ASSESSMENT METHODS FOR SOIL CARBON

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Preface

The international workshop on "Assessment Methods for Soil C Pools" was held at The Ohio State University, Columbus, Ohio, in November 1998. Approximately 50 participants from 10 countries presented research information on recent advances in methods for assessment of different carbon (C) pools in soil. The participants were drawn from Australia, Brazil, Canada, Ecuador, France, Germany, Kenya, Russia, Sweden, and the United States. This workshop was the fifth in a series of workshops (the arid regions: Tunis, Tunisia, October 1997; tropical ecosystems: Belem, Brazil, December 1997; cold regions: Columbus, Ohio, March 1998; rangeland: Las Cruces, New Mexico, September 1998) that addressed specific topics related to carbon sequestration in these ecoregions. Organization of these workshops emerged as a recommendation of the second international symposium on "Carbon Sequestration in Soils" held at The Ohio State University in July 1996.

The workshop deliberations included presentation of approximately 50 papers under seven general themes: (i) assessment of C pool (13 papers); (ii) soil sampling and sample preparation (8 papers); (iii) analytical techniques (8 papers); (iv) soil erosion and sedimentation (4 papers); (v) remote sensing, GIS and modeling (4 papers); (vi) scaling procedures (10 papers); and (vii) economic analysis (3 papers). All papers published in this volume were reviewed by the editorial committee and revised by the authors.

The 41 contributor chapters of this volume are divided thematically into seven sections, with introductory and concluding chapters (Section I, Introduction, and Section VIII, Synthesis) written by the editors. Section II, Soil Sampling and Sample Preparation, contains 7 chapters. Section III, Assessment of Carbon Pools, comprises 4 chapters. Section IV, Assessment and Analytical Techniques, consists of 15 chapters. Section V, Soil Erosion and Sedimentation, consists of 4 chapters. Section VI, Modeling and Scaling Procedures, contains 8 chapters. Section VII, Economics and Policy Issues, comprises 3 chapters.

The organization of the symposium and publication of this volume were made possible by the cooperation and funding of the USDA Natural Resources Conservation Service, the Agricultural Research Service, and The Ohio State University. The editors thank the authors for their outstanding efforts to document and present their information on the current understanding of soil processes and the carbon cycle in a timely fashion. Their efforts have contributed to enhancing the overall understanding of pedospheric processes, and how to better use soils as a sink for carbon while also managing soils to minimize pedosphere contributions of carbon dioxide and other greenhouse gases to the atmosphere. These efforts have advanced the frontiers of soil science and improved the understanding of the pedosphere into the broader scientific arena of linking soils to the global carbon cycle, soil productivity, and environment quality.

Thanks are also due to the staff of Lewis Publishers/CRC Press for their timely efforts in publishing this information to make it available to the scientific community. In addition, valuable contributions were made by numerous colleagues, graduate students, and OSU staff. We especially thank Ms. Lynn Everett for her efforts in organizing the conference and for handling the flow of papers to and from the authors throughout the review process. We also offer special thanks to Ms. Brenda Swank for her help in preparing this material and for her assistance in all aspects of the symposium. The efforts of many others were also very important in publishing this relevant and important scientific information in a timely manner.

The Editors

CHAPTER 36

Predicting Broad-Scale Carbon Stores of Woody Detritus from Plot-Level Data

M.E. Harmon, O.N. Krankina, M. Yatskov and E. Matthews

I. Introduction

Woody detritus in the form of dead tree parts such as boles, stumps, branches, and coarse roots is an important store of carbon in forest ecosystems (Harmon and Chen, 1992). Not only does this material represent a large and frequently overlooked pool (Harmon et al., 1986), but also it is a crucial component of heterotrophic respiration (Turner et al., 1996). In recent years methods to study the size and dynamics of these detritus pools have been developed and applied to various ecosystems (Harmon et al., 1999). Despite an increase in these plot-level efforts, however, no reliable inventory-based estimates exist at the regional, national, or global scales (Turner et al., 1996; Kurtz et al., 1992).

In this chapter we review plot level methods and then present a series of complementary methods that can be used to estimate potential steady-state and actual stores of woody detritus at regional to global scales. These include (1) correction and conversion factors for incomplete inventories; (2) dead:live wood expansion factors; (3) predictions of steady-state stores from input:decomposition rate-constant ratios; and (4) adjustments to include disturbance regimes.

II. Types of Woody Detritus

Woody detritus or debris takes many forms in forested ecosystems (Figure 1). The most useful distinctions are based on the size (length and diameter) and position (standing, downed, buried in soil) of the detritus. Other systems, such as those used in fire fuels, depend upon the moisture time lag, but are operationally divided by diameter (Fosburg, 1971). Unfortunately the use of these terms to describe woody detritus has been quite unstandardized, leading to major problems in comparisons. The most important distinction concerning size is between the coarse and fine fractions. This distinction often depends upon the ecosystem being examined, but a frequently used size "break point" is 10 cm diameter at the large end of a piece (Harmon and Sexton, 1996). Given the increasing number of pieces per unit area as diameter decreases, another useful size breakpoint is at 1-cm diameter. 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, the cut-off between fine and coarse woody detritus is often at 1-cm diameter.

The term woody detritus or woody debris should be used to include all the forms of dead woody material above- and belowground. Aboveground woody detritus can be divided into coarse- or fine-

Figure 1. Examples of woody detritus in forest ecosystems: A. coarse, downed wood in an old-growth, *Pinus contorata*, forest; B. standing dead wood following wildfire in *Pinus contorta forest*; C. remnant, charred wood after intense wildfire (note that woody detritus was the only aboveground component remaining); D. woody slash left after timber harvest in Pseudosuga/Tsuga forests in 1930s; and E. stumps and other slash left after pasture conversion in Mexico tropical forests. (From Rosenberg et al., 1999. With permission.)

fractions. The minimum dimensions for coarse woody detritus are usually 10-cm diameter at the large end and 1.5 m in length. Pieces smaller than these size limits 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 a 45° angle. In addition to snags, we also recognize stumps in managed settings. Vertical pieces resulting from natural processes should always be called snags. The term stump is used for short, vertical pieces that were 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. Belowground woody detritus has been rarely studied (McFee and Stone, 1966), but we recommend this 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 belowground wood is primarily based on whether you can tell its origin (similar to the distinction between O1 and O2 layers in the organic soil layers).

III. Plot Level Measurements

Harmon et al. (1999), Harmon and Sexton (1996), and Harmon et al. (1986) provide thorough reviews of plot-level methods including the relative merits of different approaches — we will therefore provide only a brief review of plot level protocols here.

A. Mortality or Input Rates

Inputs of woody detritus take several forms: (1) that associated with tree mortality and (2) that associated with pruning of branches and roots. The majority of coarse wood inputs are associated with tree mortality. 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 detritus inputs are the diameter at breast height and species of the dead tree at the time of plot remeasurement. Biomass equations are then used to compute the amount added. Coarse woody detritus inputs are highly variable in both time and space. As a first approximation, data should not be dependent upon the inclusion or exclusion of a single tree. If one desires to be within 10% of the live stem mortality rate (defined here as the percentage of tree stems dying each year), then at least 10 trees have to die within some combination of area and time. On the basis of observed rates of mortality 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 could measure the input of fine woody detritus directly, it is difficult given that many trees die standing. Therefore inputs of fine woody detritus can 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). A relatively small fraction of the downed fine woody detritus is input from branches that have snapped off by windstorms or 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 are actually new inputs of woody detritus (i.e., a change from live to dead wood); rather, these represent a change in the form of woody detritus (i.e., suspended to downed). 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.

B. Decomposition Rates

There are several methods to determine rates that woody detritus decomposes, forms soil organic matter, and immobilizes or releases nutrients. Two frequently used approaches are: (1) chronosequences which give a short-term snap shot of processes and (2) a time series approach which is a long-term effort yielding excellent resolution of temporal patterns and processes. In a chronosequence one ages as many pieces as possible in various states of decay and examines how a parameter such as density changes through time. Dates can be determined from fall scars, seedlings, living stumps, and records of disturbance (e.g., fire, insect outbreak, windstorm, thinning). This approach has been used extensively for coarse woody detritus (e.g., Graham, 1982; Grier, 1978; 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: (1) conversion of volume measurements into mass or nutrient stores; and (2) to determine the rate mass is lost or nutrients are immobilized or released. If the aim is to use a decay chronosequence to estimate rates of mass loss or nutrient release, then the data must be adjusted for past fragmentation losses to estimate these rates correctly (Harmon and Sexton, 1996). Although chronosequences produce results quickly, there are serious temporal resolution problems caused by errors in dating and estimates of initial conditions of the dead trees. A time series circumvents these problems by examining how a cohort of pieces progresses through time, thereby avoiding the substitution of space for time. Although the method requires substantial investments in effort and time, it lends itself nicely to process studies. In addition to examining a chronosequence of pieces, one can also indirectly estimate decomposition rates of woody detritus from a chronosequence of different aged stands (e.g., Gore and William, 1986; Spies et al., 1987) by assuming each stand-creating disturbance left a similar amount of material. In many cases this assumption is not justified and can lead to significant uncertainty concerning decomposition rates. Finally, the ratio of input to stores can be used to indirectly estimate decomposition rate constants of woody detritus assuming the pool is in steady-state (Sollins, 1982). This is subject to the same errors as for fine litter, compounded by the fact both inputs and stores of woody detritus are highly variable.

C. Fine Woody Detritus Stores

Several alternative methods exist for measuring fine woody detritus stores (Harmon et al., 1999; Harmon and Sexton, 1996). The most straightforward is harvesting and weighing material within small plots (<4 m^2). Downed fine woody detritus can also be estimated using planar transects in which the number of pieces in size classes is recorded and then converted to stores using the mean diameter and bulk density of the size class. Unfortunately, the latter two parameters are rarely measured or reported (see Harmon and Sexton, 1996); therefore, stores estimated by this method have questionable accuracy. Moreover, although the planar transect estimates the volume of downed, surface wood, it does not measure other important forms of woody detritus including dead branches or dead coarse roots.

D. Coarse Woody Detritus Stores

For coarse woody detritus (<10-cm diameter and < 1 m long) it is impractical to remove and weigh pieces. Therefore, for downed logs, standing dead trees, and stumps it is more usual to record piece dimensions within fixed area plots (Harmon et al., 1987) or along planar transects (Warren and Olsen, 1964; Van Wagner, 1968; Brown, 1974) to estimate volume. This parameter is then converted to mass

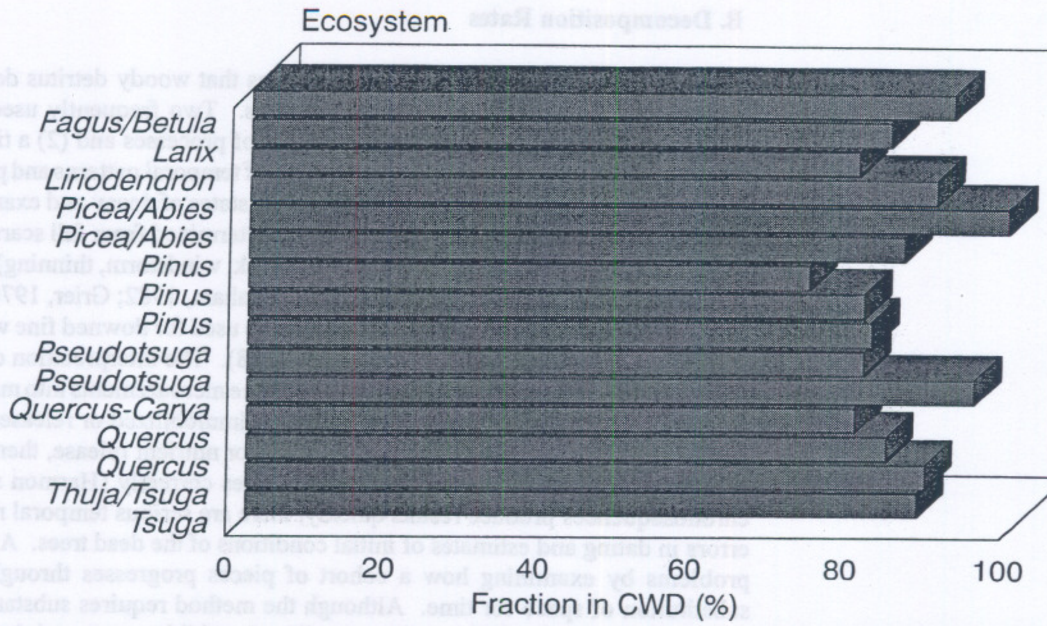

Figure 2. Fraction of total aboveground woody detritus in the coarse fraction. (Modified from Harmon et al., 1986.)

and/or carbon using decay class specific bulk density and carbon concentration values. If planar transects are used, one must measure the volume of standing dead trees and stumps with a plot-based system.

IV. Correction, Conversion, and Expansion Factors

Measurements are rarely taken or reported in the forms required for broad-scale analysis. It is therefore necessary to either correct the data for missing components (e.g., coarse wood to total woody detritus), to convert one set of units to another (e.g., volume to mass), or to base estimates of woody detritus on other related pools. We term each of these correction, conversion, and expansion factors, respectively.

A. Correction Factors

Inventories of woody detritus are rarely complete and therefore corrections to total stores are usually required. While making corrections, it is important to bear in mind that some forms of woody detritus are highly correlated while others are not. For example, size classes of woody detritus are often highly correlated (Figure 2). This is probably because as trees die, the proportions of 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 expected for suspended fine wood versus snags. There is also probably a good correlation between aboveground woody detritus and dead coarse roots as this is largely controlled by the structure of living trees. Perhaps the worst correlation between forms of woody detritus is for standing or suspended material and downed

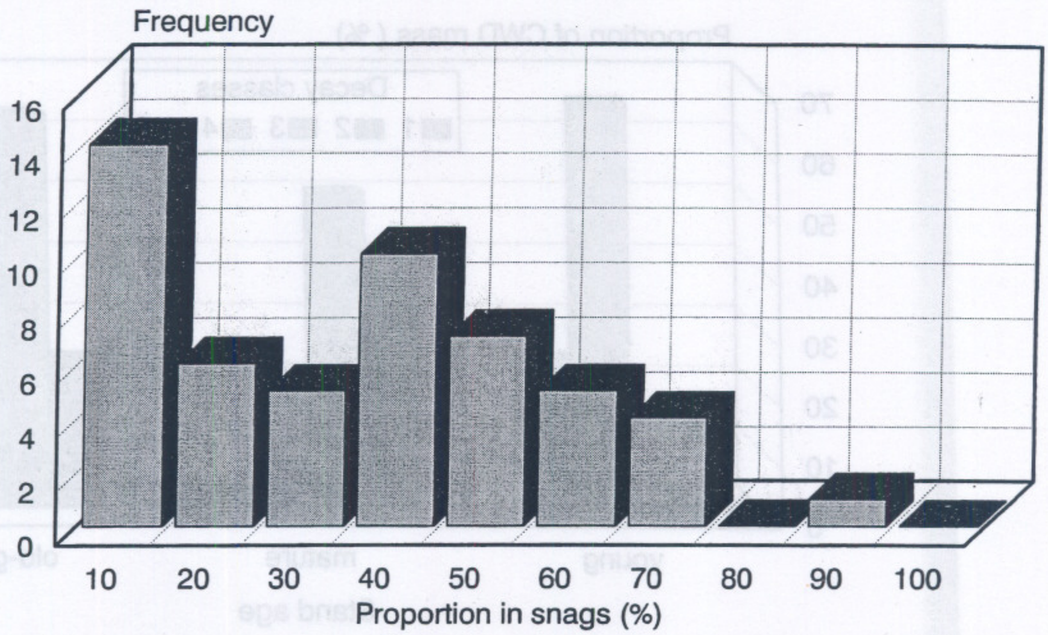

Figure 3. Frequency distribution of the fraction of coarse woody detritus in snags (i.e., standing dead trees) for *Pseudotsuga/Tsuga* forests of the Pacific Northwest. (Based on Wright, 1998.)

material. Even within a single forest type, such as the frequently studied *Pseudotsuga/Tsuga* forest of the Pacific Northwest, it is not unusual to find that snags can make up as little as 2% to as much as 98% of the coarse dead wood biomass (Figure 3). Another correction that is difficult to make is to account for missing decay classes. Many woody detritus inventories are focused on estimating merchantable volume and thus only consider the less decomposed material. Unfortunately the fraction of undecayed wood can range from being high immediately following a disturbance to very low in young forests (Figure 4).

B. Conversion Factors

The most commonly used conversion factor is to convert volume to mass or carbon. The volume of large woody detritus estimated from the dimensional data or along transects can be converted to mass and nutrient stores using decay class specific bulk density data for various stages of decay (Table 1). These values can be taken from the literature, although potential errors exist by not using site-specific values. Using an existing or establishing a new decay class system requires that physical characteristics be used to distinguish between decay classes. These include: 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 if the branch stubs can be moved.

Mortality is another parameter often requiring conversion factors as it is not unusual for mortality to be reported as stems, basal area, volume, or mass lost per unit time. Fortunately the latter three variables are equivalent when expressed in relative terms as they are all correlated (i.e., basal area is

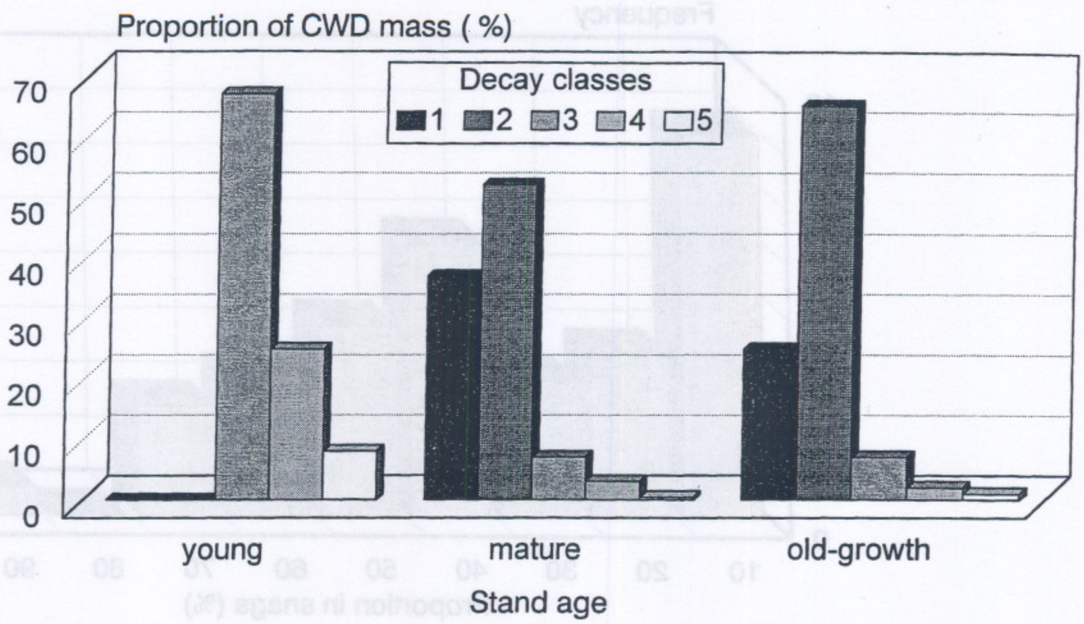

Figure 4. Fraction of coarse woody detritus in 5 decay classes for *Picea* forests in Northwestern Russia. Class 1 is the least and class 5 is the most decomposed woody material. Based on data from Krankina and Harmon (1999).

often used as a proxy for volume and mass is volume times wood density). The number of stems is not, however, well correlated to either volume or mass. Unfortunately the bulk of mortality numbers are expressed as relative stems lost per unit time. We assume here a conversion factor of 1; exact conversion factors from stem to mass input awaits more studies that report mortality in both forms.

C. Expansion Factors

The most commonly used expansion factor used is the ratio of dead to live wood (Harmon and Chen, 1992; Harmon et al., 1993; Matthews, 1997). These ratios are usually developed using field measurements of both dead and live wood mass (Krankina and Harmon, 1995). The basic logic behind these ratios is that given our much greater knowledge of live wood stores, this ratio allows one to make an estimate from that database. The major problem with these ratios is that they are best used for older stands as the ratio ranges from near infinity for recently disturbed forests (i.e., where little live wood exists) to a fairly stable number less than 1 in old-growth forests to close to 0 in forests where timber salvage and thinning are practiced (Krankina and Harmon, 1995). Although convenient, these ratios have not been estimated for more that a handful of ecosystems. Based on a sampling of 50 stands in the Pacific Northwest (Wright, 1998), it would appear that dead:live ratios are distributed as negative exponential to log-normal distributions (Figure 5).

Table 1. Density of woody detritus by decay classes and species (mean and standard error in parentheses) for Northwest Russia; class 1 is the least and class 5 the most decomposed.

Species	Decay class	Density (Mg m^{-3})
Birch		
	1	0.480 (0.010)
	2	0.442 (0.016)
	3	0.235 (0.023)
	4	0.125 (0.020)
	5	0.094 (0.003)
Spruce		
	1	0.347 (0.017)
	2	0.309 (0.015)
	3	0.207 (0.018)
	4	0.110 (0.023)
Pine		
	1	0.384 (0.018)
	2	0.311 (0.019)
	3	0.236 (0.012)
	4	0.111 (0.018)
	5	0.108 (0.004)

(After Krankina and Harmon, 1999.)

In addition to being a convenient number, use of the dead:live ratio has a theoretical basis. If it is assumed that the forest is approaching a steady-state then the inputs equal the outputs (Olson, 1963). The outputs are defined as:

$$\text{Output} = k\ \text{Dead}_{ss} \qquad \text{(Eq. 1)}$$

where k is the decomposition rate-constant and Dead_{SS} is the mass of dead material are steady-state. Therefore:

$$\text{Dead}_{ss} = \text{Input}/k \qquad \text{Eq. (2)}$$

If we relativize the inputs by assuming the steady-state live biomass (Live_{SS}) is equal to 1 then:

$$\text{Dead}_{ss} = m/k \qquad \text{Eq. (3)}$$

where m is the mortality rate-constant. As Live_{ss} is equal to 1, equation 3 is equivalent to the dead:live ratio. This allows one to take advantage of the great number of mortality and decomposition rate-constants that have been reported.

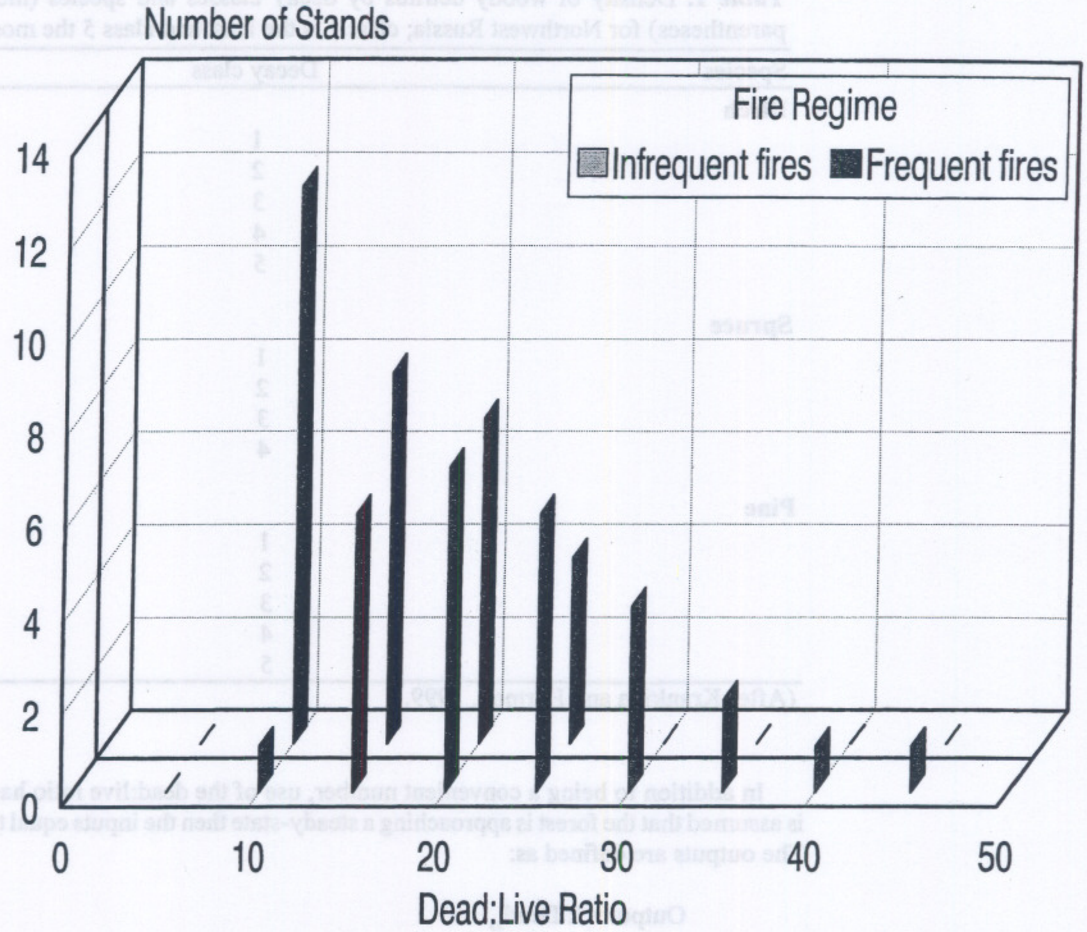

Figure 5. Frequency distribution of the dead:live wood ratio for *Pseudotsuga/Tsuga* forests of the Pacific Northwest. (Adapted from Wright, 1998.)

V. Estimating the Effects of Disturbance

Although the steady-state is a useful concept, it is rare that ecosystems reach this condition. At a regional scale a more realistic condition includes areas in various ages since the time of last catastrophic disturbance. By modeling the relative change of live and dead wood stores over succession one can estimate how to adjust the steady-state stores.

As with using mortality and decomposition rate-constants to estimate the steady-state dead:live wood ratio, we can simplify the calculations by setting $Live_{ss}$ equal to 1.0. The live biomass ($Live_t$) at any time (t) can be described by a Chapman-Richards function:

$$Live_t = (1 - \exp[-B_0 t])^{B_1} \qquad \text{Eq. (4)}$$

where B_0 and B_1 are parameters describing the rate of live biomass accumulation. Changes in dead wood mass relative to the steady-state live mass can be calculated from the input (I) versus the decomposition loss (k):

$$\Delta\, dead_t = I - k\, Dead_{t-1} \qquad \text{Eq. (5)}$$

Inputs to the dead wood pool occur either as "normal" mortality associated with competition, wind, an other non-catastrophic forms of death or because of disturbances that kill the entire forest. In the former case inputs are:

$$I = m\, Live_t \qquad \text{Eq. (6)}$$

where m is the mortality rate constant. In the latter case inputs are:

$$I = (1 - d)\, Live_t \qquad \text{Eq. (7)}$$

where d is the proportion of the live mass remaining after the disturbance.

This relatively simple model can be used to estimate the dynamics of dead and live wood after a catastrophic disturbance (Figure 6). The simplest case is for old-field succession where both live and dead mass start at 0 (Figure 6a). In this case live and dead mass accumulation parallel each other. A more complicated situation occurs after a catastrophic natural disturbance. Assuming the disturbance removes a minimum of wood (e.g., wind throw), $Dead_0$ is equal to the sum of 1 and the dead:live ratio (Figure 6a). This is followed by a monotonic decline to the steady-state dead:live ratio. When the disturbance removes a fraction of the woody mass (e.g., timber harvest) $Dead_0$ can range anywhere between 0 and 1+dead:live. Current timber harvest, for example, might remove 70% of the live biomass leading to a value of $Dead_0$ of 0.5 (Figure 6b). Dead mass declines and in some cases may drop below the dead:live ratio at steady-state. This is because the replacement of dead wood lags behind decomposition in the middle stages of succession (Harmon et al. 1986, Spies et al., 1987). Perhaps the most complicated case is when forests are converted to intensive, short-rotation forestry. Here the live mass does not recover to the steady-state level and a large fraction of the mortality is removed as intermediate timber harvest in thinning and salvage. This leads to a decrease in the dead:live ratio to a value much lower than the steady-state value. The final successional pattern, not shown, is found after forest clearing for agriculture. In this case dead mass continues to decline as non-woody plants dominate the ecosystem.

Using these successional patterns to adjust steady-state estimates requires information about the age structure of patches created by catastrophic disturbances. Although it would be best if the specific age structure was used, in many regions this is not known. Therefore one may assume that the proportion of each age class is equal to the inverse of the mean interval between disturbances in a region. The mean dead:live ratio for each region with natural disturbance is calculated as:

$$Dead{:}Live_{mean} = \mathbf{D'A} \qquad \text{Eq. (8)}$$

where **D** is a vector describing the dead:live ratio of each age class and **A** is a vector describing the proportion of each disturbance age class. It is also possible to use this approach to estimate the carbon stores of live woody biomass with natural disturbance regimes by substituting **L**, a vector describing the relative live carbon store for each age class, for vector **D**.

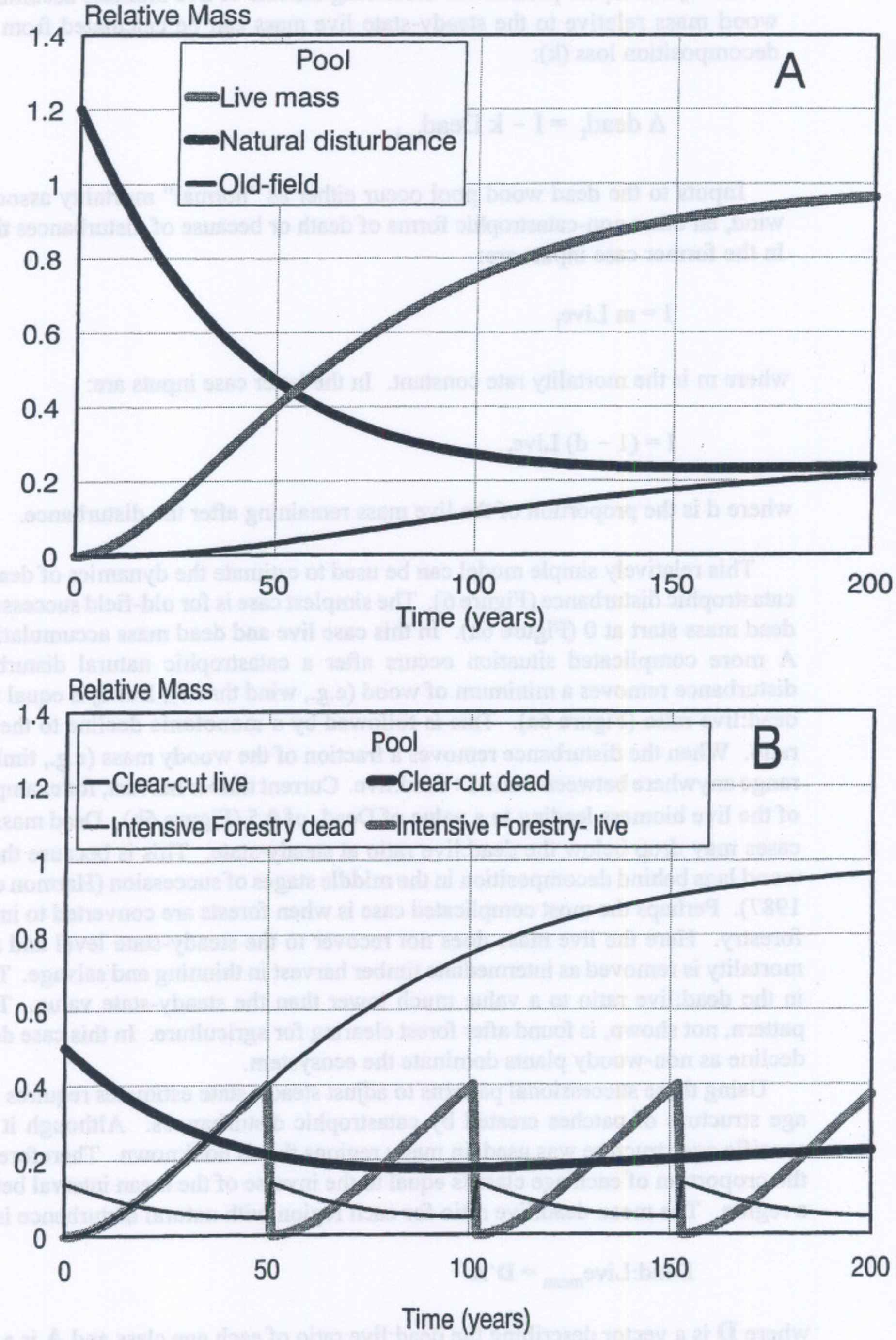

Figure 6. Change in woody detritus stores relative to live woody stores following catastrophic disturbances. A. Temporal patterns during old-field succession, or following a catastrophic natural disturbance or B. various types of timber harvest.

VI. Application to Broad-Scales

Having described how broad-scale calculations can be made we will demonstrate their use by estimating global level stores of woody detritus. We present a progression of estimates, proceeding from steady-state estimates based on stores averages to those based on observed dead:live ratios to those based on mortality and decomposition rate-constants. We then move on to include natural disturbance regimes considered typical of large regions and finish by making reductions for the forest area historically removed for agriculture. Our calculations are based on a compilation of data from the literature and from unpublished values from our research (http://www.fsl.orst.edu/lter/pubs/-globalcwd.htm). For biomes without reported data, we assume values from similar biomes. Other assumptions are presented with the actual calculations. The biome areas and undisturbed live biomass used in this analysis follow those of Matthews (1997).

A. Steady-State Estimates

The most straightforward steady-state estimates at the global scale would involve averaging the old-growth or primary ecosystem woody detritus mass for each biome and applying that to the biomes total area. As most studies only report downed material, we therefore applied a correction factor of 25% to all biomes except evergreen forests in which we assumed snags comprised 40% of the total coarse woody detritus. We also increased all numbers by 20% to account for the fact that fine woody detritus, especially dead coarse roots, are not usually reported. After these correction factors were applied, mean carbon stores in all forms of woody detritus range from as little as 1.5 Mg C ha^{-1} in evergreen woodland to as much as 55 Mg C ha^{-1} in evergreen forests (Table 2). Unfortunately, there are three biomes in which numbers have not been reported and several others with only a few studies. Nonetheless, the generally accepted pattern that stores increase in forests from tropical to deciduous to evergreen forests is supported. Applying these mean areal carbon stores to the total biome area yields as undisturbed forest steady-state global total of 157 Pg C (Table 3). This is in comparison to a total of a total of 552 Pg C of live biomass or a global dead:live ratio of 0.28.

Our second estimate of steady-state woody detritus stores is based on observed dead/live ratios. Unfortunately, the database for these calculations is even scantier than for stores, with a total of 35 observations. From this limited sample it would appear that tropical and deciduous forests are relatively similar with values of 0.14 and 0.15, respectively. Evergreen forests have the largest sample, with a mean of 0.25; evergreen woodlands appear to be even higher, although there are too few samples to have confidence in this value. Applying these number to the undisturbed live woody carbon stores gives an undisturbed forest carbon store in woody detritus of 114 Pg C which indicates a mean dead:live ratio of 0.21.

Our final estimate of steady-state woody detritus stores is based on dead:live ratios calculated from the mortality:decomposition rate-constant ratio. The first component of this calculation is the mortality rate-constant for which there is considerably more data (N=108) than stores or dead:live ratios (Table 2). Tropical forest have the highest values (0.0167 $year^{-1}$) followed by deciduous (0.012 $year^{-1}$) and then evergreen forests (0.01 $year^{-1}$). The lowest value is for evergreen woodland, with a mortality rate-constant of 0.004 $year^{-1}$. The overall trend in mortality rate-constants appears to be an increase with productivity. We therefore used this general relationship to "guestimate" values for the biomes without data. Decomposition rate-constants, the second component of this calculation also decreased from tropical (0.176 $year^{-1}$) to deciduous (0.080 $year^{-1}$) to evergreen forests (0.032 $year^{-1}$). Deciduous shrubland appears to have the highest decomposition rate-constant, possibly due to the presence of termites, which rapidly remove woody material. Although tropical forests have the highest decomposition rate-constants of any major biome, the distribution of values appears bimodal

Table 2. Area, mean undisturbed woody biomass, woody detritus, dead:live ration, mortality, and decomposition rates for biomes dominated by woody plants (numbers in bold are from literature)

Biome[a]	Area (ha × 10^6)	Average undisturbed live biomass (Mg C ha^{-1})	Woody detritus observed (Mg C ha^{-1})	Dead:live ratio	Mortality rate-constant ($year^{-1}$)	Decomposition rate-constant ($year^{-1}$)
Tropical forest	**1323**	**116.4**	**12 (1.5)[b] 19**	**0.14 (0.08) 3**	**0.0167 (0.001) 40**	**0.176 (0.050) 16**
Evergreen forest	**1631**	**109.7**	**55 (8.4) 40**	**0.25 (0.05) 14**	**0.010 (0.001) 44**	**0.032 (0.003) 33**
Deciduous forest	**1722**	**106.5**	**21.9 (3.5) 33**	**0.15 (0.03) 16**	**0.012 (0.002) 22**	**0.080 (0.013) 23**
Evergreen woodland	**497**	**61.2**	**1.5 (NA)[c] 2**	**0.36 (NA) 2**	**0.004 (NA) 2**	0.01 (NA) 0
Deciduous woodland	**735**	**45.6**	2 (NA) 0	0.36 (NA) 0	0.004 (NA) 0	**0.02 (NA) 1**
Evergreen shrubland	**226**	**27.0**	2.8 (NA) 0	0.50 (NA) 0	0.005 (NA) 0	0.01 (NA) 0
Deciduous shrubland	**145**	**28.0**	**2.8 (NA) 1**	0.25 (NA) 0	(NA) 0	**1.06 (NA) 1**
Xeromorphic formations	**3595**	**22.9**	2.8 (NA) 0	0.25 (NA) 0	0.010 (NA) 0	0.03 (NA) 0

[a]Definitions of biomes follow Matthews (1983); [b]Mean (standard error), N, if N = 0 then the value is estimated; [c]NA is not applicable.

Table 3. Undisturbed steady-state estimates of total woody detritus carbon stores for biomes dominated by woody plants

Biome[a]	Observed woody detritus (Pg C)	Observed dead:live ratio (Pg C)	Mortality:decomposition-rate constant ratio (Pg C)	Adjusted for natural disturbances (Pg C)
Typical forest	15.9	20.5	13.9	13.3–14.0
Evergreen forest	89.7	42.5	53.2	50.1–61.7
Deciduous forest	37.7	22.1	22.0	22.0–21.3
Evergreen woodland	0.7	8.7	9.7	13.0–15.7
Deciduous woodland	1.5	9.6	10.7	14.3–17.3
Evergreen shrubland	0.6	2.4	2.4	2.8–3.3
Deciduous shrubland	0.4	0.8	0.3	0.4–0.5
Xeromorphic formations	10.1	7.5	10.0	10.1–13.4
Global total	**156.6**	**114.2**	**122.3**	**131.1–148.4**

[a]Definitions of biomes follow Matthews, 1983.

(Figure 7), with a peak at <0.04 year^{-1} and another at >0.12 year^{-1}. This may be a reflection of two groups of species, one containing compounds toxic to fungi and insects in their heartwood and a second group that has little decay-resistance. Evergreen and deciduous ecosystems appear to have unimodal distributions of decomposition rate-constants.

Dead:live ratios modeled from mortality and decomposition rate-constants appear to be generally similar to observed values (Figure 8). Given the lack of a rigorous global database it is difficult to determine which is correct and whether the slightly lower ratio for tropical forests or the higher ratio for evergreen forests estimated by rate-constants is correct or not. The total woody detritus carbon store using this method is estimated to be 122 Pg C and the mean dead:live ratio is 0.22. As this estimate is based on the largest database we will use this in all subsequent calculations that adjust for disturbance effects.

B. Natural Disturbance Effects

We used equations 4 to 8 to estimate the influence of natural catastrophic disturbances on woody detritus stores. We used a range of mean intervals between these disturbances with evergreen forests having the most frequent and tropical forests the least frequent disturbances (Table 4). We also assumed that tropical forests would recover their biomass the fastest, while woodlands and evergreen shrublands were the slowest. We also assumed that the lag required to start producing biomass increased as site severity increased (i.e., parameter B_1). Adjusting for these disturbance effects gener-

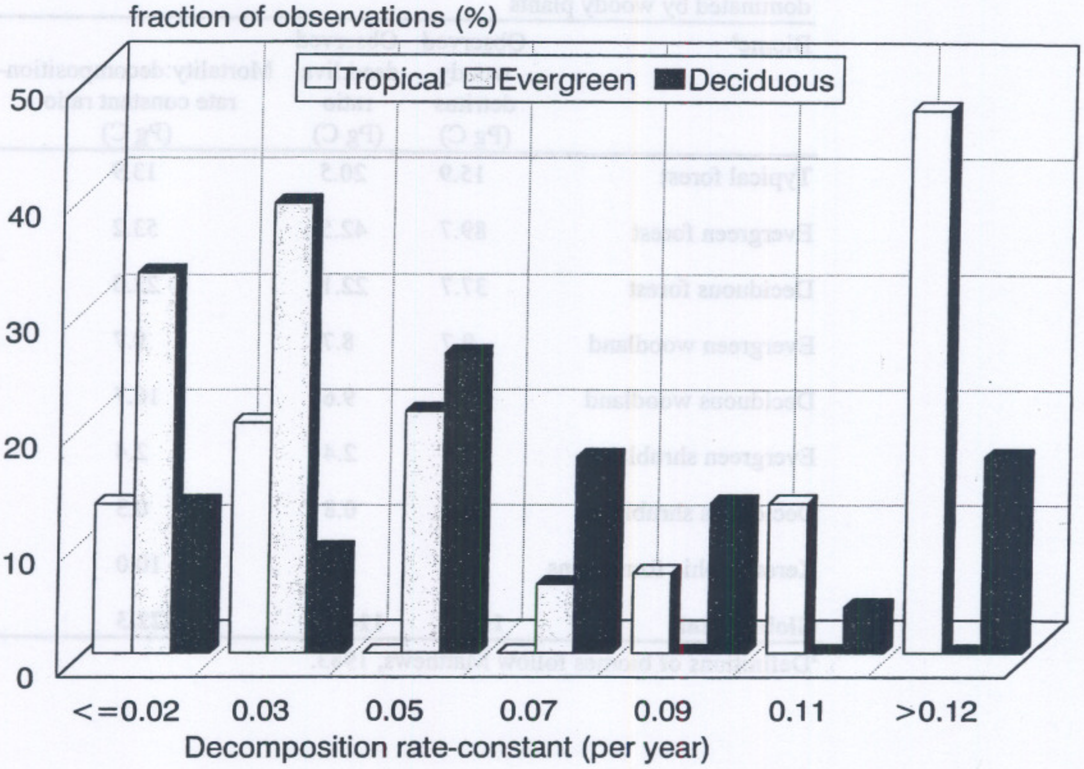

Figure 7. Frequency distribution of decomposition rates from tropical, evergreen, and deciduous forests.

ally increases the dead:live ratio, however, for tropical and deciduous forest the effect is minimal. This is probably due to the long interval between disturbances which allows woody detritus to stay near the steady-state value for much of succession. In contrast, in biomes where decomposition is slow and the interval between disturbances is short the disturbance adjusted dead:live ratio can be much higher than the non-disturbance ratio. Using these adjusted ratios yields a global store of woody detritus ranging from 131 to 148 Pg C, for the longest and shortest intervals between disturbance, respectively. Applying the same logic to live biomass yields a range of 344 to 420 Pg C. Disturbance therefore creates dead wood at the expense of live wood (Figure 9).

C. Agricultural Removals

Assuming that woody detritus in agricultural lands cleared prior to the 1950s has completely decomposed, we can adjust for this effect by reducing the land area for each biome that is now in agricultural land use. This would indicate that there was 113 to 129 Pg C in woody detritus in the middle of this century. For live biomass a range of 295 to 362 Pg C is indicated. We have not calculated the effects of post 1950s agricultural clearing, but is has probably influenced live stores more than woody detritus stores.

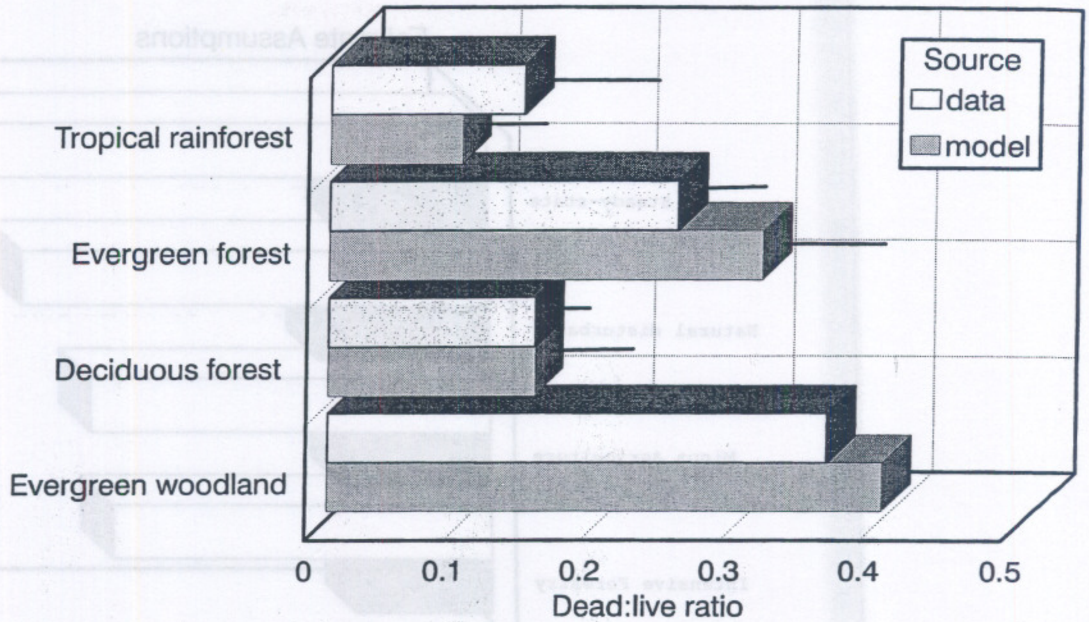

Figure 8. Comparison of observed versus modeled dead:live ratios for biomes with values reported.

Table 4. Parameters used to model the effects of natural disturbance on woody detritus stores (see Equations 4 to 8)

Biome[a]	Disturbance interval[b] (years)	B_0 ($year^{-1}$)	B_1 (dimensionless)	Steady-state dead:live ratio	Disturbance adjusted dead:live ratio
Tropical forest	500–1000	0.033	2	0.095	0.095–0.096
Evergreen forest	150–300	0.015	2	0.313	0.321–0.363
Deciduous forest	500–750	0.015	2	0.150	0.150–0.152
Evergreen woodland	200–300	0.01	3	0.400	0.535–0.646
Deciduous woodland	200–300	0.01	3	0.400	0.535–0.646
Evergreen shrubland	200–300	0.01	4	0.500	0.566–0.683
Deciduous shrubland	100–200	0.033	2	0.100	0.127–0.157
Xeromorphic formations	100–200	0.015	3	0.333	0.335–0.445

[a]Definitions of biomes follow Matthews, 1983; [b]after Harmon et al., 1993.

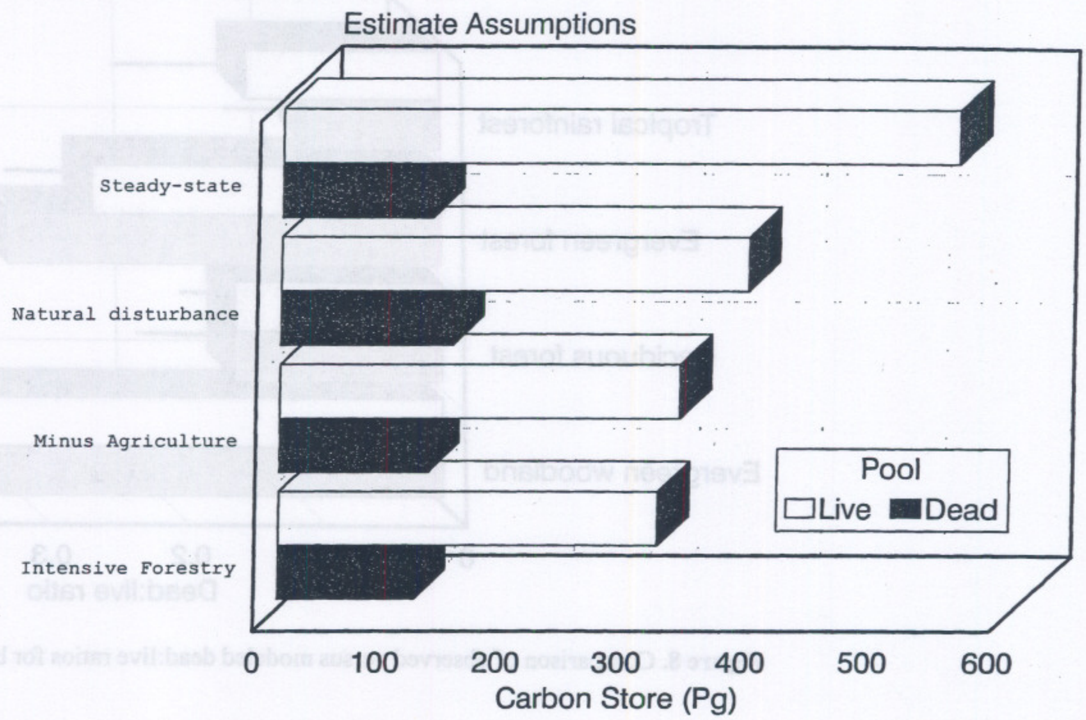

Figure 9. Comparison of live and woody detritus carbon stores for various assumptions concerning disturbance.

D. Intensive Forestry

Intensive forestry practices of short-rotations, thinning, and dead wood removal are estimated to be occurring in 10% of the worlds forest land (Dixon et al., 1994). Assuming the majority of this is taking place in evergreen forests would mean that 36% of those forest are currently under intensive management. We modeled this effect using a 50-year rotation length and assuming 50% of the mortality is harvested, and 50% of the live carbon is removed at the time of harvest. This indicates a dead:live ratio of 0.075 relative to the steady-state live mass of 1.0. That is instead of storing an equivalent of ≈30% of the maximum live carbon, the intensively managed forest stores only 7.5%. Moreover, the average live mass is reduced to 11% of the maximum. Applying these value to evergreen forests indicates the current global woody detritus store is 104 to 118 Pg C. Using a similar approach for live biomass yields a total of 283 to 340 Pg C when intensive forestry is taken into account. Using completely different methods Dixon et al. (1994) estimated a current live wood store of 359 Pg C globally. Unfortunately, they do not give a woody detritus estimate.

VII. Discussion

Despite the wide range of estimates that we calculated (113 to 156 Pg C) they are considerably narrower than those made by Harmon and Chen (1992) and Harmon et al. (1993) which spanned an order of magnitude (50 to 500 Pg C). They are all higher than the 66 to 80 Pg C estimated by Matthews (1997). These earlier estimates applied many of the same methods, but the difference is that new estimates of mortality and decomposition rate-constants have been published in the intervening years.

Regardless of the method all estimates indicate the bulk of the carbon is stored in evergreen forests. Together tropical and deciduous forests comprise a similar fraction to evergreen forests. All other biomes together appear to contribute ≈10 to 25% of the total global woody detritus store. Given the scarcity of data of any sort for these biomes, some future investment in these areas might improve global estimates significantly.

Given small number of samples used in each approach it is difficult to rate them as to their reliability. It is very likely, however, that the direct biomass approach is more prone to overestimate than the ratio approaches. First, the reported stores of woody detritus in ecosystems are neither random nor systematic. As with many fields, sampling tends to be taken in areas where large amounts of woody detritus occurs. In conifer forests, for example, many samples have been taken in the Pacific Northwest. We tried to eliminate this effect by averaging studies within regions first. Second, direct estimates of woody detritus tend to be correlated to the mass of living wood and hence the productivity (Krankina and Harmon, 1995). Using dead:live ratios eliminates some of this bias so that small stature forests contain more appropriate amounts of woody detritus. Our method of adjusting for disturbance effects makes theoretical sense, and increased stores as expected. Its primary shortcoming is the lack of specific information on the disturbance regime for many biomes.

VIII. Conclusions

In recent years, methods to study the size and dynamics of these detritus pools have been developed and applied to various ecosystems. Despite an increase in plot-level efforts, no reliable inventory-based estimates exist at the regional, national, or global scales. We presented a series of complementary methods that can be used to estimate potential steady-state and actual stores at regional to global scales. These include: (1) correction and conversion factors for incomplete inventories, (2) dead:live wood expansion factors, (3) predictions of steady-state stores from input:decomposition rate ratios, and (4) adjustments to include disturbance regimes. These methods indicate that global stores of carbon in woody detritus could be 114 to 157 Pg in the absence of disturbance, 131 to 148 Pg with natural disturbance, and 114 to 129 Pg after pre-1950s deforestation is considered.

The estimates of woody detritus stores we present are quite crude, but they strongly indicate several points. Considerable woody detritus is present at the global level, with the bulk of it stored in evergreen forests. Globally these estimates exceed those for surface litter (50 to 60 Pg C) and are roughly half of that estimated for peat. Although smaller than the commonly accepted store for soils (≈1500 Pg C), woody detritus is highly sensitive to natural disturbance and management by humans. This analysis indicates better inventories of dead woody detritus and measurement of its dynamics would considerably improve the overall understanding the role of carbon stores in the terrestrial biota.

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