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CONSEQUENCES OF TREE MORTALITY TO THE GLOBAL CARBON CYCLE

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ABSTRACT

Tree mortality and accumulations of woody detritus are important, but unstudied facets of the global carbon (C) cycle. Ecological studies from undisturbed temperate and tropical forests indicate woody litter inputs associated with tree mortality range between 0.16-5.0 Mg C/ha/yr. Mortality rates in forests appear to be positively correlated with ecosystem productivity and time since disturbance. United States Forest Service Continuous Forest Inventory data indicate that tree mortality in the United States increased over the past five decades from 52 to 65 Tg C/yr. However, mortality is increasing in some regions (eastern United States), while decreasing in others (Pacific Northwest) because of changes in forest-age structure. Globally, there are few measurements of tree mortality. Stand and Continuous Forest Inventory data were used to estimate turnover rates of live woody biomass for forests. Applying these ratios to current live biomass estimates indicates that 1.2-9.1 Pg C/yr is added globally to detrital pools by dying trees within intact forests. An additional 0.9-1.8 Pg of woody C may be added to the detrital cycle by catastrophic disturbances. The combined dead tree input is 7-39% of the 28 Pg C/yr added by fine litterfall. At these rates of input, coarse woody debris would reach a steady-state mass of 60-232 Pg C. However, because past land conversions reduced mortality and woody detritus, considerable carbon could be sequestered in forests recovering from clearing.

INTRODUCTION

Examination of any current global carbon budget (Post et al., 1990; Houghton and Woodwell, 1989) reveals a very startling point: dead trees do not exist! The tacit assumption in most, if not all, global carbon budgets is that although > 80% of the globe's living biomass is woody (Woodwell et al., 1978), very little of this material becomes litter. We will demonstrate that this assumption is unfounded and has led to a major underestimate of global detrital stores.

Excluding dead trees has several profound impacts upon understanding global carbon dynamics. First, the size of the terrestrial detrital pool has been underestimated (Harmon and Chen Hua, 1991). If woody detritus was in equilibrium, this might not be a major concern; however, land use changes have placed woody detritus in disequilibrium (Schiffman and Johnson, 1989). For example, logging within Pacific Northwest forests has halved carbon storage in this region (Harmon et al., 1990). Fully one-third of the difference between carbon stores in a plantation forest and an old-growth forest is due to the reduction of woody detritus (dead tree) carbon (Harmon et al., 1990). This reduction is not unique to this region, but probably applies to most boreal, temperate and tropical forests. If this is true, past calculations of carbon flux from forest clearing are underestimates. Conversely, this would imply that a large, unaccounted for carbon sink could be occurring in forests recovering from past harvest (Harmon and Chen Hua, 1991; Lugo and Brown, in press).

Another problem with excluding dead trees from global carbon budgets involves the future pattern of detrital stores. Most assessments of climate change upon detrital stores are comparisons of steady-state solutions under current and projected future climates. These studies generally indicate a greater storage of carbon under a warmer climate (Chapin and Matthews, 1992), primarily as a result of higher productivity. In contrast, analysis of transient responses to climate change indicates a large pulse of carbon may be injected into the atmosphere during the transition between these two steady-states (Neilson, personal communication). To a large degree, the temporal dynamics of this transient pulse will be controlled by the decomposition of woody plants killed by catastrophic disturbances (i.e., fire), or increased stress.

In the following paper, we will examine the role dead trees play in the current global carbon cycle. Coarse and fine woody detritus are formed from the death of twigs, branches, roots and boles of trees and other woody plants. The diameter used to separate coarse- and fine-fraction woody detritus is 10 cm. For the purposes of this review, we will exclude fine root turnover from our analysis, although the fine roots of many trees and shrubs are in fact woody and can exceed lead litterfall in some forest ecosystems (Vogt et al., 1986). We first review the characteristics of woody detritus that make its behavior different from other forms of litter. We then examine factors controlling tree mortality at the stand and regional levels. Finally, we estimate the input of carbon via dying trees to the global detrital system and examine its implications for the overall global carbon cycle.

CHARACTERISTICS OF WOODY DETRITUS

The decay and input dynamics of woody detritus are quite distinct from those of leafy detritus. Decay rates of woody detritus can be more than an order of magnitude less than leafy litter (Harmon et al., 1986). This has several implications for successional dynamics and C stores. First, fine litter and woody litter will store equal amounts of carbon at steady-state if woody inputs are an order of magnitude lower than fine litter inputs. These differences in decay rate also imply woody litter will take more than ten times as long to reach steady-state once input rates have stabilized.

In addition to differences in decay rates, the period required to reach maximum input rates following disturbance is considerably longer for woody than leafy litter. Input rates for leafy litter usually peak at the time of crown closure, which is as little as five years in tropical and deciduous forests (Bormann and Likens, 1979; Brown and Lugo, 1990) and up to 50 years in coniferous forests (Gessel and Turner, 1976). In contrast, woody litter inputs do not peak until the old-growth stage of succession, and this may take > 100 years even in tropical forests (Brown and Lugo, unpublished). This implies that stores of woody detritus will not reach steady-state levels for at least a century following disturbance.

Despite the fact that disturbances, including logging, create a large quantity of woody detritus, it is not unusual for this component to be overlooked in successional or ecosystem process models or carbon-sequestration assessments of climate change. We suggest that the conservation of mass applies even to dead trees. In the case of natural catastrophic disturbances (i.e., wind and fire), woody detritus can be the largest single carbon pool immediately following disturbance. In a Douglas-fir forest, for example, woody detritus comprised 25% of the total ecosystem carbon before a crown fire and 75% afterward (Agee and Huff, 1987). For most disturbances, this large increase is obvi-

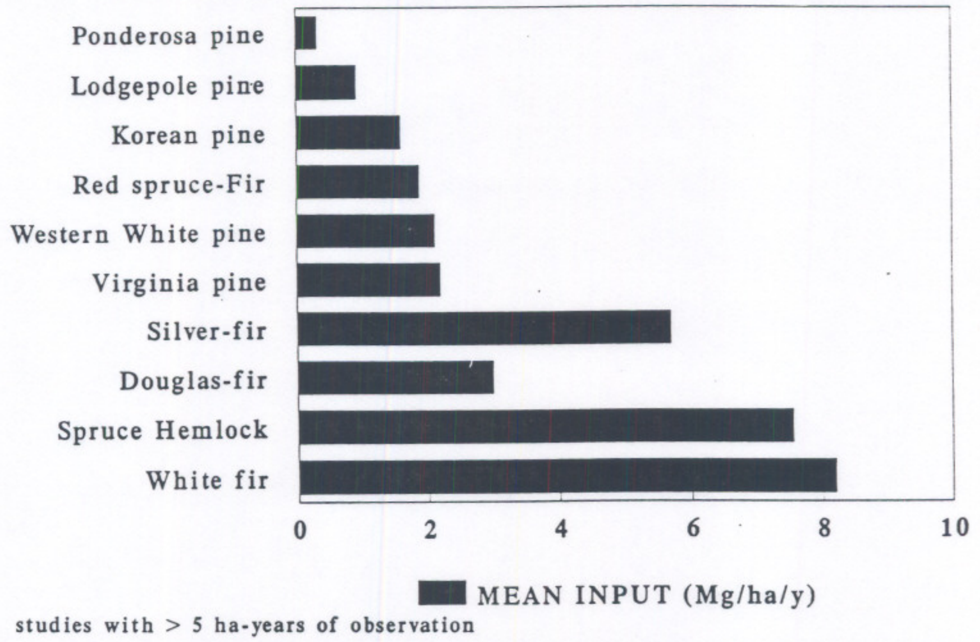


Figure 1. Woody detritus input associated with tree death in conifer forests. Only mature to old-growth forest with at least five hectare-years of observation are displayed.

ously a result of the large mass in trees being suddenly transferred to the woody detrital pool. However, in the case of fires, woody detritus is less apt to burn than leafy litter. This is especially true for the coarse- fraction material, which even under the most severe fire conditions is rarely burned completely (Sandberg and Ottmar, 1983).

STAND LEVEL STUDIES

Ecologists and foresters have been measuring forest growth for centuries; however, there are very few published mortality measurements based on direct observation (Franklin et al., 1987). The most reliable data are from large permanent plots (> 1 ha area) with individually marked trees observed for at least five years. Although numerous data sets meeting these criteria exist, many of them remain unpublished or analyzed solely from a population perspective. It is hoped that this trend will not continue.

Although it is unlikely stand level studies will ever be numerous enough to estimate global mortality rates directly, they are quite useful in understanding the causes of mortality and how stand structure, age, and productivity affect rates. Perhaps the best set of stand level plots available at this time is from the Pacific Northwest, a region where large-scale (>0.5 ha) permanent plots have been observed for more than 20 years (Franklin et al., 1987). Woody detritus inputs (including all tree parts except leaves) associated with tree death range an order of magnitude from <0.16 Mg C ha/yr in ponderosa pine to >4 Mg C ha/yr in white fir forests of California (Figure 1). In contrast, fine litterfall in these stands only differs by a factor of two from 1-2 Mg C/ha/yr (Vogt et al., 1986). Both fine litterfall and tree mortality in mature to old-growth conifer forests appears positively correlated with site quality. Plotting total above-ground NPP (net primary production, equal to the sum of biomass increment, mortality and fine litterfall) against tree mortality for mature to old-growth forests indicates that there is a general correspondence (Figure 2). For a given amount of above ground NPP, however, conifer forests produce far more woody detritus than deciduous or tropical forests. In particular, Pacific Northwest conifer forests produce almost three times the "expected" amount of tree

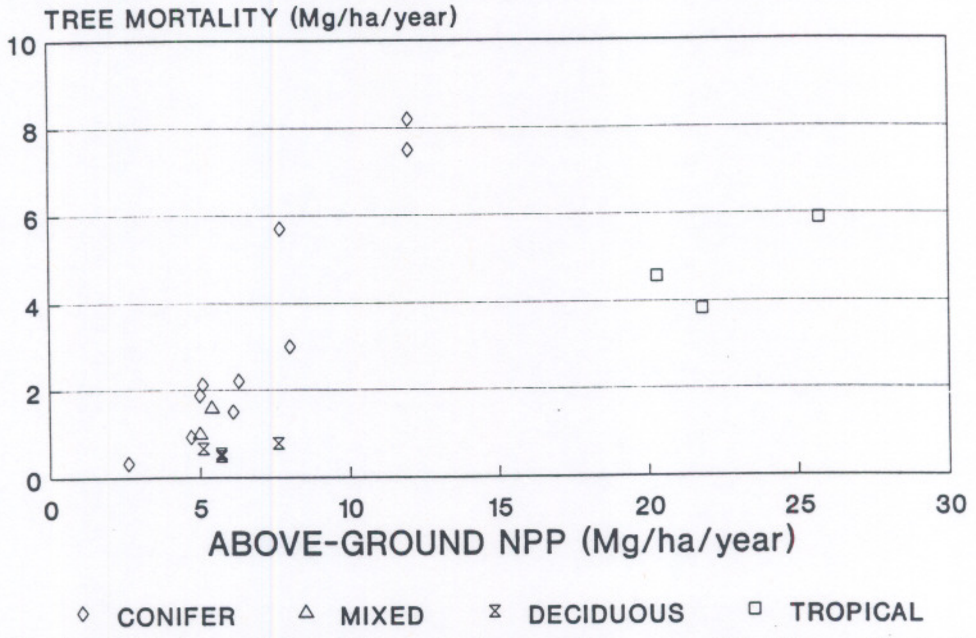


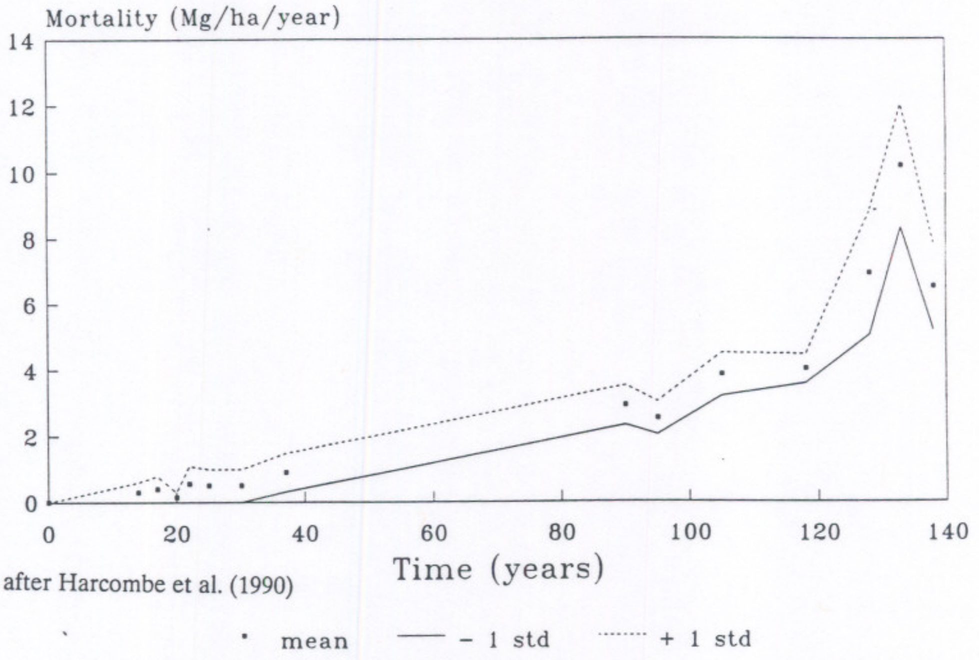
Figure 2. Woody detritus input associated with tree death versus above-ground Net Primary Production (NPP). The NPP was calculated as the sum of biomass increment, litterfall and tree mortality.

mortality litter. This difference may be attributed to, in part, from the greater longevity, and thus biomass, of these forests; a greater amount of biomass may therefore offset lower NPP.

The lower mortality rate in less productive forests does not necessarily mean that dead woody detrital stores will be lower in these forests. Dead wood stores in tropical forests might be quite similar to those in boreal forests because productivity and decomposition rates are positively correlated on a global scale--both increasing toward the tropics. There are exceptions to this pattern as some temperate regions (i.e., the Pacific Northwest) can also have high productivity. Woody decomposition rates are strongly influenced by fungi-toxic compounds in heartwood and excess moisture, factors that may not be correlated to latitude. Few boreal genera contain fungi-toxic compounds, whereas they are extremely common in tropical hardwoods. Moreover, excess moisture may limit wood decay in some tropical forests, but it is frequent in cool humid regions such as the Pacific Northwest.

Another factor that profoundly influences the amount of tree mortality is stand age (Figure 3). Although the number of stems dying is often highest during the middle stages of succession (Knox et al., 1989), it would appear that woody litter input increases with forest age (Harcombe et al., 1990). This discrepancy may result from differences of population and detrital input dynamics. The large number of stems dying during the middle stages of succession are small individuals with little mass. In contrast, fewer trees die in older forests, but they are much larger and not biased toward the smallest individuals of the population (Knox et al., 1989).

The non-linear patterns of tree mortality inputs during succession, coupled with slow decomposition, mean that woody detrital stores rarely reach a steady-state. Disturbances add a large amount of woody detritus, yet the following young forests do not produce much woody detritus. This leads to a large decrease in woody detrital stores early in succession that may equal or exceed the carbon sink created by regrowing trees (Harmon et al., 1990). If mortality rates remain low during the middle stages



after Harcombe et al. (1990)

Figure 3. Changes in tree mortality as a function of stand age for a western hemlock/sitka spruce ecosystem. Two series of permanent plots were used.

of succession, woody detrital stores may decrease below old-growth values (Spies et al., 1988). Eventually, the mortality rates return to old-growth amounts, leading to an additional sink of carbon in the ecosystem. For example, in the sitka spruce/western hemlock forest, another 100 to 150 Mg C/ha may be stored in dead wood in the next 200 to 300 years. This amounts to an additional sink of 0.5 Mg C/ha/yr in a forest that has reached a "steady-state" living biomass (Harcombe et al., 1990).

Table 1. Expansion factors used to convert the volume of growing-stock mortality from Waddell et al. (1987) to total woody mortality.

Expansion factor	Conifer	Deciduous
Growing stock to Total volume (a)	1.053	1.667
Wood density (Mg/m^3)	0.45	0.55
Wood to Total mass (b)	1.62	1.62

(a) Based upon ratios of total to growing stock volume (Bechtold, 1984).
(b) Includes bark, branches, roots.

REGIONAL STUDIES

Stand level ecological plots are not numerous or representative enough to be unbiased estimates of mortality rates on a regional or continental scale. Timber inventories generally fit these criteria; however, few countries apparently include non-catastrophic mortality. This probably results from a methodological limitation because permanent plots are needed to estimate mortality, and most timber inventories are one-time surveys. An exception is the U.S. Forest Service Continuous Forest Inventory (CFI), which has recorded mortality in permanently marked plots since the 1950's. We have converted these data (Waddell et al., 1987) from loss in cubic volume of growing stock to carbon using various correction factors for non-merchantable trees, wood density and non-merchantable parts (Table 1). We have also used the fine-litter input rates estimated by Meentemeyer et al. (1982) and the area in forest land (Waddell et al., 1987) to estimate fine-litter inputs for the same area examined for tree mortality.

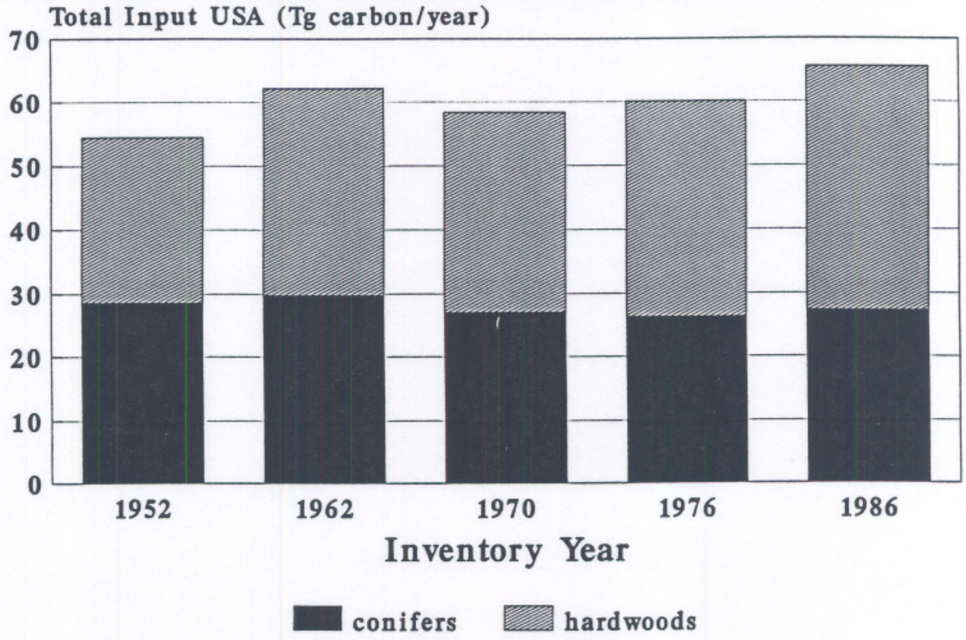


Figure 4. Woody detritus input associated with tree death in U.S. forests in the past 50 years.

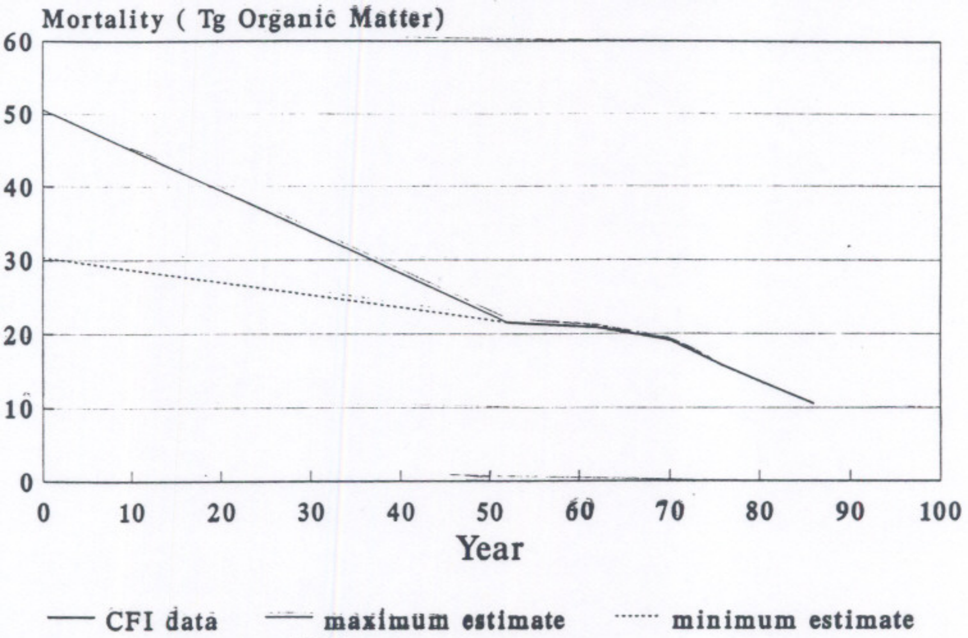
Continuous Forest Inventory data indicate that the rate of tree mortality in the United States has increased in the last five decades from 52 to 65 Tg C/year (Figure 4). This is < 10% of the total above-ground inputs, which at first glance would support the notion that tree mortality input could be overlooked with little consequence. This perspective is very misleading, however, because woody litter has a very slow decay rate and consequently can form a large amount of detrital stores. For example, applying the known differences in leafy and woody decay rates for two typical forests (i.e., an eastern deciduous and a cold coniferous forest) we find that woody detritus comprises 40 to 50% of the above-ground detrital stores in a steady-state condition.

The cause of the slight increase in tree mortality in the United States is difficult to unravel given the large-scale changes in pollution stress and age-structure that have occurred. Examination of regions indicates that the overall increase is driven by increases in the eastern United States that offset large decreases in the Pacific Northwest. We feel this pattern parallels shifts in forest age structure; regions with decreasing mortality rates are being converted to younger forests, whereas regions with increasing mortality rates are generally increasing in age.

Regardless of the current causes of increasing mortality, it is important to note that current tree mortality rates are far below pre-European levels. The effect of forest harvest on mortality rates is most clearly seen in Oregon and Washington, a region where the area extent of old-growth forests has decreased in the last 50 years. The CFI data show mortality has declined two-fold during this period (Figure 5). Extrapolating back to the turn of the century, when these forests were first beginning to be developed, indicates there has been a three- to five-fold decrease in the mortality rate.

GLOBAL ESTIMATES

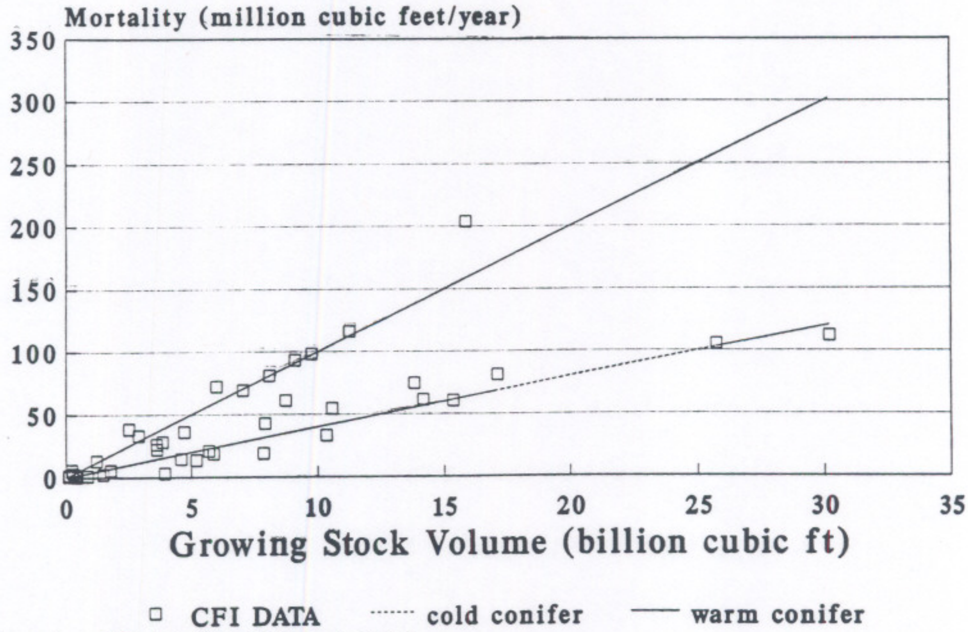
Ideally, one would base global estimates of tree mortality upon forest inventories; however, until more government agencies collect or publish these types of data, direct estimates will not be possible. We have therefore used an alternative approach to estimate mortality in intact stands based upon the ratio of mortality and growing stock volume (Figure 6). This ratio amounts to a turnover rate for the living canopy



based upon Waddell et al. (1987) and Harmon et al. (1986)

Figure 5. **Estimated historical changes in tree mortality during the last 90 years in the Douglas-fir region of Oregon and Washington.**

that can be multiplied by the living biomass data to crudely estimate the mass of mortality. Note that in our current estimates, forest age structure is not used; more accurate estimates could be made if age-class specific turnover rates were used in conjunction with age-class specific biomass data. For the temperate and boreal biomes, we used the U.S. CFI data, and for humid tropical biomes, we used data from Brown



based on CFI data (Waddell et al., 1987)

Figure 6. **Cubic mortality of growing stock versus growing stock for conifers in the United States. Each point represents the value for a state.**

Table 2. Mortality turnover rates of major forest regions of the world.

Region	Mortality turnover rate (%/yr) (a)		
	mean	minimum	maximum
Cold conifer (b)	0.43	0.17	1.00
Cold deciduous (b)	0.87	0.52	1.48
Warm conifer (b)	0.95	0.52	1.28
Warm deciduous (b)	0.64	0.42	0.93
Tropical close (c)	1.58	0.13	4.93
Tropical open (c)	0.22	0.08	0.35

(a) Calculated as the ratio between the mass or volume of mortality and the growing stock mass or volume.

(b) Based upon US Forest Service CFI data for individual states; range is the lowest and highest value for states in given forest type.

(c) Based upon stand data from Bown and Lugo (11).

and Lugo (unpublished) to estimate these turnover rates. The living biomass data were taken from Woodwell et al. (1978) and Brown et al. (1989).

Examining mortality turnover rates from five different regions indicates considerable variation within and between regions (Table 2). Coniferous forests have two distinct populations: eastern pine-type species with 0.95%/yr and cold coniferous forests with 0.43%/yr. This is consistent with the stand level results that indicate higher mortality with increasing productivity. The opposite appears true for deciduous forests in that cooler, less productive forests have a higher turnover rate (0.87/yr) than warmer deciduous forests (0.64/yr). This pattern may reflect the overall advantage that conifers have in cooler climates. Alternatively, this pattern may reflect the switch in successional status of conifers and deciduous trees with latitude. That is, conifers are generally short-lived early seral species in low latitudes, whereas deciduous trees play this role in higher latitudes. The tropical Venezuela data indicate that both dry and moist tropical forests have perhaps twice the rate of turnover of temperate forests, suggesting a positive correlation between turnover rate and productivity.

Applying these ratios to the biomass data indicates that globally 1.2-9.1 Pg C/yr is added to detritus via tree mortality within intact stands (Table 3). By far the largest amount appears to

Table 3. Global detrital input associated with tree mortality.

Ecosystem	Area (a) (10^6 km^2)	Live carbon (a) (Pg)	Catastrophic return interval (centuries)	Mortality Input Normal (b)	Mortality Input Catastrophic (c)
Tropical closed	12.0 (h)	122	7-15 (d)	1.91 (0.16-6.04)	0.08-0.18
Tropical open	7.3 (h)	26	7-15 (d)	0.06 (0.02-0.1)	0.02-0.04
Temperate evergreen	5.0	79	2-5 (e)	0.75 (0.41-1.01)	0.16-0.39
Temperate deciduous	7.0	95	10-15 (f)	0.61 (0.40-0.88)	0.06-0.09
Boreal	12.0	108	1-2 (g)	0.46 (0.18-1.08)	0.54-1.08
Total	48.5	743	3-7	3.79 (1.17-9.11)	0.86-1.78

(a) Based upon Woodwell et al., 1978; Brown et al., 1989.

(b) Mean (minimum-maximum), calculated using the mean, minimum and maximum mortality turnover rates Table 2.

(c) Calculated by dividing the range of return intervals in years into the live biomass.

(d) Based on Sanford et al., 1985.

(e) Based upon Kilgore (1978) and Christensen (1978).

(f) Based upon Seischab and Orwig, 1991.

(g) Based upon Heinselman, 1978.

(h) Based upon Lanly, 1982.

be dying in closed tropical forests that have both high turnover rates and high biomass stores (due to extensive areal extent). Boreal forests are less important globally, but still may be adding as much as 1 Pg C/yr from intact stands.

These estimates are low, of course, as they do not include contributions from catastrophic disturbances. Unfortunately, there are few estimates of natural rates of catastrophic disturbance on a global scale upon which to base our calculations. We approach this problem in two ways. First, one might consider the return interval required to have catastrophic mortality equal to within stand mortality. This would indicate whether setting non-catastrophic and catastrophic mortality rates equal is a reasonable assumption. The return interval would be the reciprocal for the estimated turnover rates of intact stands. This indicates a catastrophic-disturbance return interval as short as 43-200 years in tropical forests and as long as 200-600 years in boreal forests. The return interval for boreal forests seems reasonable in that it implies 2 to 6 x 10^6 ha/yr are disturbed, less than the 8 x 10^6 ha/yr estimated for a decade with high fire occurrence (Stocks, 1990). In contrast, the return intervals for temperate and tropical forests is unrealistically short. A more reasonable estimate from these regions can be made by using published return intervals (Table 3). This indicates catastrophic disturbances may be adding another 0.85 to 1.78 Pg/yr globally. Thus total tree mortality input for the globe would appear to be in the range of 2.03-10.89 Pg C/yr.

Global estimates of fine litterfall (Meentemeyer et al., 1982) are about 28 Pg/yr, thus woody detrital inputs are relatively small compared with that well-known input. Nonetheless, woody detrital flows are important in two regards. The first is that this flow is about equal to fossil fuel burning. The idea that flows this large are being ignored, as ecologists "balance" the global carbon budget (Post et al., 1990), is mind-boggling. The second point is that while the input rate may be small relative to leafy litter, the storage in woody detritus may far exceed that of leafy litter because of the much lower decomposition rate of woody material. We have calculated the potential steady-state carbon store in woody detritus using the range of input rates (Table 3) and estimated decay rates (i.e., tropical = 10%/yr, temperate evergreen = 3%/yr, temperate deciduous = 7.5%/yr, and boreal 2%/yr). This calculation indicates that given an input of 2 to 11 Pg C/yr, a steady-state store of 64 to 232 Pg of woody detritus carbon results. Ecologists have thus been ignoring a detrital pool that at least equals and most likely far exceed the 70 Pg of fine litter carbon (Post et al., 1990).

CONCLUSIONS

Our estimates of the detrital input associated with tree mortality are preliminary, and to an order of magnitude only. They do indicate, however, that a major flow in the global carbon cycle has been ignored. We question whether the global carbon budget can be balanced when flows as large 2-10 Pg C/yr are ignored. Our analysis indicates global detritus may be underestimated by an amount roughly equal to the carbon stores in peats. Given that past forest harvest and clearing have greatly reduced woody detrital stores globally, this pool may have been a significant source of carbon in the past and a potentially significant future carbon sink in the present. However, until we have better estimates of tree mortality and woody detrital decay rates, the exact contribution from woody detritas to the global carbon cycle will remain a mystery.

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