Eglitis 1989).

CONCLUSION

Our intent in preparing these guidelines has been to provide a flexible scheme by which those new to woody detritus studies can produce information that is comparable to ongoing work in this field. While we have tried to give the reader the benefit of our experience over 20 years of woody detritus research, there are many aspects of quantifying the amount and dynamics of woody detritus in forest ecosystems for which no suitable method yet exists. We have offered potential solutions for some of methodological shortcomings but, in many cases, researchers may need to plunge in on their own to find something that actually works! This will not be our last attempt to gather and consolidate methods. We welcome comments on what we have presented here or suggestions of new methods for the next edition. Finally—GOOD LUCK!

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