Chapter 8
Woody Detritus Mass and its Contribution to Carbon Dynamics of Old-Growth Forests: the Temporal Context

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8.1 Introduction

Woody detritus is an important component of forested ecosystems. It can reduce erosion and affects soil development, stores nutrients and water, provides a major source of energy and nutrients, and serves as a seedbed for plants and as a major habitat for decomposers and heterotrophs (Ausmus 1977; Harmon et al. 1986; Franklin et al. 1987; Kirby and Drake 1993; Samuelsson et al. 1994; McMinn and Crossley 1996; McCombe and Lindenmayer 1999). Woody detritus also plays an important role in controlling carbon dynamics of forests during succession. Along with live woody parts of trees, dead wood or woody detritus is a large pool undergoing a relatively large change in stores during succession (Davis et al. 2003). In contrast, carbon in the mineral soils represents a large store, but generally changes slowly [see Chaps. 11 (Gleixner et al.) and 12 (Reichstein et al.), this volume]. Moreover, the organic layer lying above the mineral soil can change very rapidly, but generally represents a small proportion of total forest carbon stores.

Woody detritus takes many forms. Fine woody detritus (FWD), with the exception of roots, is typically less than 7.6–10 cm in diameter, the former being based on lag-times of fire fuels. For woody roots the size break is usually 2 mm, which is based on conventions on the maximum size of live fine roots. Coarse woody detritus (CWD) exceeds these diameters (usually >7.6 cm), but also typically must exceed a length of 1 m. Woody detritus is present in the form of roots, stumps, branches (including attached dead branches), standing dead (i.e. snags), and downed material. Very few inventories measure all these forms and size classes, standing and downed "dead" material being the most commonly measured.

This chapter reviews what is known about how aboveground woody detritus mass changes over forest succession. To understand the quantity and quality of woody detritus in old-growth forests it is also necessary to understand the preceding stages of succession. Moreover, to understand how succession starts it is necessary to understand the amount of woody detritus present at the time of disturbance. This review starts with the processes that underlie these changes, considers how these processes control amounts of woody detritus in old-growth forests and then

combines these processes to examine the expected theoretical trends during succession. Observed changes, largely through the use of chronosequences (substitution of space for time) are compared to model predictions of mass and net changes in stores. Finally, I conclude with suggested improvements to reduce uncertainties concerning trends in woody detritus mass during succession and the role it plays in forest carbon dynamics.

8.2 Underlying Processes

8.2.1 Disturbance

Disturbances, events that significantly restructure the forest, are a logical point to start an analysis of secondary succession. What exactly constitutes a disturbance is scale dependent (Pickett and White 1985). In the context of this chapter, disturbances are events that significantly restructure forests at the level of stands. Although "partial" disturbances such as thinning, low intensity fires, and insect attacks clearly fall under disturbances at some scales, the majority of observational and theoretical studies on woody detritus have considered only "catastrophic" or "stand-replacing" disturbances – ones that kill the majority of trees. This chapter therefore emphasizes the latter type of disturbance. Gap dynamics, a smaller scale form of tree-level disturbance important in old-growth forests, is treated below under mortality.

Stand-replacing disturbances restructure forests in two ways and both control the nature of the legacy of material left, which influences much of the succession that follows. First, by killing trees, disturbances create woody detritus. Second, disturbances can remove woody detritus (e.g. fires and timber harvest). The maximum input of woody detritus occurs when none of the formerly live material is removed (e.g. windthrow or insect-kill). Disturbances related to pathogens such as fungi, may also have very high levels of woody detritus input, although some losses may occur during the process of trees dying, especially if the pathogen decomposes wood. The minimum woody detritus input occurs for intensive timber harvest, with the removal of stems, branches, and roots. However, it would be more typical for harvest systems to leave branches, roots, and unmerchantable parts of the stems, which probably amounts to at least one-third of the live tree biomass (Harmon et al. 1996). Fires remove far less live wood, but this highly variable process is likely to change from ecosystem to ecosystem, and fire to fire. Except in extremely severe fires, it is unlikely that much of the large diameter live wood burns.

Some disturbances also remove woody detritus present at the time of the disturbance. In the case of timber harvest, merchantable woody detritus is often removed in salvage operations. Fire is the disturbance most likely to remove woody detritus, but little is known about the amounts involved. Consumption of woody detritus increases as moisture and piece diameter decrease, and as the degree of decay increases (Brown et al. 1985; Rienhardt et al. 1991). In most situations the consumption of large woody detritus is linked to consumption of the forest floor because woody detritus alone does not generally provide a continuous enough fuel bed to support a

fire on its own. The burning forest floor interacts with large wood detritus providing the energy feedback required to maintain dead wood consumption (Harmon 2001). This is important because it means that, without deep forest floor layers, large pieces of woody detritus may not be completely consumed.

In regions where there is a significant difference in the decomposition rates of standing versus downed wood, the type of disturbance can influence the longevity of the legacy woody detritus (i.e. that left by the disturbance). For example, if standing wood decomposes slower than downed wood (which would be typical of drier climates), then fires, insects, and pathogen-related disturbances might create a lag or slower initial phase in the decomposition of the legacy wood. Disturbances that create downed wood, such as timber harvest and windthrow, might lead to a more rapid loss of legacy wood. Conversely, if standing wood decomposes faster than downed wood (typical of wet, cool climates) then disturbances that create standing dead wood would have an initial rapid loss of legacy wood followed by a slower phase as trees fall to the ground. Disturbances that create substantial amounts of downed woody detritus in this situation might have legacy wood disappear at a slower rate than those creating snags.

The nature of disturbances also determines the decomposition rates of legacy wood in more direct ways. The presence of a wood-decomposing pathogen might impact future decomposition rates by short-circuiting decomposer colonization; hence disturbance of an old-growth forest with high incidence of heart-rot may lead to faster decomposition than disturbance of a younger forest with few incidences of heart-rots. Attacks by insects such as bark beetles may also speed the colonization process, although only by a few years given that trees dying from all causes are rapidly attacked by these insects (Kirby and Drake 1993). Fire is likely to slow decomposition, but this may only be true for wood that is in the intermediate stages of decomposition (Harmon 2001). Fire charred trees are typically attractive to wood-boring insects, and many species specialize in finding fire-killed trees. Wood fully colonized by decomposers is also likely to be little affected by charring, although decreasing albedo is likely to heat the wood and lead to faster biological activity. Charring is most likely to slow decomposition in woody pieces that have the decayed portions fully removed by fire, thus eliminating the normal colonization sequence.

The size of material input by disturbance is dependent on the age of the forest being disturbed. The largest size pieces should result from old-growth forests being disturbed. Repeated harvests of forests at short intervals would likely result in the smallest material being input by disturbance, because of the removal of larger diameter stems and the smaller size of the trees.

8.2.2   Forest Re-Establishment

The ultimate source of new or de novo woody detritus following disturbance is the forest that follows. While it is beyond the scope of this chapter to review all aspects of this process, perhaps most important is the rate the new forest re-establishes. In cases where a seedling bank is present or species can sprout, forest re-establishment

can be quite rapid. If seeds must disperse and germinate, and seeding survival is low, then re-establishment could be extremely slow. Tree planting can speed the recolonization over natural rates, although not all plantings are successful. Regardless of the average rate of forest re-establishment, there can be a considerable range between the slowest and fastest rates observed in a landscape (Yang et al. 2005).

There are several important aspects of re-establishment regarding woody detritus. The faster the re-establishment rate, the faster leaf area can be redeveloped and the faster net primary production (NPP) can return to predisturbance levels. This means biomass recovers more quickly and, as some of the new trees die, the losses from legacy wood can be replaced faster. Re-establishment also influences the species of trees present, and if the decomposition rates of species differ, then this can also influence woody detritus mass during succession. The species present during the succession can also influence the rate of NPP and mortality, both of which can influence woody detritus mass (cf. Chap. 5 by Wirth and Lichstein, this volume). The temporal pattern of NPP during succession can strongly influence the amount of de novo woody detritus present. As forests re-establish, NPP generally increases and eventually levels out. There is, however, considerable evidence that there is a decline in NPP as forests continue to age (Ryan et al. 1997). The mechanism responsible for this decline and its extent is not well understood [see Chaps. 4 (Kutsch) and 7 (Knohl), this volume, for a critical appraisal of NPP decline]. However, if present, this pattern of declining NPP once a certain age is reached is likely to introduce non-linear patterns to woody detritus mass during succession and may mean that woody detritus in the old-growth is lower than the mid-succession phase.

8.2.3 Mortality

Mortality is the process that creates woody detritus. It occurs by natural or by human-related causes. It can occur as single tree parts (e.g. branch pruning), as single individuals, or as entire stands (i.e. as landscape units). In this chapter I have used disturbances to account for mortality processes that kill an entire stand. At the level of individual trees and parts, I refer to this process as "regular" mortality, recognizing there is a continuous gradient of mortality from tree parts to trees to stands. Gap formation, the process of mortality for single or small groups of trees, is an important form of mortality creating many aspects of old-growth structure including the small-scale spatial variability of woody detritus.

Mortality has been difficult to study because it is highly variable in time and space (Franklin et al. 1987). To understand this process, one needs to observe a population frequently over time to determine rates and causes, although some stand reconstruction methods can give rough approximations of long-term rates (McCune et al. 1988). In models of mortality there is a tendency to only consider self-thinning, but trees are often killed by causes unrelated to density-dependent

mechanisms, such as wind, ice damage, insects, pathogens, and outright accidents [e.g. the second highest cause of death in Pacific Northwest forests in the United States is being crushed by another tree or snag (Franklin et al. 1987)]. Considered over the life of a stand, the inputs of woody detritus from self-thinning, gap dynamics, stand level disturbances, and other density-independent causes are probably quite similar in amounts – they just occur at different stand ages (Harmon et al. 1986).

Despite the difficulty in studying and understanding this process, it is clear that average mortality rates in older forests vary significantly from ecosystem to ecosystem. At the continental scale, the tendency is for mortality to increase with productivity, although the cause of this relationship is not clear. Tropical forests have the highest mean mortality rate-constants (0.0167 year^{-1}) followed by deciduous (0.012 year^{-1}) and then evergreen forests (0.01 year^{-1}) (Harmon et al. 2001). There is also a change in the proportion of mass dying over succession. In forestry circles, mortality rates are commonly thought to be highest in older forests, but in natural stands proportional mortality rates (i.e. expressed as a proportion of live mass dying) actually tend to be highest during the self-thinning stage of succession. For example, in the Pacific Northwest region, proportional tree mortality rates in old-growth forests appear to be one-third to one-half those of the self-thinning stage (Franklin et al. 1987). Mortality may appear to be lower in younger stands from a forest management perspective because much of the mortality is "captured" by thinning and salvage, whereas in old-growth forests much of the mortality is not utilized. While thinned and salvaged trees are utilized, these trees have still died in terms of ecosystem function.

The absolute amount of input to woody detritus via regular mortality generally increases during succession (Fig. 8.1), although the pattern of increase depends on the biomass present and the proportion dying in each phase of succession. The simplest case would be if the proportion of trees dying remains constant. Here, the input from mortality should mirror that of biomass, increasing and then stabilizing as biomass stabilizes. While it is likely that proportional mortality rates changes during succession, the complete development of stands has generally not been observed. Hypothetically, once trees establish after disturbance, proportional mortality should be low because tree-to-tree competition is low. As stands enter the self-thinning phase, the proportion of trees lost to mortality may increase as competition increases. This might lead to a temporary increase in absolute mortality inputs; however, the smallest trees are most likely to die in the self-thinning phase of stand development and this may offset the higher proportion of stems dying. Once trees reach their maximum crown diameter it is likely that density-independent mortality becomes more important, leading to a decrease in the proportional mortality rate as stands enter the old-growth phase. Mortality rates in the old-growth stage of succession are likely controlled by species longevity, the presence of pathogens and insects, and susceptibility to wind. Despite a decreased proportional mortality rate in the old-growth stage, high biomass in old-growth stands should lead to a high rate of absolute mortality inputs.
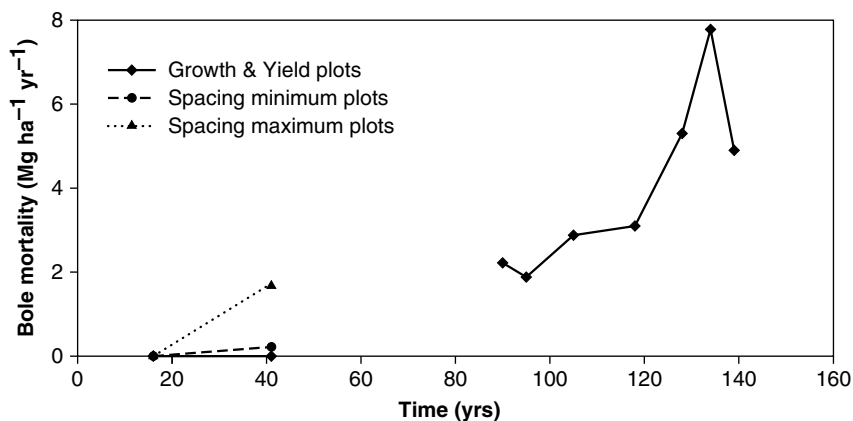
Fig. 8.1 Change in regular mortality input over succession for a *Picea-Tsuga* forest in coastal Oregon (after Harcombe et al. 1990)

Theoretically, as stands age, more and more NPP is allocated to replace biomass lost via mortality. This has been confirmed in relatively old forests in the Pacific Northwest where NPP is roughly equal to mortality losses (Harmon et al. 2004; Acker et al. 2002) and live tree biomass has remained relatively constant for decades (Franklin and DeBell 1988; cf. also Chap. 14 by Lichstein et al., this volume). It is not exactly known how a simultaneous decline in mortality and NPP in ageing stands effects biomass, but theoretically these parallel changes might lead to a stabilization of biomass around an asymptote. As mentioned above, if tree mortality cannot be replaced by new growth in very old forests, then it is possible for biomass and subsequently dead wood mass input to decline as forests age. However, this pattern of biomass decline seems to be of lower importance than previously thought [see Chaps 5 (Wirth and Lichstein) and 14 (Lichstein et al.), this volume].

8.2.4 Decomposition

Decomposition is the most important natural process controlling the loss of woody detritus. Many factors control its rate, ranging from the chemical and physical nature of the wood, to the environment at the micro- and macro-levels, and the decomposers involved (Harmon et al. 1986). There is a basic assumption that most wood decomposition involves respiration. While most likely true, fragmentation and leaching can lead to significant losses from pieces of woody detritus (Harmon et al. 1986; Spears et al. 2003). It should be borne in mind, however, that these two losses are not losses at the ecosystem level. This means that, at least theoretically,

current estimates of woody detritus decomposition rates are overestimating ecosystem losses. In practical terms, the size of this overestimation is likely small because fragmentation rates are often based on volume losses, and some volume losses are caused by respiration losses (Harmon et al. 2000), and leachates may decompose at high rates once they leave the wood and may not accumulate in the soil (Spears et al. 2003).

It is well known that different tree species produce woody detritus that decomposes at very different rates (Harmon et al. 1986). In some cases these differences can approach an order of magnitude even when the site conditions are identical (Harmon et al. 2005, 1995), but more typical might be a two-fold difference in the rate-constants describing decomposition. Differences in species are due largely to differences in heartwood decay resistance, with the heartwood of some species containing substances toxic to decomposers (Scheffer and Cowling 1966). Given that heartwood decay resistance is unlikely directly related to seral status (i.e. some pioneer species are decay resistant and some are not), it is possible for decay resistance to increase or decrease during succession (see Chap. 5 by Wirth and Lichstein, this volume).

Size also influences decomposition; however, there are many contradictory reports on its effect, which can be explained but only by understanding the interaction of size with species decay resistance and microclimate of the woody detritus. Under humid conditions in sites where excessive drying is not an issue, decomposition rate declines hyperbolically as piece diameter increases (Harmon et al. 1986; Mackensen et al. 2003), due in part to increases in the surface area to volume ratio as diameter increases (Fig. 8.2). However, it is also clear that the rate of decline is steeper for species that have decay resistant heartwood, because at small diameters all species lack heartwood, and the sapwood and bark of species
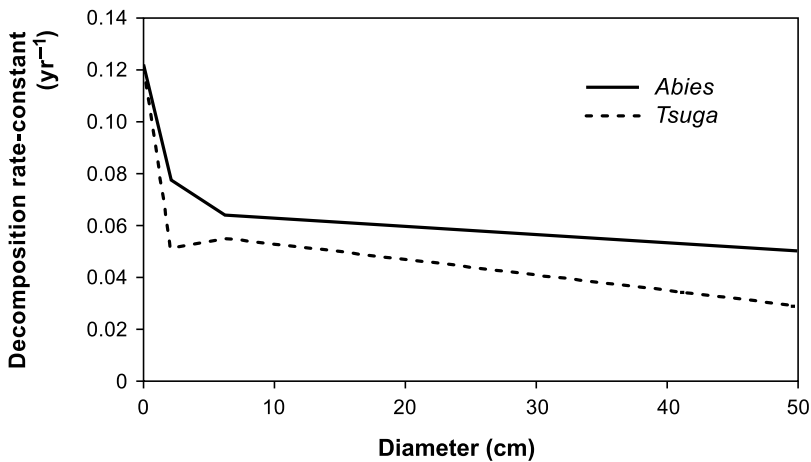

Fig. 8.2 Change in the decomposition rate-constant for woody detritus as a function of piece diameter (M.E. Harmon, unpublished data)

are usually quite similar in decay resistance. Therefore, for species with highly decay resistant heartwood, the larger the diameter, the more heartwood is present (Hillis 1977), and thus the overall decay resistance increases with diameter (Harmon et al. 1986). In climates or microclimates with excessive drying it is possible that smaller diameter wood decompose slower than larger diameter wood, because the smaller the diameter, the faster the drying rate. Given all these possibilities it is not surprising that one study contradicts another.

The effect of size on decomposition is potentially important because the size of woody detritus inputs changes over succession, with larger pieces being added as the forest ages. It is therefore likely that the largest pieces are added in the old-growth stage of succession due to density-independent mortality. In contrast, the smallest pieces are probably added during the self-thinning stage of succession as the smallest individuals are most likely to die.

As with any form of detritus, climate is an important control of decomposition rates. Examined globally, mean decomposition rates for coarse woody detritus decreases from tropical (0.176 year^{-1}) to deciduous (0.080 year^{-1}) to evergreen forests (0.032 year^{-1}) (Harmon et al. 2001). However, some of these differences are confounded with differences in species decay resistance. Plotting species with and without decay resistance against mean annual temperature indicates that the decomposition rate-constants of the former species increases as temperature increases, with a Q_{10} (i.e. the increase in rate-constant with a $10°C$ increase in temperature) in the range of 2.7–3.4 (Fig. 8.3; Yatskov et al. 2003). Interestingly, across the same range in mean annual temperature decay resistant species had a Q_{10}
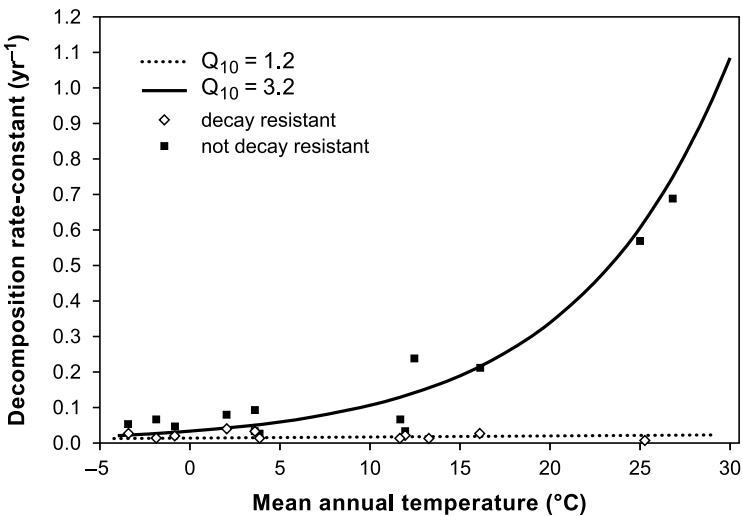

Fig. 8.3 Change in decomposition rate-constant (k) for coarse woody detritus in Russia as a function of mean annual temperature (after Yatskov et al. 2003). Q_{10} refers to the rate the decomposition-rate constant increases for a $10°C$ increase in temperature

of 1.2, indicating there was little increase in the decomposition rate constant with temperature. While the most obvious climatic control at the global level appears to be temperature (Mackensen et al. 2003), moisture balance can be important at a local scale (Harmon et al 2005). While the response of decomposers to moisture in wood is relatively straightforward, predicting the moisture is not. Below the fiber saturation point (~30% moisture content, water : dry weight basis) decomposer activity is limited (Fig. 8.4; Griffin 1977). As moisture content increases above fiber saturation, decomposer activity increases and eventually approaches an asymptote. However, when moisture reaches the point where pore spaces fill with water, the diffusion of oxygen becomes limiting, and this leads to a decrease in decomposer activity.

The moisture balance of wood is obviously controlled by precipitation amounts, but also by temperature and solar radiation, as well as by the size and exposure of the material. These factors interact in complex ways that have yet to be examined adequately. For example, standing wood (e.g. snags) is generally drier than downed (e.g. logs) or buried wood, but how this influences decomposition depends on the macroclimate. In climates that have low precipitation or a high potential to evaporate water, the moisture balance of standing dead material is likely to be low enough that decomposition is slowed. In the same situation downed wood, due to its greater protection, is likely to be less limited by excessive drying. This means that in dry climates, disturbance and mortality types that create standing dead wood are likely to lead to slower initial decomposition than those that create downed wood. These relationships change when the climate has very high precipitation and/or a low potential to evaporate water. Here downed wood may retain too much water to
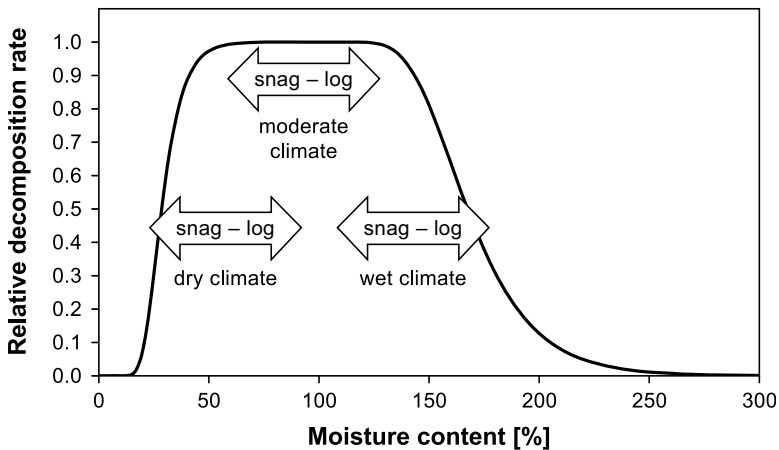

Fig. 8.4 Relationship between relative decomposition rate and moisture content (water to dry mass basis) for coarse woody detritus. Snags are always drier than logs due to their greater exposure to drying and lower interception of precipitation. The *arrows* indicate the range of conditions in three different climates (dry, moderate, wet)

support active decomposition and downed material will decompose slower than standing material. These relationships are also influenced by size, with larger diameter pieces retaining water longer than smaller diameter ones. Therefore, even in wet climates exposed smaller diameter pieces may be subject to excessive drying.

In addition to the position of the wood (i.e. standing versus downed), the age of the forest is likely to influence the moisture content of woody detritus. Increased exposure to solar radiation caused by disturbance should increase drying rates, leading to woody detritus in old-growth forests being moister than recently disturbed stands. However, as with position, the effect on decomposition is likely to depend on the macroclimate. In excessively wet climates, increased solar radiation is likely to speed decomposition, whereas in dry climates it is likely to retard decomposition. These effects may also depend on the rate of vegetation growth. Janisch et al. (2005) found little difference in log decomposition rates in harvested versus old-growth forests, a finding attributed to the rapid growth of vegetation that shaded the decomposing wood in recently harvested forests.

Perhaps the least understood control of decomposition rates is of the decomposer organisms; their effects are rarely considered in ecosystem models. The most general effect of organisms involves the lag introduced by their colonization of woody detritus (Harmon et al. 1986). Given the size of some of tree stems, it can take many years for decomposers to spread throughout (Kimmey and Furniss 1943; Buchanan and Englerth 1940). This leads to a lag in decomposition that could last decades. To some degree, these colonization effects are captured by decay resistance and moisture balance. For example, high decay resistance of heartwood leads to lower colonization rates in some species of dead trees, and thus to a lower decomposition rate. Likewise for waterlogged wood, the environment reduces the ability of decomposers to colonize and grow (Griffin 1977). When these factors are not an issue (i.e. in species with low decay resistance or environments were moisture is not limiting), the lag caused by colonization effects per se might last a decade or less (Harmon et al. 1986). The presence of macro-invertebrates, especially termites, can greatly change decomposition rates (Ausmus 1977). One of the reasons woody detritus in semitropical and tropical forests disappears quickly, at least for the species with minimal decay resistance, is the presence of termites (Harmon et al. 1995). The type of fungi present, and the degree to which stable material is formed, can also alter the decomposition rate. In particular, the presence of white-rot versus brown-rot fungi can determine whether lignin is degraded during the course of decomposition, with the former being able to degrade this substance and the latter not (Gilbertson 1980). This means that wood is not completely degraded by brown-rot fungi, and a substantial fraction of the initial mass (20–35%) may eventually be stored in the forest floor. In contrast, white-rot fungi decompose all wood constituents leaving little residue. The type of fungi present may also influence the decomposition rate; there is evidence that white-rots decompose wood faster than brown-rots (Harmon et al. 2005), although the generality of these observations needs to be further tested.

8.2.5   CWD Amounts in Old-Growth Forests

The amount of organic matter in woody detritus observed in old-growth forests spans several orders of magnitude, ranging from around 10 to 350 Mg ha^{-1} (Harmon et al. 1986, 2001; Harmon 2001). This range reflects differences in input rates versus decomposition rate-constants (Olson 1963). In general, as the NPP of old-growth forests increases, the live biomass, and the input of mortality increases. Thus, more productive old-growth forests can be expected to have more woody detritus than less productive ones. Those old-growth forests with lower decomposition rate-constants should have more woody detritus than those with higher ones; moreover, decreases in decomposition rate-constants can compensate to some degree for lower inputs rates via tree mortality. To eliminate productivity related differences, it is useful to compute the ratio of dead to live wood in old-growth forests (Harmon et al. 2001; Harmon 2001). These ratios average from 0.15 for tropical and deciduous forests to 0.25 for evergreen conifers, although values as low as 0.03 and as high as 0.65 have been observed (Harmon 2001). Aside from making an inventory of dead versus live wood stores, the dead to live wood ratio can be determined from the ratio of the mortality and decomposition rate-constants (Harmon 2001). Based on average mortality and decomposition rate-constants of forests, this ratio could range between 0.09 and 0.31, slightly wider than the means indicated by inventories. The dead to live wood ratio also indicates the potential for woody detritus to increase when a stand-level disturbance occurs. The range in mean ratios observed implies a four- to seven-fold increase depending on the forest.

8.3   Theoretical Trends

As discussed above, many processes control woody detritus mass over succession. Since these processes interact one can gain considerable insight by using a very simple model (Table 8.1) that tracks three carbon pools: (1) the live trees C_L, (2) the legacy woody detritus created and left by a disturbance C_{DL}, and (3) the de novo wood created from regular mortality of the live trees C_{DN}. In this model, the live tree mass is controlled by the balance of inputs via aboveground woody NPP (here simply termed NPP) and the output via regular mortality. It is assumed that disturbances kill all the trees in a stand. Legacy woody detritus mass is controlled by inputs from disturbance and the amount of previously dead material that is left by the disturbance. Losses from this pool are controlled by decomposition. De novo woody detritus mass is controlled by inputs from regular mortality (including those from gap formation) versus losses from decomposition. This model was pro-grammed on a spreadsheet using an annual time step. The following simulations examine the effects of the various processes described in Sect. 8.2 on the pattern of woody detritus mass over time. In the first simulation, I assumed all the

Table 8.1 Equations and parameters used in the basic model simulations to examine temporal patterns of aboveground woody detritus following a stand replacing disturbance. The parameters are typical of a Pacific Northwestern forest

State variable	Equation
Net primary production	$NPP_t = NPP_{max}[1 - \exp(-r_{NPP}t)]^{L_{NPP}}$
Live carbon	$C_{L,t} = C_{L,t-1} + NPP_t - m \cdot C_{L,t-1}$
Legacy woody detritus	$C_{DL,t} = C_{DL,t-1} \cdot \exp(-k \cdot t)$
De novo woody detritus	$C_{DN,t} = C_{DN,t-1} + m \cdot C_{L,t} - k \cdot C_{DN,t-1}$
Parameters[a]	Value/units
Maximum NPP (NPP_{max})	3.5 Mg C ha^{-1} year^{-1}
Rate of NPP increase (r_{NPP})	0.1 year^{-1}
Lag parameter for NPP increase (L_{NPP})	2
Mortality rate-constant (m)	0.01 year^{-1}
Decomposition rate-constant (k)	0.02 year^{-1}

[a]Deviations in these parameters for specific simulation runs are discussed in the text

rate-constants controlling processes are time invariant and call this the basic model. In the following simulations I modified how these rate-constants changed over succession; the rational and values for the particular modifications are described under each simulation. Since I am most concerned about the relative patterns of change, I simulated a Pacific Northwest system to illustrate the general points using the parameter values listed in Table 8.1 It is therefore best to consider the time axis to be relative; the development of tropical forests would be faster and boreal forests slower. For a more realistic evaluation of specific ecosystems I refer the reader to Chap. 5 by Wirth and Lichstein (this volume).

The case in which all the process rate-constants remain unchanged reveals the fundamental system dynamic (Fig. 8.5). As expected, legacy (residual) wood decreases during succession and de novo increases. The shape of the total woody detritus curve is highly dependent on the amount of legacy wood removed. When none of the legacy woody detritus is removed, there is a reverse J-shaped curve with the amount of woody detritus in the middle stages of succession falling below that of the later stages (Fig. 8.6a). The depth of this mid-successional low point depends on the rate at which trees re-establish (Harmon et al. 1986); with slower rates of re-establishment having a lower dip than faster rates. While this type of curve is generally referred to as U-shaped in the literature, this is because many studies missed the initial period of very high mass. Regardless of name, the shape of the curve changes as the amount of legacy removed increases. When the amount of legacy wood equals that found in old-growth forests, the curve becomes more U-shaped, with the heights of the two arms more symmetrical than for the reverse J-shape. When all the legacy wood is removed the shape changes to a S-shape reflecting the sigmoid curve of the underlying live biomass. It should be noted that the shape of these curves is modified by the degree disturbance creates a distinct pulse of input. Simultaneous input creates the initial sharp peaks simulated here. However, Lang (1985) demonstrated that when the disturbance-related pulse is
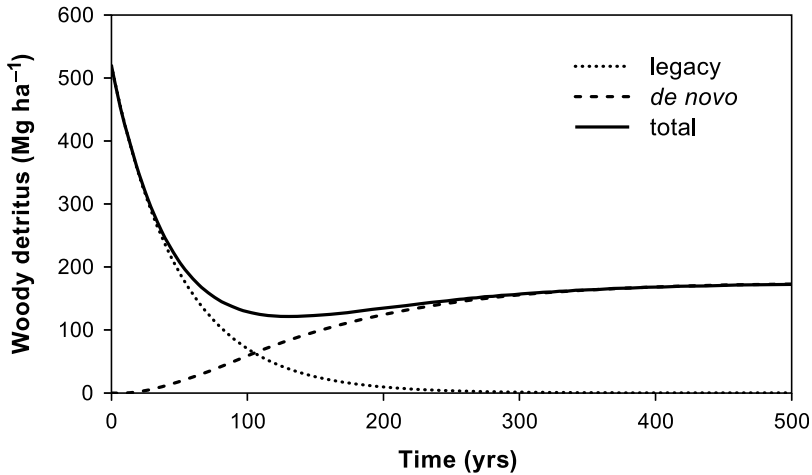
Fig. 8.5 The basic model of woody detritus mass during succession. Legacy mass is left by the disturbance and decreases as a negative exponential. De novo wood is continuously created by mortality in the new forest and also decomposes as a negative exponential function. Note that, in this example, dead wood in the old-growth stage >250 years is composed entirely of de novo wood

spread over time, the initial peak exhibits a broad shoulder and thus woody detritus mass can gradually increase as the disturbance progresses. Once the disturbance input ends, woody detritus mass decreases following the trend predicted by the basic model.

Based on classic ecosystems theory (e.g. Olson 1963) the average amount of woody detritus in old-growth forests will increase as decomposition rate-constants decrease and the mortality rate-constants increase (see Sect. 8.2.4). However, the shape of the successional curves is also dependent on the decomposition and mortality rates of the ecosystem in question. If all the legacy wood is left, then increasing the decomposition rate-constants causes the minimum to occur earlier and reach a lower value. As legacy wood is removed, the timing of the minimum is less subject to change than the value of the minimum; the latter decreases as the decomposition rate-constant increases. Changing the mortality rate-constant tends to have the opposite effects. When all the legacy wood remains, increasing the mortality rate-constant increases the minimum value and delays its timing. As legacy wood is removed, the effect of increasing the mortality rate-constant is to shorten the time required to reach the minimum, but does not seem to greatly influence the minimum mass.

The effect of delaying forest regeneration was explored by changing the timing of NPP recovery to 30 years. As long as some legacy wood is left by the disturbance, a delay in regeneration lowers the minimum mass curves (Fig. 8.6b). However, as the fraction of legacy wood left decreases, a regeneration lag also causes the minimum to occur later in succession. This is because the more important de novo wood becomes, the stronger the lag on regular mortality inputs becomes. The effect of
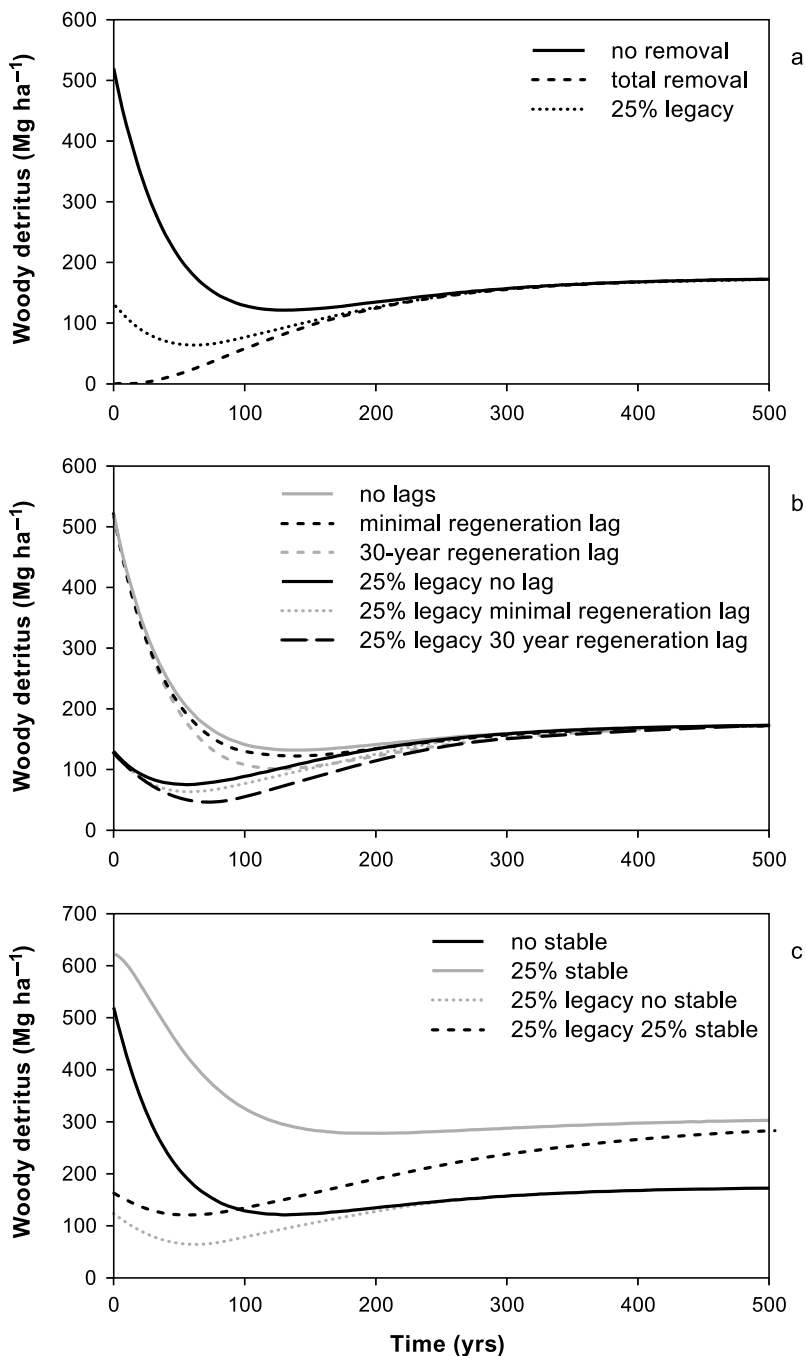
Fig. 8.6 a Predictions of the basic model with various proportions of remaining legacy wood. The shape of the mass curve changes from a reverse-J, to a U, and to an S-shape as more legacy wood is removed. **b** Effect of regeneration lags on the mass of woody detritus for the

regeneration lags is most noticeable when all the legacy wood is removed as it parallels the lagged curve for live biomass. This set of experiments indicates that depending on the amount of legacy wood and the length of the regeneration lag, old-growth woody stores may be the highest (no legacy wood) or lowest (abundant legacy wood and no regeneration lag) during succession.

If brown-rot fungi are the primary decomposers in a forest, then a stable material (i.e. lignin) may be left during decomposition. To simulate this situation I assumed an equivalent of 25% of the wood formed to be stable material, based in part on the fraction of lignin in the wood. I also assumed that this stable material decomposed at 0.005 year^{-1}, which is one-quarter the rate-constant assumed in the basic model. The inclusion of a stable fraction leads to more woody detritus during succession regardless of the amount of legacy woody (Fig. 8.6c). This indicates that old-growth forests dominated by brown-rot decomposers should have more woody detritus than those with only white-rots. This difference should increase as the fraction of stable material increases and the difference in decomposition rates between the stable and other wood increases. The presence of a stable fraction can change the successional curve shape. For example, in the case where legacy wood is reduced by 75%, the presence of a stable fraction leads to a very long period of woody detritus accumulation into the old-growth stage.

As stated in Sect. 8.2.1, the form of mortality and the climate may create lags in legacy wood decomposition. This would be typical of disturbances creating standing dead trees in a dry climate. To simulate this situation I assumed legacy woody detritus had a lag of 10 years before maximum rates of decomposition were reached. In an environment with high precipitation and/or low evaporation rates, the converse might happen with standing dead wood decomposing faster than downed wood. Specifically, in cases where disturbance created standing dead wood, the legacy wood might decompose slower as wood fell to the ground. To simulate this case I allowed standing wood to decompose at twice the rate of downed wood and had all standing wood fall to the ground between 10 and 20 years after disturbance. These simulations indicate that lags have a greater effect on the temporal pattern of woody detritus than an initial period of elevated decomposition rates (Fig. 8.7a). As would be expected, lags increase the amount of woody detritus during succession relative to when decomposition rate-constants are unchanging, causing the reverse J- and U-shapes to become shallower. If the decomposition lag is extended (in these simulations to 30 years), it is even possible for the lag to offset the expected dip in the curves. Thus it would appear that when there are long lags in decomposition of residual wood, that woody detritus mass is likely lowest in old-growth forests whenever there is little removal of legacy wood.

Fig. 8.6 (Continued) case where either all or 25% of the legacy remains. The *no lags* simulation represents the basic model. **c** Effect of including a stable phase of wood decomposition for the cases where either all or 25% of the legacy wood remains. The *no stable* cases represent the basic model
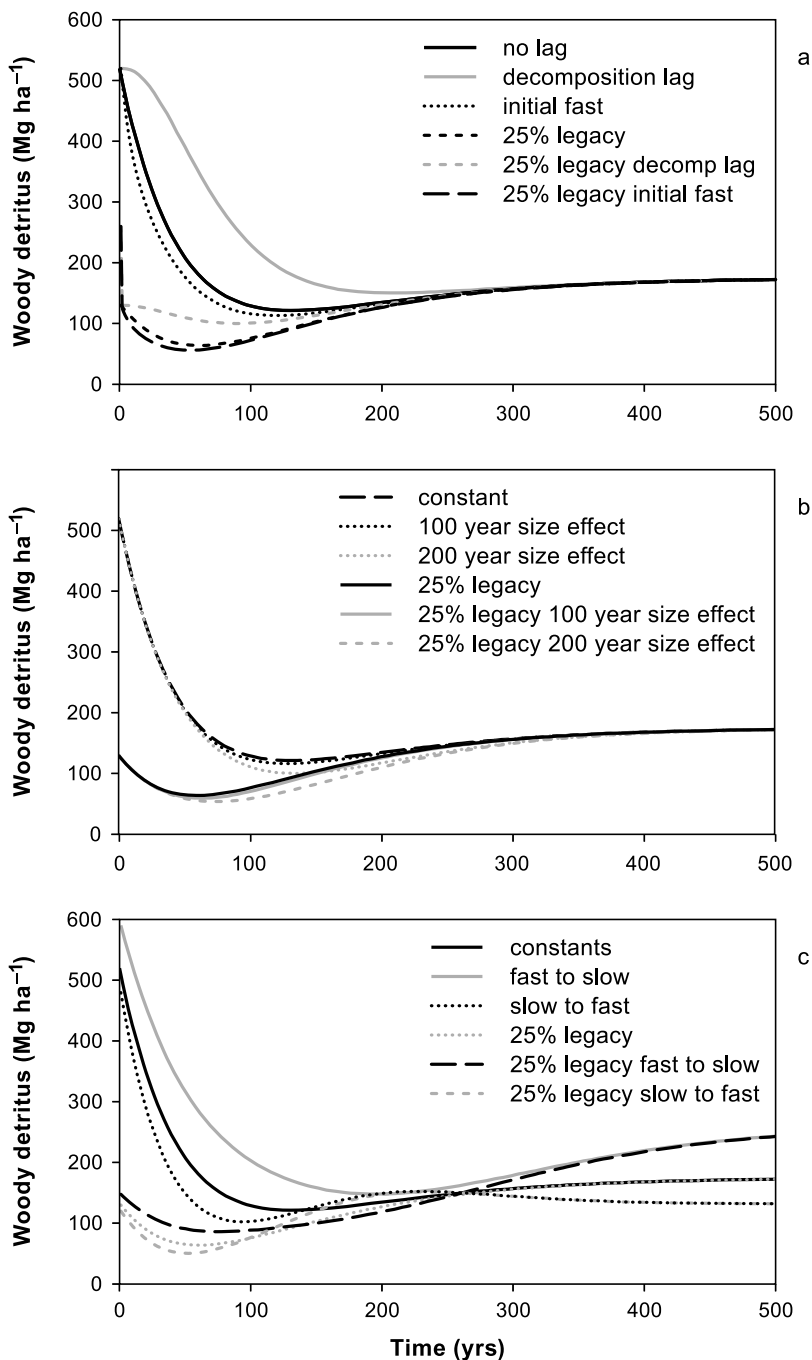
Fig. 8.7 a Effect of changing decomposition rates due to changes in position (i.e., snags becoming logs) for the case where either all or 25% of the legacy wood remains. The disturbance was assumed to create snags. In the decomposition lag case, snags were assumed to decompose slower

Decomposition rate-constants of the de novo woody detritus is likely to change over time, because as the forest grows the size of woody detritus also increases, leading to a decrease in decomposition rates assuming there is sufficient moisture. To simulate this I decreased the rate of decomposition of de novo woody detritus five-fold as forests aged, in one case up to 100, and in another case up to 200 years (Fig. 8.7b). Simulations indicate that the longer it takes for decomposition rates to decrease, the longer and deeper the decline in woody detritus during the middle stages of succession. This is because the higher decomposition rate-constant early in succession delays the rate at which de novo wood accumulates. If the decrease in decomposition rates associated with size increase takes 100 years or less, then the effect of decomposition-size dependence is relatively minor. If this decrease in decomposition rates takes 200 years, then the mass is around 20% lower at the minimum point and this minimum occurs around 20 years later. Increasing the difference in decomposition rate-constants between the smallest and largest wood ten-fold (or twice the initial experiment) does not change the timing of the minimum mass, although it does reduce the minimum mass amount. In the case of the 100- and 200-year transitions periods, the minimum is 10% and 30% lower, respectively than the basic parameterization. A ten-fold difference from the smallest to largest pieces of wood is probably at the upper limit of differences one could expect, and it is also likely that the majority of the changes in size would occur in less than 200 years. These simulations show that, while there is a size effect, it is small compared to other factors.

Another change during succession is caused by replacement of one tree species with another, particularly if the decomposition rate-constants of the species differ. In this set of simulations I assumed that species decomposition rate-constants differed from each other by a factor of two, and that half-way through the simulation the mixture of the species was 50:50. I examined two cases, one in which a decay-resistant species was replaced by a decay non-resistant species and vice versa. These simulations indicated that the potential effect of species replacement is quite complex, causing secondary periods of woody detritus loss (Fig. 8.7c). This complexity results from the fact the late-successional species dominates the legacy wood and the early-successional species dominates the early phases of the de novo wood. This causes the effects of the early- and late-successional species to offset each other somewhat early in succession; specifically, as the fraction of legacy wood left increases the late-successional species comprises more and more of woody detritus in the early phases of succession. The simulations indicate that the effect of the early-successional species is strongest in the middle phases of

Fig. 8.7 (Continued) than logs, simulating a dry climate. In the initial fast case, snags were assumed to decompose faster than logs, simulating a very wet climate. **b** Effect of size changes in decomposition rates assuming smaller diameter wood decomposes faster than large diameter wood for the case where either all or 25% of the legacy wood remains. The transition from small to large diameter wood takes either 100 or 200 years, representing different rates of growth. **c** Effect of changing species composition during succession on woody detritus mass for the cases where either all or 25% of the legacy wood remains. *Fast to slow* indicates a fast decomposing species ($k = 0.0265$ year^{-1}) is replaced by a slow one ($k = 0.0135$ year^{-1}) and vice versa

succession because de novo input approaches the maximum at this point. In the case where the late-successional species decomposes slowly, the legacy wood is greater than when the late-successional species decomposes quickly. This is because of differences in the old-growth store. When the pioneer species decomposes slowly, it is possible to have a peak in woody detritus mass in the middle of succession, and this peak becomes more evident as the fraction of legacy wood left increases and as the difference in species decomposition rates increase. These simulations indicate that when old-growth trees species have faster decomposition rate-constants than early-successional species, it is possible for woody detritus stores to decrease as stands enter the old-growth stage.

Declines in NPP as forests reach the later stages of succession were explored by decreasing NPP by 20 and 50% between an age of 150 and 300 years. As with species change, declining NPP can introduce complexity into the woody detritus temporal pattern (Fig. 8.8). The greater the decline in NPP, the lower the mass after the disturbance, regardless of the amount of legacy wood is left (this is because mortality inputs are lower in the old-growth phase). The decline in NPP also leads to a secondary decline in woody detritus that is proportional to the decline in NPP. These simulations indicate that either a reduction in NPP or an increase in decomposition rate-constants as forests age could lead to mid-successional forests having more woody detritus than old-growth forests.

Repeated disturbance was explored by changing the interval of disturbance from 500 years in the base case to 50 and 100 years. In one set of simulations all the legacy woody detritus was retained, and in another, representing intensive forestry, 75% of the legacy wood and 50% of the regular mortality was removed by harvest. These simulations indicate that the shorter the disturbance interval, the less woody
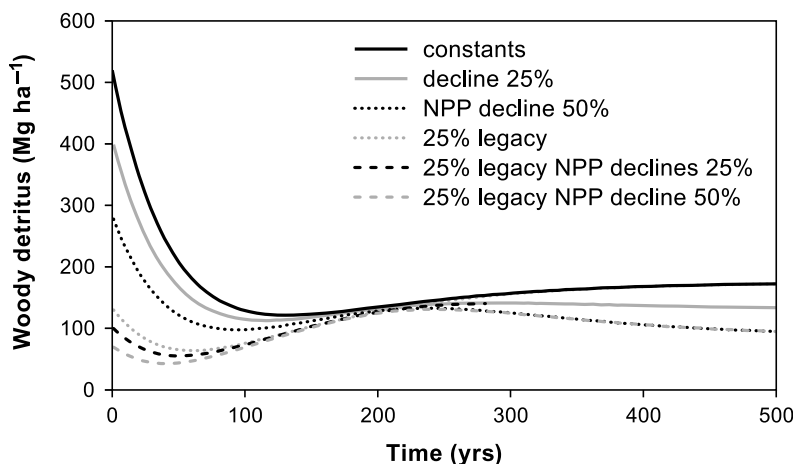

Fig. 8.8 Effect of a 25% and 50% decline in net primary production (NPP) during the latter phases of succession on woody detritus mass for the cases where either all or 25% of the legacy wood remains

detritus occurs during succession (Fig. 8.9a). This pattern is due to two factors. First, the shorter the interval, the smaller the forest is when it is disturbed and less is input as legacy wood. Second, the shorter the interval, the less likely that de novo wood will accumulate. When the interval of disturbance was reduced to 50 and 100 years, the average amount of woody detritus is 45 and 59% of the average of the 500 year interval, respectively. Harvest of legacy and de novo wood greatly reduces the amount of woody detritus, with the maximum never exceeding the amount occurring during the natural succession (Fig. 8.9b). Moreover, the average mass of woody detritus of intensively harvested forests is 10% and 17% of the 500 year natural cycle for 50 and 100 year harvest intervals, respectively. These simulations may indicate why old-growth forests are often considered to have the maximum store of woody detritus. However, the other simulations indicate that
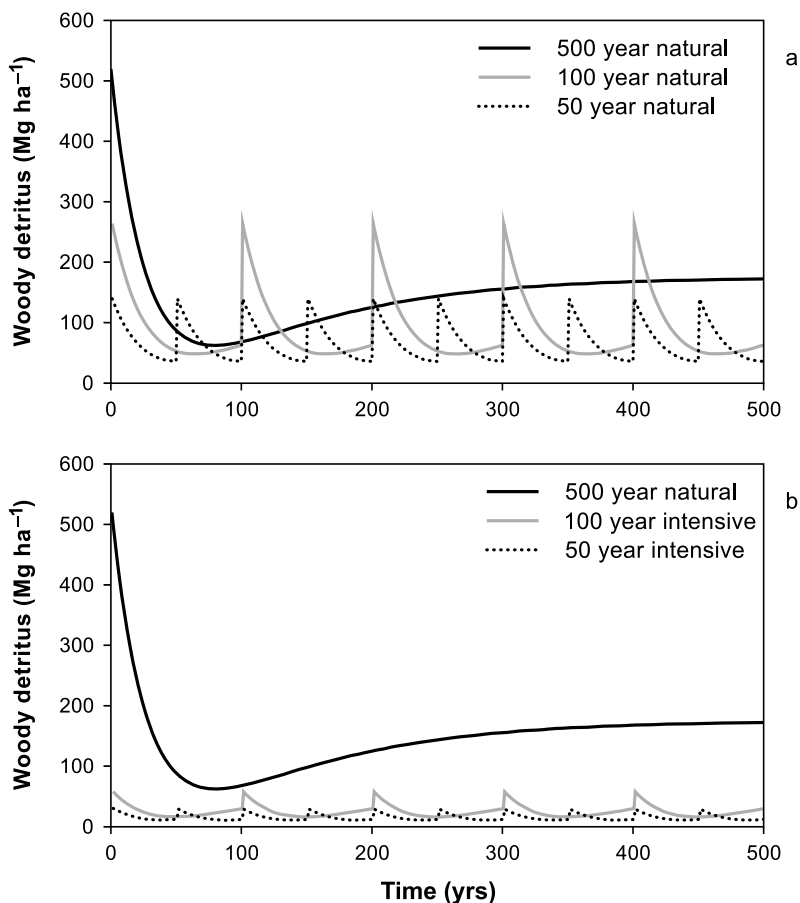

Fig. 8.9 Effect of repeated disturbance on woody detritus mass for (**a**) natural disturbance cycle that leaves all the legacy wood, and (**b**) an intensive harvest system that removes 75% of the legacy and 50% of the mortality of the post-disturbance forest

following natural disturbance this may not be the case, especially if considerable legacy wood is left by the disturbance. Other factors, such as the length of regeneration lags, differences in the decomposition rates of early and late seral trees, and the degree to which NPP decreases as stands age, may cause old-growth forests to have less than the maximum stores of woody detritus during succession.

8.4 Comparison of Theoretical and Observed Temporal Trends

8.4.1 Studies Matching the Classic Model

Both reverse J- and U-shape trends in woody detritus biomass, predicted by the so-called classic model, have been commonly observed in field studies using chronosequences (Table 8.2, and see Fig. 5.9 in Chap. 5 by Wirth and Lichstein, this volume). While the U-shaped curve is more commonly observed, this is often due to the fact that many studies do not sample directly after disturbance and consequently miss the initial peak in mass.

The Pacific Northwest is one of the best studied regions regarding woody detritus successional patterns. Agee and Huff (1987) sampled stands 1 to 515 years after catastrophic fires in moist Pacific Northwest conifer forests and found a distinct reverse J-shaped curve with initial aboveground woody detritus 7.5 times higher than the minimum amount of woody detritus that occurred in forests 110 years of age. Intermediate amounts of woody detritus, equivalent to one-third the initial pulse, were present in forests 515 years after disturbance. Spies et al. (1988) reported a U-shaped woody detritus mass curve in moist conifer forests of the Pacific Northwestern United States. Spies et al. (1988) estimated the initial mass of woody detritus would have been at least nine times larger than at 40 years of age, indicating a reverse-J shaped for fire disturbed stands. Accumulation of de novo wood in this system started 50 years after the disturbance, whereas most of the legacy wood had disappeared within 100 years, leaving the lowest mass in forests of 100–150 years of age. Similar patterns were observed by Janisch and Harmon (2002) in a chronosequence of harvested and fire-disturbed conifer forests in southwestern Washington State. For forests originating from harvest, a U-shaped curve of woody detritus mass was followed, with de novo wood beginning to accumulate noticeably after 70 years. This also roughly corresponded to the time of the minimum mass. By using live masses observed in old-growth forests and observed decomposition rates of legacy wood, the analysis of Janisch and Harmon (2002) indicated that a fire-disturbed forest would have followed the reverse-J shape.

Several eastern hardwood forests appear to follow the classic model prediction. Gore and Patterson (1986) examined the mass of downed woody detritus in cut and uncut northern hardwood forests in New England and found evidence for a reverse-J shaped curve with a minimum between ages of 20 and 60 years. Examining their regional

Table 8.2 Summary of findings from woody detritus chronosequence studies. Some of the individual chronosequences are also shown graphically in Wirth and Lichstein (Chap. 5, Fig. 5.10)

Biome	Main genera	Time period (years)	Stands (number)	Disturbance	Temporal pattern	Reference
Standing and downed woody detritus sampled						
Conifer	Abies	0–70	37	Fire-wave	Reverse-J[a]	Lambert et al. (1980)
Conifer	Abies, Picea	33–110	26	Harvest	U-shaped	Sturtevant et al. (1997)
Conifer	Picea	4–152	7	Fire	Reverse-J[a]	Manies et al. (2005)
Conifer	Picea	20–250	91	Fire	Reverse-J[b]	Harper et al. (2003, 2005)
Conifer	Pinus	2–383	16	Fire	Reverse-J	Wirth et al. (2002a, b)
Conifer	Pinus, Picea, Abies	11–426	71	Fire	Reverse-J	Clark et al. (1998)
Conifer	Pseudotsuga, Tsuga	1–515	6	Fire	Reverse-J	Agee and Huff (1987)
Conifer	Pseudotsuga-Tsuga	40–90	166	Fire	Reverse-J	Spies et al. (1988)
Conifer	Pseudotsuga-Tsuga	8–500	36	Harvest, fire[c]	U-shape	Janisch and Harmon (2002)
Deciduous	Acer, Fagus, Betula	10–>110	23	Harvest	Reserve-J	Gore and Patterson (1986)
Deciduous	Acer, Fagus, Betula	1–110	6	Harvest	U-shape	Roskoski (1980)
Deciduous	Nothofagus	2–191	9	Mixed	Mixed	Carmona et al. (2002)
Deciduous	Quercus, Carya, Acer	70–110	10	Harvest	U-shaped	Shifley et al. (1997)
Tropical	Mixed	9–>200	23	Slash and burn	U-shaped	Saldarriaga et al (1988)
Downed woody detritus sampled						
Conifer	Mixed[d]	0–360	4,840	Fire	Mixed	Brown and See (1981)
Conifer	Picea	1–30	3	Wind	Reverse-J	Knohl et al. (2002)
Conifer	Pinus	0–79	5	Harvest, fire[e]	U-shape	Howard et al. (2004)
Deciduous	Nothofagus	10–>150	12	Wind	Reverse-J	Davis et al. (2003)
Deciduous	Quercus, Carya, Acer	1–100	3	Harvest	Reverse-J	Idol et al. (2001)

[a]With a broad initial peak
[b]With decline in the old-growth phase
[c]Stands >60 years disturbed by fire
[d]Pinus, Pseudotsuga, Tsuga, Abies, Larix
[e]Oldest stand disturbed by fire

synthesis in more detail indicates that there is some evidence for a U-shaped curve as well, particularly for the data from Roskoski (1980), which were from a series of harvested stands where much of the live biomass was harvested. A reverse-J pattern of woody detritus mass was also found by Idol et al. (2001) in oak-hickory forests of Indiana with a minimum mass in forests 16–100 years after harvest.

There appears to be some support for the classic model in Russian forests. Wirth et al. (2002a, 2002b) observed successional changes in woody detritus in Siberian pine forests disturbed by fire that are consistent with the reverse J-shape curve with initial woody detritus stores six-fold higher than that found in forests over 100 years of age. Legacy wood in this system had largely decomposed by 100 years, and woody detritus appears to increase between the ages of 100 and 400 years of age, despite the fact that recurring surface fires appear to consume about 75% of the de novo wood.

South American forests observations support the classic model to some degree. Saldarriaga et al. (1988) found a U-shaped temporal pattern in woody detritus following slash-and-burn agriculture in moist tropical forests of Columbia and Venezuela. Although the youngest stands sampled were 9–14 years since clearing, considerably more woody detritus mass was found here than in forests that had been disturbed 20 years before. Interestingly, the accumulation of de novo wood appears to start soon after this point in time because forests disturbed 30 years ago have almost as much woody detritus as those disturbed 9–14 years before. Carmona et al. (2002) found support for a range of curves in temperate forests in Chile, with stands that had been logged having 4–50% of the woody detritus mass of that found in those that had only been burned. In stands with substantial removal of wood, early-successional forests had lower amounts of woody detritus than mid-successional or old-growth forests, suggesting an S-shaped accumulation curve. In forests disturbed only by fire, a reverse J-shaped curve appeared to be followed, with mid-successional forest having the least, and unlogged old-growth intermediate amounts of woody detritus mass.

8.4.2   Studies Not Matching the Classic Model

There have been cases where the reverse-J and U shaped curve for the temporal development of woody detritus mass has not been followed. This often occurs as an artifact of woody components measured or how the data are reported. For example, Brown and See (1981) found little consistency of temporal trends; however, they only considered downed woody detritus. This lack of consistent pattern occurred even when the mass for different forest types was normalized, with some areas exhibiting S-shaped curves, others U-shaped curves, and others having a peak in the intermediate stand ages. This inconsistency might be expected depending on the amount of downed wood removed by disturbance and the fact that disturbances creating standing dead trees would result in major input to downed woody detritus many years after the disturbance. For example, Tinker and Knight (2000) found that

downed woody mass was similar in recently burned or harvested lodgepole pine forests in Wyoming. However, when standing dead material was included, burned forests contained at least twice the mass of woody detritus suggesting that Brown and See (1981) might have seen a reverse J-shape in stands originating from fire had they accounted for snags. Clark et al. (1998) observed a U-shaped pattern of log volume following fire in spruce-fir and pine sub-boreal forests of British Columbia. Snag basal area followed a reverse-J shape in these same forests, but given the different units reported it is difficult to determine what the overall pattern was; in relative terms, logs and snags seemed least abundant in forests of 50–100 years of age.

Another cause for the lack of correspondence to theoretical trends is that only a segment of the succession was examined. For example, Franklin (1982) observed a very gradual increase in woody detritus for forests of 150–1,000 years of age, which is consistent with the later portions of the reverse J-shaped curve. Given the live biomass observed in these stands, it is very likely that the early-successional woody detritus mass would have been four- to six-times higher than they observed in the older ages. In another case, Knohl et al. (2002) observed an exponentially decreasing pattern of woody detritus mass after windthrow in a Russian boreal forest. However, the oldest forest examined was 28 years of age, and thus far younger than required for significant de novo woody detritus to accumulate. A similar decrease in woody detritus over succession was observed by Howard et al. (2004) in harvested southern boreal Jack pine forest of Canada, where mass decreased at least three-fold from an age of 0 to 29 years. Given that de novo woody detritus stores were five-fold higher in a 79-year-old forest that had been disturbed by fire, this might indicate that more of an S-shaped (as opposed to reverse J-shape) curve occurs in these forests following harvest. Shifley et al. (1997) reported that second-growth Missouri hardwood forests contained half the volume of downed wood of old-growth forests. This pattern is consistent with the accumulation of de novo wood, although without additional age classes it is difficult to ascertain. Davis et al. (2003) observed a negative exponential decrease to an asymptote in southern beech forests of New Zealand, and while this might be consistent with a reverse J-shaped curve, it is quite different from the classic version of this curve, with the minimum and oldest forest masses being similar.

In some cases, the peak of initial woody detritus can be quite broad, causing a departure from the classic model. This broad peak can be caused by the nature of the mortality or the presence of decomposition lags. Lambert et al. (1980) observed a variation of the reverse J-shape in a balsam fir forest in New England that was subject to fir-wave mortality. However, the pulse of input was drawn out over a decade by the gradual mortality process. After this pulse occurred, the mass curve displayed a decrease to a minimum in 50 years after the onset of mortality. In fire-killed black spruce forests of Canada, Manies et al. (2005) observed that woody detritus mass remained relatively constant for the first 30 years. This was probably caused by the very low decomposition rate of snags, but once these fell to the ground mass declined rapidly, reaching a minimum 70 years after the fire. Between

70 and 150 years after the fire, a small increase of woody detritus mass indicated a variant of the reverse-J shape.

Not all the U-shaped curves "confirmed" in the literature are strictly supported by the reported data. Sturtevant et al. (1997) reportedly found a U-shaped curve of woody detritus volume in a chronosequence of harvested stands in boreal forest of Newfoundland; however, the curve suggested by their observations is more of an S-shape. This is likely caused by the fact that their youngest stand sampled was 33 years of age and, after 50 years, most of the woody detritus was de novo wood. Had younger forests been sampled, it is most likely their assertion of a U-shaped curve would have been supported directly.

There is some evidence that temporal patterns of woody detritus mass can be quite complex during succession with secondary periods of decline. Harper et al. (2003, 2005) reported that black spruce forests of Quebec do not follow the classic temporal patterns. Those growing on sandy soils appear to follow the reverse J-shape for log volume, but since snags were reported in terms of basal area it is difficult to estimate a total volume pattern. Those forests growing on clay soils show an initial decrease in log volume followed by an increase in intermediate stages, with a decline as forests age further. Combining this data with the snag volume reported in Hély et al. (2000) suggests that the overall pattern of woody detritus abundance is similar. It seems likely that there is a decline in total woody detritus volume associated with paludification (i.e. the process of bog expansion resulting from rising water tables as a consequence of peat growth) given that live biomass in these forests declines from age 100 years to 200 years (Paré and Bergeron 1995). This would be similar to the theoretical pattern observed when NPP declines greatly as stands age (Fig. 8.8). Since paludification also decreases the amount of live wood present at the time of the disturbance, the low amounts present 32 years post-disturbance might be a consequence of this change in NPP as well (Hély et al. 2000). Sturtevant et al. (1997) also suggested that late succession boreal forests in Newfoundland could have a decline in woody detritus mass associated with changes in structure from even- to uneven-aged stands.

8.5   Effect of Management

There is little question that timber harvest, salvage logging, and intensive management (i.e. harvesting over short intervals, thinning, and salvage of mortality) can reduce the amounts of woody detritus found at different stages of stand development as suggested by the basic model presented in Sect. 8.3. While shortening the disturbance regime can reduce the amount of woody detritus, the interval between disturbances must be greatly reduced for this to be the dominant effect. For example, Wright et al. (2002) examined two disturbance regimes in Oregon that differed four-fold in the frequency of fires. Interestingly they had very similar amounts of woody detritus averaged over a landscape. This suggests that the effect of management is due largely to the reduction of legacy wood. Pedlar et al. (2002)

found that recently burned hardwood-conifer mixed forests in Ontario contained three times the woody detritus of those that had been recently clear-cut harvested. However, they also found that pure conifer stands created by management contained one-sixth to one-ninth the volume of woody detritus of mixed forests. Duvall and Grigal (1999) compared chronosequences of naturally disturbed versus managed stands in the Lake States region of the United States and found that the largest relative differences occurred early in succession, with managed (i.e. harvested stands) having one-fifth the amount of woody detritus of natural stands. By the end of the harvest rotation interval examined, managed stands contained one-third the woody detritus biomass of natural stands.

8.6   Consequences for Net Ecosystem Carbon Balance

The amount of legacy wood remaining at the start of the succession has a major impact on the pattern that net ecosystem carbon balance (NECB – Chapin et al. 2006) follows after disturbance. The basic model suggests that if legacy wood is left, the initial values of NECB are negative (a source to the atmosphere); however, as the amount of legacy wood decreases, the source phase (i.e. the period that NECB is negative) is weaker in magnitude (i.e., the absolute size of the flux) and ends earlier (Fig. 8.10). The basic model also predicts that the source phase is shorter but of much higher magnitude than the sink phase. While it is common to think of woody detritus always being a source of carbon to the atmosphere, the basic model predicts that the accumulation of de novo wood actually increases the strength of the carbon sink in the later phases of succession [cf. Chaps. 5 (Wirth and Lichstein) and 21 (Wirth), this volume]. The majority of published studies on forests disturbed by harvest or natural processes indicate an increase in carbon
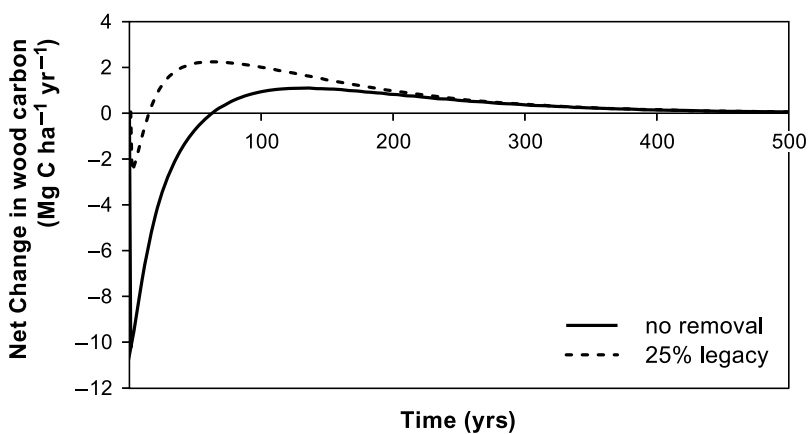

Fig. 8.10   Net change in total woody carbon stores predicted by the basic model for the case when all or 25% of the legacy wood remains

stores associated with accumulation of de novo dead wood during the middle stages of succession (8.2). The simulation experiments conducted here indicate that this pattern is also likely to be true for all cases except when: (1) a fast-decomposing species replaces a slow-decomposing species during succession, or (2) NPP decreases markedly during the latter phases of succession. In both these cases a secondary period of net carbon loss as the forest enters the old-growth stage is possible. At first glance, removing legacy wood appears to create a net sink over the succession, but this conclusion is misleading unless the majority of the wood removed by harvest is permanently stored. A more realistic interpretation would account for the fate of removals in terms of decomposition, losses in manufacturing and use etc., all of which would tend to put the overall forest sector system (i.e. the forest and forest products) in carbon balance.

Unfortunately, few studies have measured atmospheric carbon flux directly after a disturbance. Knohl et al. (2002) measured atmospheric carbon exchange from July to October in a Russian boreal forest that had been windthrown 2 years prior to the study. The decomposition of woody detritus comprised one-third of the total ecosystem respiration and caused these forests to be a source of carbon to the atmosphere. Clark et al. (2004) measured atmospheric flux for a chronosequence of harvest slash pine plantations in Florida and found that recently harvested forests were a strong net source to the atmosphere, but by year 10 forests were net sinks.

Despite the number of chronosequences sampled for woody detritus mass, few studies have reported masses for both live and dead wood. Therefore the ability to check the predictions of the basic model regarding successional patterns of NECB is limited. In the Eurosiberian boreal region, harvested forests remain carbon sources to the atmosphere for their first 14 years (Schulze et al. 1999). Examining the trends in NEP (net ecosystem production) of fire-disturbed Scots pine forests in Siberia based on changes in live and dead biomass (including woody detritus) indicated that forests remained a net source to the atmosphere for 12–24 years and then became net sinks (Wirth et al. 2002b; Fig. 8.11). This analysis also indicated that NEP approached zero when the forest exceeded 300 years of age. In the Pacific Northwest, harvested forests remained a net source to the atmosphere for 15 years despite the removal of the majority of the legacy wood (Janisch and Harmon 2002). Using an empirical model, this study estimated that the source phase would have lasted 40–50 years if all the legacy wood had remained. In accordance with Wirth et al. (2002b), Janisch and Harmon (2002) estimated that the sink phase would have lasted until an age of 300 years. It would be expected that the timing of this pattern of source–sink switching would shorten approaching the tropics. This is supported by the findings of Gholz and Fisher (1982) from a 35-year long chronosequence in Florida slash pine forests. In this case, a harvested forest switched from a net source to a net sink with respect to the atmosphere within 3 years, with the source phase having twice the magnitude (i.e. absolute size of the flux) of the sink phase. Based on the rate of woody detritus loss between ages of 9 and 20 years, this rapid pattern of loss may also be true for the tropical post-pasture succession examined by Saldarriaga et al. (1988); however, their chronosequence started 9 years after disturbance and NECB is generally positive after this time.

8.7   Reducing Observational Uncertainties

The simulation model results show that many factors can change the pattern of woody detritus mass over succession relative to the classic model, but that the fundamental pattern shape is determined by the amount of legacy wood remaining. There are observations consistent with the classic model as well as those suggesting that other factors may influence the pattern of accumulation. However, it is also clear that observational studies could be improved to elucidate whether some of the more subtle predictions occur. There are several aspects that would make chronosequence data more useful in this regard:

1. To detect changes in the non-linear curves suggested by the models it is necessary to have more than three to four points in time sampled. The minimum times to sample would be: (1) right after the disturbance, (2) at the lowest point, (3) as the mass approaches the final maximum, and (4) for a very old forest to help check if there is a final decline in mass. Pinpointing these optimal times would be difficult in most systems and so a greater number of stand ages would be preferable. A related comment is that many studies sample chronosequences long after the disturbance occurred, thus making it difficult to determine the overall pattern of woody detritus mass accumulation.
2. Standing and downed debris need to be sampled and reported in the same units (either volume or mass) to quantify the total woody detritus trend. Ideally, tree mass would also be determined to allow to estimate changes in total wood carbon stores over succession. Sampling both standing and downed wood is important since there is no fixed relationship between their abundance, in part because disturbances and subsequent stand development can create a wide range of mixtures. Mass is the most appropriate unit to examine changes in carbon stores as volume is more conservative than mass (Duvall and Grigal 1999) and unless the degree of decay during succession can be estimated, a fixed volume to mass conversion factor, which would give the same relative temporal pattern as volume, must be used. Predicting the state of decay is difficult because it is likely to be highly non-linear and so it is necessary to record at least the average state of decay during sampling (and it is even better to determine this on each piece of wood sampled). Separating woody detritus into legacy and de novo wood is very helpful in creating an empirical model of the system (e.g. Spies et al. 1988) and interpreting the total mass pattern.
3. Chronosequences are a relatively fast way to determine successional changes in woody detritus mass; however, they have several shortcomings. It is extremely important that the productivity, soils, and climate of the stands sampled are as similar as possible. Since this is difficult to achieve, replicate stands of similar age helps to minimize some of these problems. It is also important that the disturbances initiating the succession are comparable. While mismatching disturbances in chronosequence (e.g. Howard et al. 2004; Carmona et al. 2002) can provide insights, the results have to be interpreted very carefully when the amounts of legacy wood differ. While using a time series to observe an entire

forest succession sequence is not realistic in the short-term, more could be learned by examining short-term changes of forests arranged along a chronosequence (Wirth et al. 2002a). This would result in a vector of change and allow one to quantify NPP as well as mortality inputs and decomposition rates, all of which would provide considerable insight into the processes underlying changes in mass. This approach has been applied to CWD decomposition and changes in forest floor mass to reveal far more details than can be detected using a chronosequence approach alone (Harmon et al. 2000; Yanai et al. 2000).

8.8   Conclusions

Woody detritus is an important, but until recently understudied, part of forest ecosystems. While often considered solely a feature of old-growth forests, woody detritus is present in all forests. The way this material changes over succession follows a predictable pattern, strongly influenced by the nature of the disturbance. The classic model predicts that when disturbances leave most of the legacy wood, the temporal pattern generally follows a reverse-J shaped curve and as legacy wood is removed this evolves to a U-shaped curve; if the entire legacy is removed it follows an S-shaped curve. This suggests that the commonly held view that old-growth forests always contain the maximum amount of woody detritus is not always true – the relative amount in old-growth forests depends strongly on the amount of legacy wood present at the start of succession. There are likely many variations on the classic model predictions; however, the only cases in which the basic shapes are not likely followed include: (1) the replacement of an early-successional species with high decay resistance by a late-successional species with low decay resistance, and (2) a forest in which there is a substantial decline in NPP late in succession. In these two cases there are possible secondary, but minor, decreases in woody detritus mass late in succession that may have implications for carbon sequestration. In the case of repeated harvest, the shorter the interval between disturbances and the more legacy wood that is removed, the lower the average woody detritus mass becomes. Chronosequence studies have confirmed the basic pattern predicted by the simple, classic model, and in at least one case suggest that a secondary decline in woody detritus mass due to decreases in NPP. Field studies using changes in mass and eddy flux also indicate the presence of woody detritus early after disturbance causes forests to be net sources to the atmosphere. The time forests switch from a net source to a net sink is controlled by the amount of legacy wood left and by the rate at which the new forest re-establishes. However, to fully understand these changes and their consequences for forest carbon balances, the temporal resolution of chronosequences needs to be improved and these measures need to be combined with measurements over time.

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