



The role of woody detritus in biogeochemical cycles: past, present, and future

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Abstract Woody detritus (WD), created by mortality of trees and their associated parts, is an important component of forested ecosystems with roles in energy flow, hydrologic and geomorphologic processes as well as in carbon and nutrient cycling. Although likely to be increasingly important as forest systems respond to climatic and other human induced changes, WD-related science is just beginning relative to other aspects of forested ecosystems. WD differs from other litter forms and soil in key ways (i.e., size range, rigidity, and heterogeneity) that limit the application of many paradigms currently used in studying and modeling decomposition. Thus, while temperature and concentrations of lignin and nitrogen are important controls, others factors related to moisture and its interaction with canopy openness, WD size, position relative to the soil surface, and decomposers need to be

better understood. Moreover, the unique attributes of WD decomposers need to be acknowledged as they have evolved over hundreds of millions of years to efficiently process this high lignin, low nutrient substrate. Given the heterogeneity within and among WD entities, WD behavior can be extremely non-linear, often resulting in cascades of activity rather than all or nothing behavior. Substantial improvements in understanding and modeling the respiration, fragmentation, leaching, and burial involved during WD decomposition are required to accurately assess the impact of global increases in tree mortality. Additionally understanding how the perception of WD-related processes changes with scale and organizational level is required to fully understand WD's role in past, present, and future biogeochemical cycling.

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Introduction

Woody detritus (WD) related to various trees parts that have died such as stems, branches, and coarse roots is now understood to be an important structural feature of forested ecosystems. The presence of this material influences many important processes in forested

ecosystems including those related to habitat, energy flow, water, and elemental cycles. Much of what has been learned about these roles has been “discovered” in the last 50 years. Elton (1966) was one of the first to assign importance to the presence of WD in forests, estimating that 20% of the vertebrate fauna have some habitat- or food-related relationship to this structure. Boussu (1954) recognized WD as an important element of fish habitat in streams; Anderson and Sedell (1979) did the same for aquatic insects. The first estimate of decomposition rates of large WD was made in 1970 (Odum 1970), but others soon followed (e.g., Harris et al. 1972) when assessing the stocks and flows of organic matter and nutrients in ecosystems became a major focus of the International Biome Project (IBP) (Worthington 1965; Reichle 1981). Heede (1972) and Keller and Swanson (1979) were among the first to recognize the geomorphic importance of WD. The first major review of the ecological function of coarse woody debris was published in 1986 (Harmon et al. 1986).

Much of what has been learned about the role of WD in biogeochemical cycles has accrued during the tenure of the journal *Biogeochemistry*. It is therefore appropriate to use this 35th anniversary volume to take stock of where this field of science currently lies and where it might be going. A growing motivation for new research in this field, aside from increasing knowledge in general, is to better understand the impact of higher rates of tree mortality related to climate and other human induced changes (Allen et al. 2010; Williams et al. 2013). In short, we need to move beyond documenting increases in mortality to understanding how the WD created by this process influences how ecosystems function. Therefore my objective in this commentary is to provide perspective on how WD contributes to biogeochemical cycling, what is known about the processes involved, and to advance concepts that might motivate future research. While my examples largely come from boreal and temperate forests, they hopefully represent phenomena found in all terrestrial ecosystems in which WD occurs regardless of biome or management intensity. I also have used models to illustrate hypothetical and conceptual relationships; and while admittedly they need further exploration and testing, they provide a possible starting point.

Historical perspective

Before moving on to the main thrust of this commentary, a deeper historical perspective may prove instructive on several fronts. While the “discoveries” outlined in the introduction are seemingly recent, it should be acknowledged that these processes and relationships have been going on since forested ecosystems arose on Earth 340 million years ago! The point is that we need to distinguish between when humans recognize something versus how long it has existed. In the case of WD, the scientific community, based on my review of ecological textbooks, models, and personal conversations, has had a hard time recognizing the existence of WD. The source of this reluctance is not entirely clear, but it may be related to the fact that while scientists strive to be objective, they are humans after all! Since humans are a practical species, they tend to focus on items of economic importance (live versus dead trees). Thus, the curious condition of a forest with live wood that lacks equivalent dead wood still seems to persist in many a scientist’s mind.

The presence of WD has greatly influenced the biogeochemical development of planet Earth. Lest this seem like a gross exaggeration consider the following. The formation of coal in the Carboniferous was largely due to the presence of WD, which failed to completely decompose because of either extremely moist environmental conditions (Nelsen et al. 2016) or the lack of white-rot fungi responsible for degrading lignin (Robinson 1990; Floudas et al. 2012). Although an inefficient process (Dukes (2003) estimated 4–39% of annual NPP of an Indonesian swamp forest enters the coalification process), the sequestration of so much carbon (C) depleted the atmospheric concentration of carbon dioxide to the point that global cooling was initiated (Feulner 2017). Since so much photosynthesis was not offset by respiration, the concentration of oxygen in Earth’s atmosphere rose to $\approx 30\%$ (Bernier 2003) likely increasing the preponderance of wildfires (Uhl et al. 2008). The appearance of WD also influenced biogeochemical cycling indirectly because its presence significantly altered riverine systems by armoring river banks and trapping sediments (Gibling and Davies 2012). If these major past effects of WD on Earth’s history have been under appreciated, then it is entirely possible current effects have been under appreciated as well.

Key features of woody detritus

WD represents a wide-range of materials from different origins. This includes stems (or alternatively trunks or boles), branches and twigs, and coarse roots. While largely associated with dead trees, WD is found on live ones as well: attached dead branches are a form of WD that can comprise a large fraction of the total aboveground WD mass (Nordén et al. 2004; Svensson et al. 2014). WD varies in its position relative to the soil: some is standing or suspended above the soil; some is downed in “contact” with the soil; and some is within the soil either because it is buried or originated in the soil (e.g., coarse roots). Finally, WD is usually subdivided into diameter classes, with < 1 cm typically included with the litter layer, 1–10 cm considered fine/small woody debris (FWD), and > 10 cm considered coarse/large (CWD).

As in many ecological systems, the behavior and structure of WD is dependent on the level of organization it is examined. In this commentary I therefore divide WD-related organizational levels into tissues (e.g., wood versus bark), individual pieces/parts, cohorts of multiple pieces/parts which were formed in the same time period, ecosystems which contain multiple cohorts formed at different times, and

landscapes that contain ecosystems differing in structure and/or disturbance history (Fig. 1).

The many forms of WD and its relatively slow dynamics make understanding WD challenging, but another complication is that WD is a material always in transition. By this I mean the properties of WD change markedly during the decay process (Fig. 2, supplemental information). The properties of live trees by comparison are relatively stable, and while trees increase in size as they grow, they largely add parts similar in character to those of earlier growth phases. It should be borne in mind that certain properties of WD, such as structural integrity, density, and size decline over time; whereas others, such as permeability, porosity, and degree of interface with soil increase. WD therefore encompasses many combinations of these properties that influence its functionality. This makes it challenging to make sweeping statements about WD’s behavior.

High lignin content is often emphasized as the distinguishing attribute of WD. While true, this misses other key differences with other kinds of decomposing organic matter including range in size, rigidity, and heterogeneity. Each has a strong influence on how WD functions. Although more specific instances of this are described in the next sections, a general overview reveals the following.

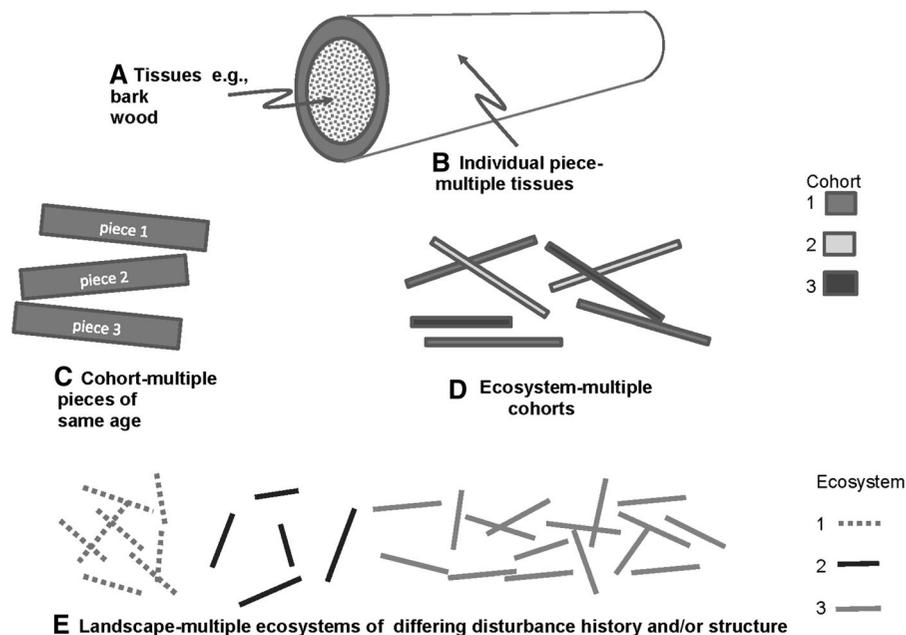


Fig. 1 Organizational levels of woody detritus

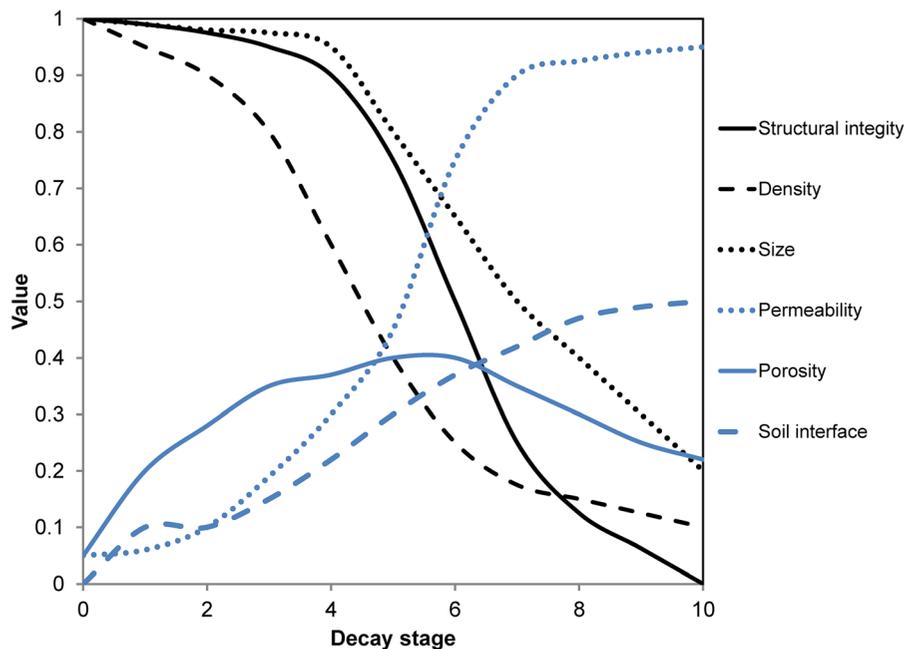


Fig. 2 Hypothetical changes in WD properties as decay proceeds (0: recently dead; 10: most advanced decay stage)

Size range

The range in size of WD (indicated by diameter) is orders of magnitude greater than for leaves (indicated by thickness). Despite the large range in the surface area of individual leaves, their thickness is limited because a key function of leaves is to exchange gases with the atmosphere and since that is achieved via diffusion leaf thickness must remain limited, typically < 1 mm (Niinemets 2001). Woody parts primarily function as support and transportation of water and solutes. Neither of these functions is impaired by large diameters, albeit they are affected by length and height (Ambrose et al. 2010). If we use the diameter of the largest existing tree as a guide to the upper diameter possible, the diameter of WD ranges from ≈ 1 mm to over 10,000 mm. Given that trees with diameters of up to 1000 mm are common, it follows that WD diameter generally exhibits a diameter range of at least three orders of magnitude in many forested ecosystems. This takes on functional significance because it influences the surface to volume ratio (this also varies 1000-fold) which strongly influences the flow of gases and water in and out of WD. Therefore the wide range in diameters means that some WD readily exchanges materials with its surroundings, whereas some does

not. Moreover, diameter influences the length of time decomposers need to colonize WD. For example, if fungi can grow in a radial direction 50 mm year^{-1} in a decomposing substrate, then most kinds of “dead” leaves can be colonized in far less than a year, but WD colonization might take between 1 and > 10 years depending on the diameter of the piece. While the colonization rate varies with biota and environment, the point remains that “dead” leaves and fine roots typically become biogeochemically active within a year, whereas some kinds of WD retain biogeochemically inactive zones for decades.

Rigidity

The higher lignin content of WD is not just of chemical importance, it has structural importance that significantly influences how WD functions. The evolution of lignin-bearing stems lead to rigidity that allowed greater height of plants and the evolution of the tree life-form (Weng and Chapple 2010). This rigidity also impacts the ecological function of woody detritus in that it suspends much of this material above the underlying litter and soil layers. This is clearest for standing dead trees and attached dead branches, which can remain many meters above the soil surface for

decades with important influences on ecosystem function (e.g., Schlesinger 1978). However, a close examination of downed WD indicates that the majority of material in this position is not in actual contact with the underlying soil (including the organic horizon). In routine tree mortality surveys conducted in the Pacific Northwest, the fraction of stem length in contact with the soil when added to the WD pool was $\approx 6\%$ (i.e., of 18,926 trees examined, 21% of stem length was downed and 31% of the downed length was resting on the soil surface (data from Franklin et al. 2020)). The reason, aside from the inherent rigidity of WD, is that newly formed WD often lands on previously formed WD, stems toppled by wind are often suspended at their base by soil and roots, and branches can suspend the smaller downed trees. Even when this does not occur, soil surface topography and profiles of the pieces of WD rarely perfectly conform to each other.

As decomposition proceeds, rigidity of WD is lost leading to fragmentation and collapse that increases contact with the upper soil horizons. Moreover, the subsequent fall of either newly formed WD or collapsing standing material can drive older, downed WD into the soil. WD can also become buried by smaller litter or overgrown by ground vegetation to become buried (Moroni et al. 2015). Based on the data on WD reported by Harmon et al. (2004) and the relative mass abundance of highly decayed classes of downed CWD ($\approx 30\%$ of downed CWD), I estimate that 33% of total WD mass is in contact with soil, but much of that mass (40%) is comprised of dead coarse roots, leaving 20% of the aboveground WD mass in contact with the soil. If surface area was considered, the proportion in contact aboveground would be even lower. While this estimate is very crude, and more ecosystem-specific estimates need to be made, the point is that the majority of WD is not directly interacting with soil in many forest ecosystems. Position is functionally important as it influences the microenvironment, but also determines the kinds of exchanges possible. Consider a common explanation of how WD functions in biogeochemical cycles: it immobilizes nutrients from the soil via fungal transport. However, if the majority of WD surfaces are not actually in contact with soil, then how is this mechanism possible for most WD?

Heterogeneity

Heterogeneity is an important aspect of many biological phenomena, but is not often considered in decomposition-related sciences. For example, while examination of most any anatomy textbook (e.g., Esau 1965) reveals leaves are clearly heterogeneous, this aspect of their structure has largely been ignored in favor of their overall characteristics such as average chemical composition and indices such as the lignin to nitrogen (N) and C to N ratios (e.g., Taylor et al. 1989). In contrast it is difficult to understand how WD functions without acknowledging the heterogeneity created by the distinctly different tissues related to this substrate. The term woody implies WD is wood; however, a substantial amount of it can actually be comprised of bark. For example, if the upper limit of relative bark thickness reported in Pausas (2015) is used (28 mm per 1 cm of diameter thickness), then up to 36% of some tree stems is comprised of bark. For two common genera, *Quercus* and *Pinus*, one would expect 2–12% of the volume to be bark (based on numbers reported by Pausas (2015)). This is an important concept because the chemical make-up of bark substantially differs from that of wood (Harmon et al. 1986) and because bark's outside position influences WD wetting drying cycles and exposure to water (Harmon and Sexton 1995).

Even within bark and wood there are substantial differences in tissues. Bark can be divided into outer and inner barks, respectively serving as passive protective covering versus active tissue involved in water and nutrient transport as well as secondary growth (Esau 1965). These differences are reflected during decomposition, with the inner bark decomposing more like leaves and the outer bark more like wood. Functional differences in living wood, reflected in sapwood versus heartwood, also influence how WD functions. Heartwood, a physiologically inactive tissue, lies within the sapwood leading to it having a different microenvironment, but also, in many tree species, heartwood contains chemical constituents that retard fungal growth (Scheffer 1966). Additionally, in branches and coarse roots, some heartwood becomes impregnated with resins, leading to a substrate that decomposes little, if at all (Chen et al. 2001). To add complexity to the heterogeneity of WD, the proportions of these tissues vary with diameter leading to the

differences among tree species increasing with diameter.

WD as a store

With the emphasis on understanding processes and their controls, it is easy to forget that stores are also integral to understanding the dynamics of WD. The store represents the cumulative net balance of inputs and outputs; therefore serves a check on how these fluxes are measured or modeled. Given that past inputs and outputs are rarely known, one has to either know the past store or make unrealistic assumptions about its status (e.g., either it was zero or at steady-state) that limit the utility of current flux estimates and measurements. Moreover, estimates of output fluxes also depend on stores. Specifically, although decomposition fluxes can be measured directly, in most cases the amount being lost from WD is measured as the percentage or proportion lost per unit time (i.e., k). If the decomposition-related flux is to be estimated from these k 's, then the stores and their characteristics (e.g., species composition, size distribution, and position) need to be known as well. To illustrate this point, consider a hypothetical *Pinus contorta* forest in the Rocky Mountains. Based on what is known about the decomposition of standing versus downed versus buried WD and differences related to WD diameter, the overall ecosystem k could vary from 0.01 to 0.03 year⁻¹ (supplemental information). Specifically, in a forest left undisturbed for a long time, the k might be ≈ 0.02 year⁻¹ because downed CWD would be the largest store. However, after a bark beetle outbreak, the k would be ≈ 0.01 year⁻¹ because standing CWD would be the largest store and it decomposes much more slowly than downed CWD. The same beetle-killed forest after salvage would have a k of 0.03 year⁻¹, because dead coarse roots would be the largest store and they decompose faster than either standing or downed CWD. In all these forests the k 's associated with positions and sizes are the same; the differences are due to very different relative abundances for the three cases examined.

As far as I know, the only element for which WD-related stores have been estimated at the global level is C. At the global level WD currently stores 73 Pg of C (Pan et al. 2011). However, this estimate is highly uncertain as stores for many regions were modeled

using constant stores per area or expansion factors. Currently there are no global estimates of WD stores that are strictly inventory based. In the future, this will hopefully occur as more governmental agencies add to the already growing database of regional inventories (e.g., Fridman and Walheim 2000; Domke et al. 2013). These data represents a significant improvement from the earliest estimates taken on research plots given that more rigorous sampling protocols were designed to give unbiased broad-scale averages. Despite these improvements, technical issues remain. Some pools, such as attached dead wood and dead coarse roots are difficult to directly inventory and have to be based on another pool that can be estimated more directly. For larger WD, estimates of volume, density (i.e., mass per volume), and elemental concentration are needed to calculate stores; however, only measurements related to volume (i.e., diameters, length), position, and decay status are part of current inventories. Unfortunately for many regions data on density and elemental concentrations are still lacking introducing substantial uncertainty into stores estimates (Campbell et al. 2019).

Given the lack of inventory data, global (and some national) estimates of WD stores are indirectly estimated using models. This modeling might utilize information about processes (e.g., Brown and Schroeder's (1999) estimate of net accumulation of WD in the eastern USA), but more often uses the ratio of WD to a pool, such as live wood, that has been more consistently inventoried (Domke et al. 2013). This ratio is usually expressed as the ratio of WD mass to aboveground live mass (Dead:Live ratio). While this ratio method has only been applied to C, there is no reason it could not be applied to other elements. The Dead:Live ratio for C based on inventories for older forests ranges at least between 0.15 and 0.5 (Harmon et al. 2001). For forest stands or landscapes approximating steady-state one can also use the ratio of the fraction of live wood dying per unit time and the decomposition k (Harmon et al. 2001; also see supplemental information for derivation of this index). As the proportion of trees dying increases, so does this ratio; conversely as the k increases, the ratio decreases. If we assume (based on tree lifespans) that 0.5–5% of the tree mass is dying each year and that the CWD decomposition rate-constant, k , ranges between 0.005 and 1.0 year⁻¹ (Harmon et al. 2020) one can estimate the potential range of the Dead:Live ratio. If we further assume that mortality rates and k are positively

correlated, then the range of potential Dead:Live ratios globally for forests in or near a steady-state would be 0.05 and 1, with the upper limit being far higher than generally assumed. Although one ratio usually is used per region, the ratio varies among ecosystem types, over succession, and among management regimes (i.e., natural disturbance versus harvest). The effect of succession on the ratio depends on the amount of WD left after disturbance: for intensive harvest regimes, in which most of the aboveground live and WD is harvested, the ratio would be lower than for forests in a steady-state; for natural disturbance systems in which the full WD legacy is left, the ratio would be substantially higher than the steady-state; and for partial WD legacies, the same is true, but to a lesser extent (Fig. 3). Hence, while the estimates provided by Pan et al. (2011) were an important step, a new estimate accounting for the effects of disturbance would provide a more realistic estimate especially now that mortality rates appear to be increasing.

Process understanding

Over the past 50 years, the general processes involved in biogeochemical cycles and WD have been explored,

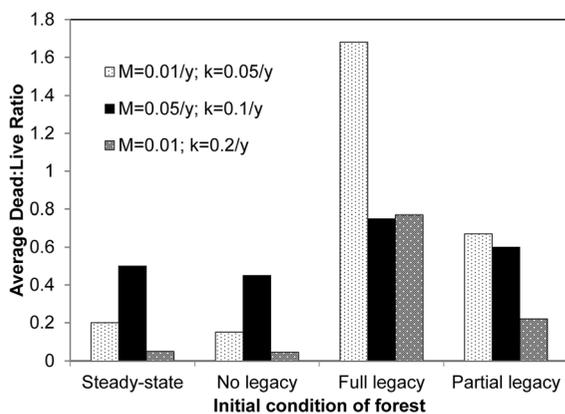


Fig. 3 The average Dead:Live ratio for disturbance regimes that leave various amounts of woody detritus (WD) for various values of M (the proportion of live wood dying) and k (decomposition rate-constant of WD). The initial conditions included: using the steady-state live and dead stores; no legacy in which the dead store were set to zero; full legacy the dead store was set to its steady-state store plus 98% of the live steady-state store; and partial legacy in which the dead store was set to its steady-state store plus 20% of the live steady-state store. In the cases other than the steady-state, the live store was initially set to 2% of its steady-state value

but much remains to be learned about the range of rates and their controls. From the least resolved perspective, WD is an input–output system with mortality as the input process and decomposition as the output process. However crude this representation, it still is lacking from many global change models in that WD is neither included nor explicitly addressed (Harmon et al. 2020). As mortality of woody plants increases (Allen et al. 2010; Williams et al. 2013) it is doubtful this perspective can continue to persist in analyses of global change. Below I focus on the decomposition process, but clearly we need improved understanding of the mortality process as well (Anderegg et al. 2013; Harmon and Bell 2020).

C turnover times

At this point in time, the global the respiration flux from WD is highly uncertain. Pugh et al. (2020) estimate that 37–81% of forest-related NPP (23.3 Pg C year⁻¹) is associated with mortality (versus fine root and leaf turnover). Assuming this mortality flux is roughly equivalent to the global WD respiration flux suggests it ranges between 8.6 and 18.9 Pg C year⁻¹. When coupled with 73 Pg C of stores globally (Pan et al. 2011) an average turnover time ranging between 3.5 and 8.5 years is suggested (or expressed as the time to decompose 95% of the WD this would indicate a lifespan ranging between 12 and 25 years). While this \approx twofold range is considerable, turnover times of downed coarse WD determined from species-level studies range 400-fold from 1 to 400 years, implying it could take anywhere between 3 and 1200 years for 95% of a piece of WD to decompose (Harmon et al. 2020).

Process controls

While some of these differences are related to climate, particularly temperature, much is related to the wide variation in size, heterogeneity, and position found within WD. Confounded with some of these factors are the decomposers themselves, which oddly are often neglected as a factor controlling decomposition! Nonetheless, some of the changes in decomposition rates associated with temperature are undoubtedly related to the presence of certain decomposers (e.g., termites) in warmer climates (Sanderson 1996). Moreover, the proportion of WD converted to organic

soil horizons is likely related to the activity of brown-versus white-rot fungi (McFee and Stone 1966). Therefore it might be fruitful to pursue a model that considers the match/mismatch between decomposer potential to degrade a substrate, the actual decomposer ability to degrade a substrate in a given environment, and the abundance of a given substrate. Presently it seems to be assumed that all three inevitably match, but it was such a mismatch that may explain, in part, the accumulation of coal (Robinson 1990).

Many of the controls of nutrient dynamics are similar to those of C; however, there are certain aspects that warrant specific mention. Critical elemental ratios have been a productive way to predict when nutrient uptake versus release occurs in litter and soil (Gosz et al. 1973; Zechmeister-Boltenstern et al. 2015). While the same may be true for WD (Lambert et al 1980), one cannot assume that the critical element ratio at which behavior switches is the same as for leaf litter, fine roots, and soils. If the critical C:N ratio is 25, starting with an initial WD C:N ratio of 500:1, the approximate midrange found in wood (Harmon et al 1986), suggests that either up to 95% of the C needs to be lost or N stores must increase 20-fold for N release to begin. However, field measurements suggest that N is released in WD when C:N reaches $> 117:1$ (Hart 1999). This implies that either $< 75\%$ of the C needs to be lost or N stores need to increase fourfold. While both C is lost and N is gained to reach either critical C:N ratio, the higher critical ratio in WD implies far less change in either before N is released from WD.

What explains the higher critical C:N ratio in WD? One hypothesis is that because some of the C is relatively inert, the effective C:N ratio is lower. It may also have to do with the decomposer organisms themselves. While the fungi in WD are often considered “soil” fungi, they are generally not the same as those in soil and probably have not been for hundreds of millions of years. It therefore would be no surprise if WD-related decomposers have evolved different tolerances and capabilities than soil-related decomposers. We have known some of these differences for some time including: high levels of internal recycling of N within fungi (Cowling and Merrill 1966); transportation of elements between WD pieces and from soil via fungal hyphae (Lodge 1993); and significant levels of N fixation in WD (Roskoski 1980; Griffiths et al. 1993). It could also be the case that decomposer organisms in WD are not C limited

and therefore mine out an element in abundance, C, to get access to nutrients that are not, such as N. Even under conditions in which nutrients should be immobilized, the fact that decomposers such as fungi form fruiting bodies can lead to nutrients being exported from WD (Harmon et al. 1994). Moreover, decomposer activity is not uniform throughout the year: mechanisms of nutrient removal such as leaching occurs in cooler, wetter seasons when decomposer activity is lower, while those related to immobilization occurs in warmer, drier ones when decomposer activity is higher. One also needs to acknowledge the effect of heterogeneity on nutrient dynamics: some parts of WD can be biogeochemically active (e.g., bark), while others are inactive (e.g., wood). In these cases the proportion of active versus inactive WD controls overall rate of activity, but does not eliminate the activity altogether. Hence, substantial losses of nutrients can occur from bark even when the wood is inactive. To understand release we need to understand the cascade of interacting zones within WD because this could lead to a loss of nutrients over time versus distinct periods of net nutrient uptake and release (Fig. 4).

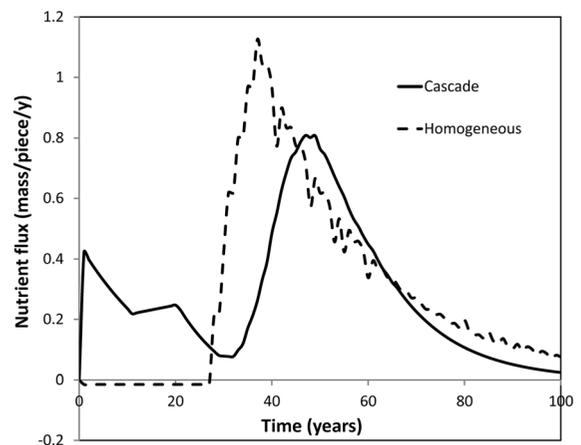


Fig. 4 Hypothetical effect of a cascade of release versus homogeneous release of nutrients from a piece or cohort of WD. A negative flux indicates a net uptake of nutrient; a positive flux a net release from the WD. Homogeneous release assumed that all the parts of the WD were the same and simultaneous. Cascade release subdivided the WD into zones with different qualities that became active sequentially (see supplemental information for additional details)

Decomposition unpacked

Despite the fact the decomposition process has been conceptually divided into respiration, fragmentation, and leaching for considerable time (Swift et al. 1979), we still do not have good estimates of the proportion that each of these pathways comprises. While all three can occur simultaneously, it is unlikely they are equally important or constant over space or time (Fig. 5). These proportions also likely vary by the level examined (i.e., individual pieces or cohorts of WD versus populations of WD that contain multiple cohorts). The assumption has been that most losses from WD are related to respiration; and while likely true in that most fragments and leachates are ultimately respired, it does not mean fragmentation and leaching can be ignored. As pointed out by Bond-Lamberty and Gower (2008), the assumption that decomposition losses are solely attributable to respiration inflates estimates the flux of CO₂ to the atmosphere.

Leaching

Given that the majority of sound wood is not water soluble and water flows slowly through this material, it seems reasonable to assume that leaching forms a very small fraction of WD losses. Specifically, Pettersen's (1984) compilation suggests an average of 4.6% (range 2–15%, N = 603) of ground wood is soluble in hot water (note that the solubility of intact wood in

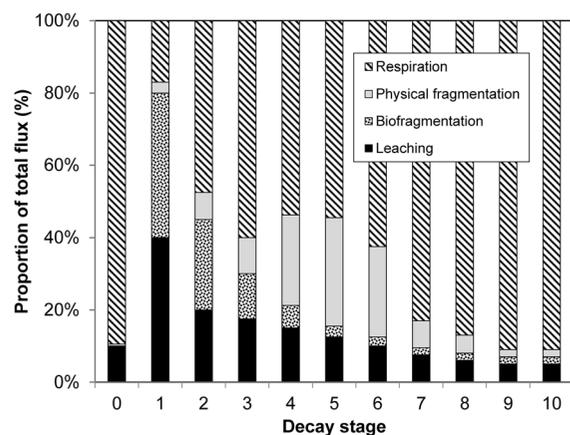


Fig. 5 Hypothetical changes in the importance of decomposition-related fluxes from a WD. Biofragmentation is caused animal activity, whereas physical fragmentation is primarily caused by gravity. Decay stages are as in Fig. 2

cooler water is probably substantially lower). The higher fraction of water soluble compounds in bark and the fact that decomposers convert non-soluble to soluble compounds suggests a higher fraction of WD can be leached than one might assume at first glance. Moreover, decomposition increases the rate of water movement through WD as insect galleries and various cracks appear in the WD. The concentration of dissolved organic carbon (DOC) in leachates from WD is higher than from leaf litter (Spears and Lajtha 2004; Kahl et al. 2012); however, the flux at the ecosystem level can be low because WD does not cover as much of the soil surface as leaf litter (Hafner et al. 2005). Given that downed WD covers somewhere between 2 and 25% of the forest floor (Harmon et al. 1986), concentrations of leachates from WD would have to be 4–50 times higher than those from leaf litter for the flux to be the same at the ecosystem level. Standing WD also likely loses leachates; and in the early phases of decomposition leaching rates from standing WD may be similar to that of live tree stemflow (Parker 1983).

Actual measurements of leaching rates from WD are rare, but those that have been made suggest that during the initial phases of decomposition (i.e., before respiration peaks), leaching can be the major pathway of loss (Harmon and Sexton 1995). Over the lifetime of a downed piece of WD \approx 5% of the losses could be via leaching (Spears et al. 2003). What is fate of this leachate? If these leachates are highly decay resistant, then one would expect a significant increase in the underlying soil C store (Spears and Lajtha 2004). Assuming that none of this leachate decomposes one can calculate the relative amount of C increase in the underlying soil depending on the initial soil C store, the diameter of the downed WD, and the fraction of losses via leaching (supplemental information). For example, for a 10 cm diameter piece of WD, the mineral soil C beneath would be expected to increase 10–39% if as little as 5% of the WD is leached, with the higher value for soils with a low initial C store (Fig. 6). The potential increases in soil C under WD would be considerably higher with 100 cm diameter pieces. Although most of these increases in soil C would likely be detectable, comparison of soil under versus adjacent to downed WD shows only a minor increase in soil C or none at all (Spears et al. 2003; Kahl et al. 2012). These observations imply that the majority of WD leachate is respired in a timeframe

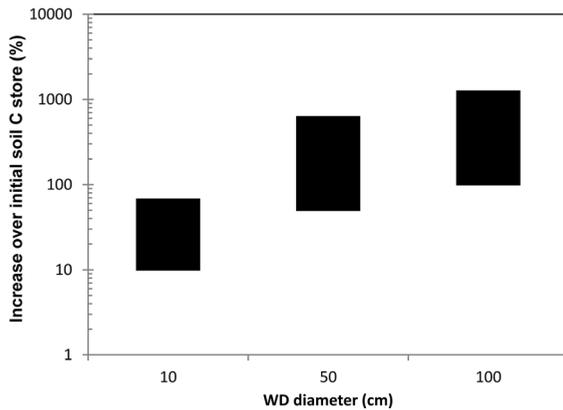


Fig. 6 Potential increase in soil organic carbon (SOC) stores from WD leachate if it does not decompose (note the logarithmic scale on y-axis). The range for each diameter is related to the fraction of WD leached (5–15%) and the initial store of SOC (25–100 Mg/ha)

comparable to the WD lifespan; therefore the hypothesis that log leachates decompose slowly needs to be revisited. Indeed, experiments in which chipped WD was added to the soil surface indicated no increase in surface SOC after 10 years and that increased leachate losses from the forest floor enhanced soil respiration (Lajtha et al. 2018).

“Log shadows” are an interesting way to envision the effect of downed WD appearing and disappearing over the soil on the spatial pattern of SOC (Dennis Knight, personal communication). This concept, along with rates of tree mortality, leaching, and leachate decomposition can be used to estimate the variability in SOC caused by the presence of WD (supplemental information). This model suggests that variation in the mortality rate introduces more spatial variability than variation in leaching or leachate decomposition rates. Interestingly, increasing the decomposition rate-constant of WD leachates increases the coefficient of variation in SOC, but it also decreases the store. This suggests that the variation in SOC introduced by WD leaching might be difficult to detect because either the store is low and highly variable, or the store is high, but exhibits low variability.

Fragmentation

Fragmentation rates, especially at the microscale, have proven difficult to determine. The fall of standing dead stems (i.e., snags), a form of macrofragmentation, has

been determined to some degree, but these estimates are more compromised than one might initially assume. The fact that there is often a lag between snag formation and snag fall means that several parameters need to be reported to describe this process; hence a single rate (the most common way of reporting) is often misleading. Moreover, even when the stem falls to the ground intact, bark, twigs, branches, and sapwood have often already fallen due to microfragmentation implying macrofragmentation-based estimates significantly underestimate fragmentation losses. For example, if the majority of bark, twigs, branches, and sapwood have fallen off when an “intact” snag finally falls, then 10–30% of the “complete” standing dead tree may have already hit the ground! The time for complete snag fall to occur probably ranges between a decade and a century (or more) and in environments in which standing and downed WD decompose at different rates, the timing of this fragmentation process can greatly influence C efflux after disturbance (Harmon et al. 2020). Another form of fragmentation that has been documented is the sloughing of bark, which can influence not only the chemical properties of WD, but also the microenvironment of the underlying wood. Complete bark loss probably ranges from a few years to many decades. If we assume 10–30% of WD is bark, then an upper limit to bark-related fragmentation processes would be similar. Micro-fragmentation of the decomposing wood by either biological (e.g., insect frass) or physical processes has rarely if ever been measured directly, but it is clear that certain assumptions (i.e., volume loss equals fragmentation loss) related to indirect estimates overestimate fragmentation losses.

Fragmentation represents a reduction in size as well as a change in microenvironment. Smaller size caused by fragmentation should increase exchange with the surrounding environment, but it is not necessarily true this speeds the decomposition rates. The fact that moisture can be too low or too high to sustain decomposition (supplemental information) means that the effect of fragmentation is dependent on the moisture availability within the microenvironment where the fragments reside. Specifically, in a dry environment fragmentation might slow decomposition as smaller fragments would dry faster. Conversely, in a wet environment fragmentation would be likely to speed decomposition as increased drying rates might reduce the period of waterlogging. Similar effects are

caused when fragmentation moves material from one microenvironment to another (Harmon et al. 2011); snagfall could speed decomposition in a dry environment, but either slow or arrest it in a very wet one.

Respiration

Of the three pathways of decomposition loss, respiration is the best studied, in part because it is methodologically easiest. Given that most respiration estimates involve measuring CO₂, the tacit assumption is that aerobic respiration dominates. Theoretically this seems justified in that white- and brown-rot decomposer fungi, the main decomposers of WD, are strict aerobes (Walker and White 2017). Nonetheless there are conditions under which CH₄, a major product of anaerobic respiration, can be produced. For example, termites, via their gut microbes, produce CH₄ (Sanderson 1996). However, CH₄ formation in xylophagous termites is much lower than in fungal-growing and soil-eating termites (Brauman et al. 1992). This is because acetogenic bacteria outcompete methanogenic ones in the hindguts of xylophagous termites. Once formed, methanotrophic bacteria could oxidize CH₄ to CO₂ within the WD or soil before it leaves the forest ecosystem (Steudler et al. 1989). It therefore remains an open question the degree to which CH₄ is released from WD into the atmosphere via termites. CH₄ could also be produced by bacteria if the WD remains water saturated over an extended period. These conditions would be commonly found in swamp forests and lakes, but the rate of CH₄ generation would likely be quite low given the fact that submerged wood can take millennia to decompose. For example, wooden trackways created through swamps of England in the Neolithic have been found (Morgan et al. 1987); as these trackways were constructed ≈ 6000 years ago an average decomposition rate < 0.02% year⁻¹ would be indicated. In upland situations, full water saturation is only seasonally possible (typically in the colder season) and even in very moist environments fully anaerobic conditions appear rarely (Hicks and Harmon 2002). Hence, it remains to be seen whether CH₄ production is as common in WD as it is in live trees (Covey et al. 2012).

Burial: a key process

Although not considered a decomposition process per se, burial occurs as decomposition of WD proceeds. With the exception of roots, which essentially start “buried”, WD is buried by a wide range of processes including: growth of vegetation (particularly bryophytes), accumulation of litter or soil on the WD surface, bioturbation, and physical processes. In the case of burial by litter, loss of the litter below the WD piece leads to the appearance that the WD has “melted” into the forest floor. Although erosion is a major physical process related to burial, WD can also be “pushed” into the underlying soil as one piece falls upon another. In some cases burial effectively stops the decomposition process leading to large accumulations of buried, partially decomposed WD (Moroni et al. 2015); therefore we cannot continue to assume that all buried WD is eventually respired. Hence some of the elevated mortality now being observed in forests may not result in greater CO₂ flux to the atmosphere. Burial would reduce exchange with the atmosphere and would effectively make WD moister; but as with fragmentation, the effect on decomposition depends on moisture level. Therefore in dry environments burial might speed decomposition, whereas in wet ones the opposite might occur. Despite being a process with considerable impact on biogeochemical cycles, burial rates have do not seem to have been measured or modeled. Conceptually it seems likely that three factors need to be considered: the relative rate of decomposition, the burial rate, and the size of the WD being buried (see model in supplemental information). Specifically, if the decomposition rate is faster than the rate of burial or the WD is large relative to the burial rate, then little WD should become buried; whereas if the burial rate is high enough to bury pieces before they decompose fully, then a great deal of WD should become buried (Fig. 7).

Combustion

Although a smaller flux than respiration, combustion of WD due to wild- and managed-fire is potentially substantial. The global flux of carbon via combustion was estimated to be 1.2–2.4 Pg C year⁻¹ (Knorr et al. 2012, 2016). Assuming half is from WD combustion and that the WD respiration flux (as estimated above) ranges between 8.6 and 18.9 Pg C year⁻¹, I estimate

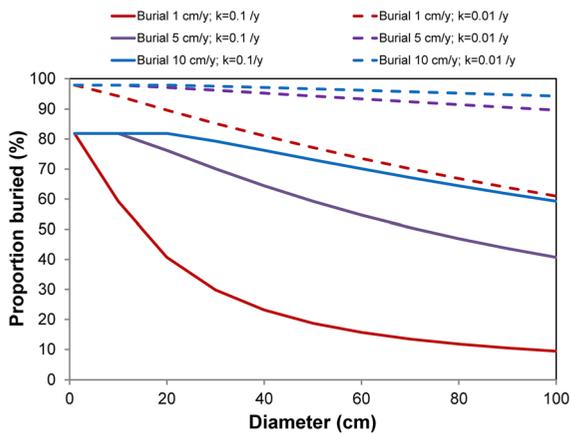


Fig. 7 The proportion of initially aboveground WD buried at the ecosystem/multi-cohort level as a function of burial rate, decomposition rate-constant (k), and WD diameter. The proportion buried was calculated as the sum of the masses buried versus the total mass added assuming a constant rate of WD input over a 300 years period. For each cohort of WD input the proportion of mass buried was assumed to be the same as the proportion of the diameter buried (e.g., at a burial rate of 1 cm year⁻¹, 10% of a 100 cm diameter WD piece would be buried in 10 years)

that combustion accounts for 3–14% of the total flux from WD to the atmosphere.

This high level of uncertainty in the fraction respired versus combusted arises from several factors. The respiration flux from WD is not well constrained, in part because of uncertainty in the store of WD, but in part because WD decomposition rate-constants (i.e., k) are highly variable, locally ranging between < 0.001 and 1 year⁻¹ (Harmon et al. 2020). Combustion estimates are also influenced by uncertainty in stores, but there is also uncertainty in the fraction consumed by fire. Knorr et al. (2012) assumed 20–40% of the WD was consumed by fires; however, field measurements have found a far wider range of 10–100% (Brown et al. 1985, 1991; Prichard et al. 2006; Hollis et al. 2011). Even less clear is how much WD is combusted versus converted to char during fires. Tinker and Knight (2000) found 8% of the CWD was consumed and an equal percentage was converted to charcoal in the 1988 Yellowstone Fire. Whether this is typical is uncertain, but of substantial importance: char from WD could form a long-term store of C as evidenced by accumulations of charcoal in many soils (e.g., Ohlson et al. 2009). In addition to the amount of char formed, the rate of incorporation into mineral soil should be an important control on its longevity

because, exposed on the surface, charcoal could be consumed by subsequent fires (supplemental information).

The factors controlling combustion losses from WD are multiple and interactive (see supplemental information for a more detailed discussion). Some, such as size, position, and decay are directly related to the form of WD present (Brown et al. 1985, 1991; Albini and Reinhardt 1995, 1997; Hollis et al. 2011). Others, such as mineral content, physical arrangement (i.e., packing), and oxygen supply are indirectly related to the form of WD (Rothermel 1972; Frandsen 1987). Factors largely independent of WD form include fire intensity and weather as these are related to a particular fire (Hollis et al. 2011). Moisture, perhaps one of the more important controls of combustion (Rothermel 1972; Frandsen 1987; Brown et al. 1991; Hollis et al. 2011), results from the interaction of antecedent weather, size, position, and decay state.

Given all these interacting factors it is little wonder that WD fire consumption rates are highly variable. The challenge has been to figure out how all these factors can be integrated! One approach has been to model each form of WD separately (e.g., Brown et al. 1985); however, this potentially results in models with different predictor variables and this hinders integration. At the other end of the spectrum is a single integrated combustion rate (e.g., Knorr et al. 2012). While certainly integrated, the basis of a particular value is not clear and a range invariably introduces uncertainty. I believe what is needed is a system that acknowledges various forms of WD as well as the influence of all controlling factors and produces an overall estimate that can be used in broad-scale analyzes. One possibility would be to rank the likeliness of combustion of the various forms of WD based on how these factors vary by WD type (see supplemental information for an example). Weighting these rankings by the abundance of the various WD pools might provide an overall estimate of the fraction potentially combusted at the ecosystem and landscape levels.

Although combustion removes WD, it also adds WD by killing vegetation. As the Dead:Live ratio for CWD is generally < 0.5 , less than half the mass of the live stems in a forest needs to be killed by fire to offset complete CWD combustion. Since combustion of CWD is rarely complete, fire is unlikely to decrease

the CWD store when fire-mortality inputs are considered.

Finally, combustion likely has an effect on decomposition, but it may not always slow decomposition as might be assumed. Two factors are hypothetically at play: the fraction of the WD that has been colonized by decomposers versus the fraction of decomposer colonized WD removed by combustion. For WD that has not been fully colonized by decomposers, combustion could “short circuit” the colonization process by removing the outermost decomposing zones. This would leave a relatively inert charred surface and a sound interior which might take many years for decomposers to recolonize. For WD in advanced stages of decomposition when colonization is complete, decomposers are likely to continue as before the fire except in the rare instances when WD is completely sterilized.

WD and nutrient cycling

While the role of WD in C cycling has received increased attention, in part, because of the recent increases in tree mortality, its role in nutrient cycling is generally downplayed because relative to leafy and fine root litter: concentrations of nutrient elements in WD are much lower; WD does not store appreciable amounts of nutrients; WD dynamics are slower; and nutrients tend to accumulate in WD, indicating long-term immobilization. While each of these points is true to some degree, I think they need to be considered in a multi-level context that goes from tissues to landscapes (Fig. 1).

Tissue versus tree level

In general, nutrient element concentrations (expressed as mass of nutrient to total mass) in woody tree parts are lower than in leaves or fine roots (Harmon et al. 1986) suggesting that at the tissue-level nutrient inputs and uptake of woody ones are lower than for non-woody ones. However, the input and store of elements also depends on organic matter stores as well as elemental concentrations. This can be illustrated by the fraction of woody parts in a tree needed to result in half of the nutrient returned to the soil coming from WD upon tree death. For example, if woody part concentrations are the same as non-woody ones, then

50% of a tree needs to be woody for nutrient flux via woody tissues to be 50% (Fig. 8). Woody parts comprise 80–95% of tree mass with the proportion increasing with forest biomass and decreasing with mean annual temperature and degree trees are ever-green (Reich et al 2014). Concentration differences between non-woody and woody parts/tissues vary among elements and their ratio is likely in the range of 2–23 (supplemental information). These ranges in these two variables suggests that in some cases woody parts contribute more nutrients than non-woody parts upon tree death and in other cases the opposite is true.

Effect of disturbances

Disturbances rearrange ecosystems so that nutrients in the live pools are shifted to dead pools. Given that timber harvest reduces the input of WD and salvage harvest removes WD in many forest ecosystems, the amount of WD, relative to other stores such as live wood, can be low. However, this cannot be used to generally conclude that WD stores of nutrient elements are always low and hence unimportant to consider. WD stores are strongly influenced by disturbance and management regimes and without specifying a number of parameters (e.g., severity of disturbance, legacy, decomposition and mortality

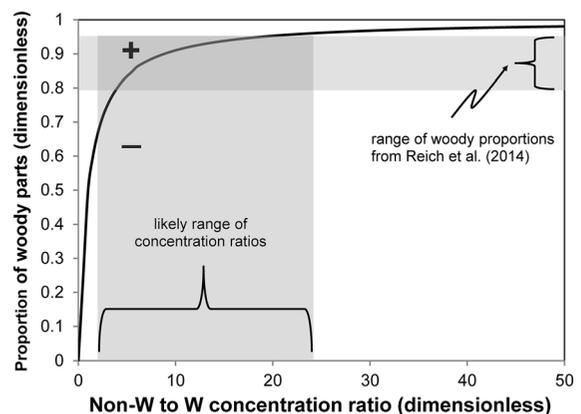


Fig. 8 The relationship between the ratio of elemental concentrations between non-woody and woody parts and the proportion of trees comprised of woody parts. The line indicates the point at which woody and non-woody parts each contribute 50% of a nutrient when a tree dies (above this line indicate woody parts contribute > 50% and below < 50%). The observed range in woody part proportions was modified from Reich et al. (2014). See supplemental information for the range of concentration ratios

rates, tree regrowth rate, etc.) one cannot predict the relative amount of WD stores present. Consider two cases. In an old-growth forest ecosystem, in which the Dead:Live mass ratio was 0.05, WD would store $\approx 5\%$ (if the elemental concentrations in live and dead woody parts were the same). Therefore the WD nutrient pool might be considered unimportant relative to the live woody stores. However, in the same forest that had just been disturbed and all the woody material was left there would be a ≈ 20 -fold increase in the WD store of the element. In fact it would be larger than the amount stored in the live wood of the old-growth case, which we have just concluded was a large store!

Given a major increase in nutrients stored in dead organic matter caused by disturbance, it is important to consider the temporal pattern of nutrient release. In Fig. 9 the hypothetical release of an element from leaf and fine roots, fine WD, and coarse WD after a disturbance killing all the trees is displayed. What we see is a cascade of release: a very large initial pulse from leaf and fine root decomposition, is then followed by a lower secondary pulse from FWD associated with twigs, branches, and coarse roots, which is then followed by a yet lower tertiary pulse from CWD. While the first pulse in this example releases the most (41% of the total), the second and third pulse are non-trivial (29% and 30%, respectively). Although the much lower peaks of the secondary and tertiary pulses relative to the primary pulse might seem to make them less important, it is interesting that these peaks correspond to the times in which the corresponding

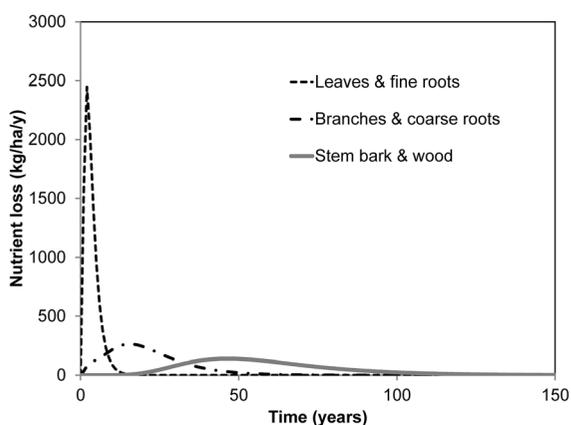


Fig. 9 Hypothetical release of a nutrient from various tree parts killed by a disturbance (note the nutrient concentrations in leaves and fine roots were tenfold higher than for bark, branches, and coarse roots and 20-fold higher than for stem wood)

live parts are increasing in recovering vegetation. Specifically, the initial, rapid, high pulse corresponds to the formation of new leaves and fine roots; the secondary pulse to the formation of new branches and coarse roots; and the tertiary pulse to the major growth period of new tree stems. Hence the cascade of nutrient release largely corresponds to the regrowth of the various tree parts. While I am not suggesting that the nutrient demands of regrowing trees are necessarily directly supplied from these forms of decomposing organic matter, losses from decomposing organic matter could be resupplying the soil store in sequence that corresponds to increases in live stores.

Post disturbance accumulation

The increase in WD in the later phases of succession could result in an extended period of accumulation of nutrient elements in forests influencing nutrient export dynamics (Fig. 10). These accumulation dynamics are influenced by both the time to recover mortality inputs (fastest for leaves and fine roots and slowest for stems), but also the rate-constants of decomposition losses (also fastest for leaves and fine roots and slowest for stems). The speed of dynamics also impacts the stores, with slower pools often having substantial accumulations, mineral soils being a case in point. Most would not conclude soil stores of C or nutrients are unimportant to nutrient cycling because of “slow dynamics”. Slower dynamics also implies a lower proportion of an element is turning over, but this is often offset by the higher mass turning over. Turnover times (i.e., the inverse of decomposition

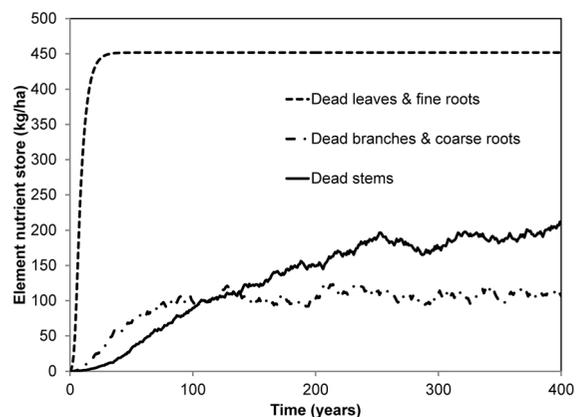


Fig. 10 Hypothetical accumulation of nutrient stores in various WD pools starting with no legacy and no subsequent disturbance

rate-constants) of WD are generally an order of magnitude higher than for decomposing leaves and fine roots. Given a tenfold difference in turnover times and identical stores of WD and non-WD, the flux of nutrients from WD would be 10% of non-WD pools. However, if the mass of WD was 10 times higher than non-WD pools, then the flux would be the same. While one should not conclude from this that nutrient fluxes from non-WD and WD pools are the same, it does suggest that one needs to move beyond turnover time to understand the role of WD in nutrient cycling.

Disturbance regime at the landscape level

To this point, I have focused on nutrient flow associated with disturbance; however, much of the flow of nutrients is also associated with so-called “normal” tree mortality as well as leaf and fine root turnover. To address this one needs to examine nutrient inputs within the context of a disturbance/management regime (Harmon and Bell 2020). A sensitivity analysis of a model accounting for nutrient inputs for woody versus non-woody parts via disturbance and non-disturbance inputs confirms that nutrient concentration is important, but so is the fractional allocation of production to woody parts (supplemental information). Interestingly, the fraction of nutrients flowing via woody parts is insensitive to both the average interval of disturbance and the severity of the disturbance. At the landscape level woody parts die either via “normal” mortality processes or disturbance regardless of the interval or severity of disturbance. This is not to say disturbance interval and severity do not influence the degree nutrients are added to dead organic matter pools in pulses versus steadily: as the average interval of disturbance increases, the proportion added in pulses decreases; conversely as disturbance severity increases the proportion added in pulses increases. As woody parts accumulate more mass than non-woody parts due to their longer turnover time, woody parts tend to have a higher proportion added via pulses than non-woody parts.

Cohort versus ecosystem levels

Given the slow dynamics of WD it makes sense that nutrient stores in WD would generally increase over time. Indeed we suggested that CWD acted as a

nutrient sponge, accumulating nutrients over time (Harmon et al. 1986). However, I wish to recant that view, in part, because accumulation depends on the level of the system examined and the initial store. This can be illustrated by a model in which various elements have different temporal patterns relative to C, including those that exhibit a phase of net uptake due to inputs from outside or inside the WD (e.g., N fixation). These cohort level dynamics are illustrated in Fig. 11a. Regardless of these cohort level temporal patterns, the degree that an element is gained or lost at the ecosystem level (i.e., a level at which multiple cohorts exist) is largely a function of the initial store. If the initial store was zero, then all elements accumulate (Fig. 11b). In contrast, if the initial store was the steady-state amount, then there is no change in the stores (Fig. 11c). Finally, if the store is elevated above the steady-state store (i.e., by a disturbance), then the stores decrease (Fig. 11d). Rather than influence whether there is a net uptake or loss of nutrients, the cohort level dynamics determine the rate that stores either increase or decrease as well as the amount they reach at steady-state. In light of these results, it might make sense to reexamine past conclusions based on a limited set of initial stores (e.g., Laiho and Prescott 1999). It would also make sense to specify the level at which the conclusion is reached because clearly what happens at the level of a piece or cohort of WD is not the same as at the ecosystem level in which multiple pieces or cohorts is considered.

Are the nutrients in WD needed?

Are the nutrients associated with WD surplus to forest ecosystem needs as seems to be generally assumed? Perhaps, but it has to be acknowledged that humans have a basic conflict of interest regarding WD given this is a potentially useful, economically important resource. Hence I am admittedly skeptical of claims that the nutrients in WD are irrelevant for maintaining forest productivity. Surprisingly, given the importance of understanding the impact of humans on forest ecosystem function, there have been few definitive, long-term field experiments that could assess the impact of WD and timber harvest on ecosystem productivity. Experiments in which WD has been added have usually involved the addition of sawdust or chips, and while this is wood, the resultant immobilization of nutrients (e.g., Rhoades et al. 2012) and

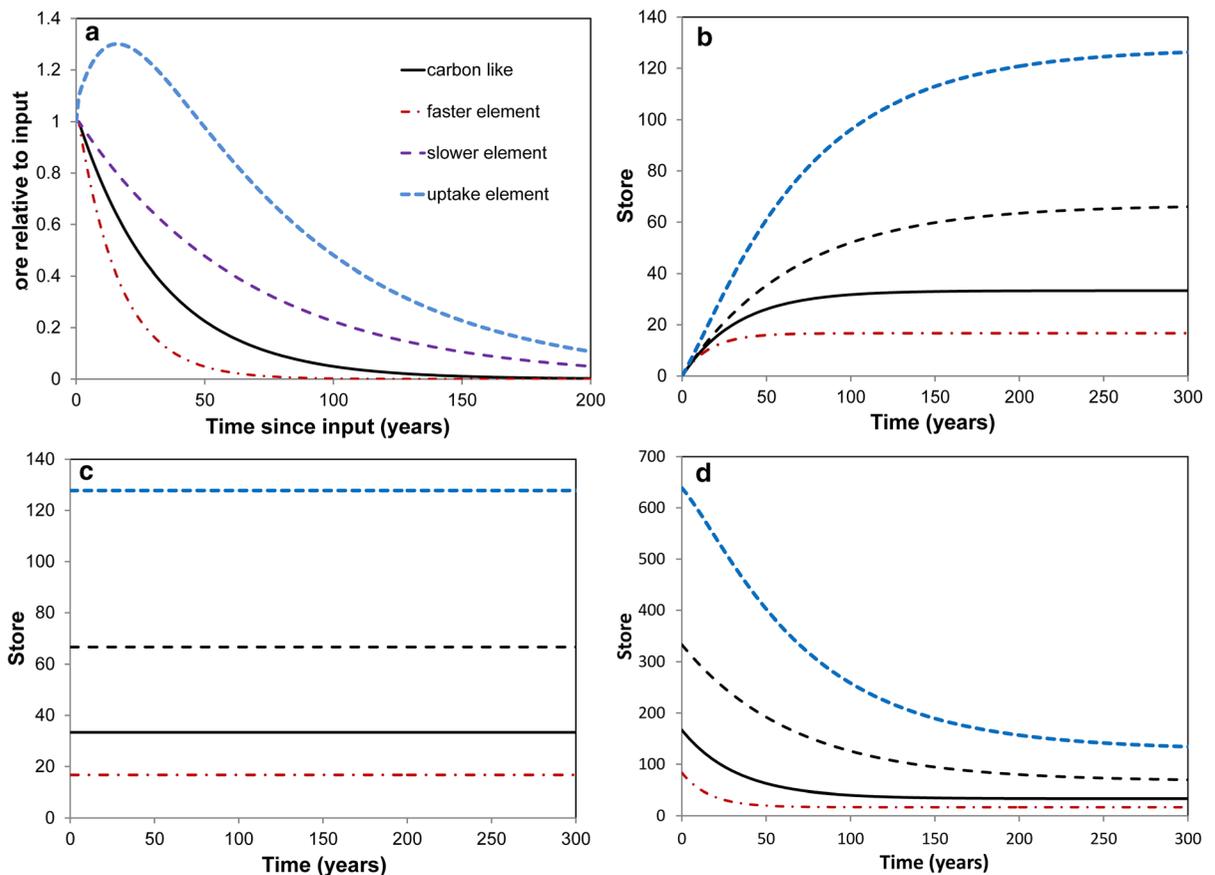


Fig. 11 Differences in nutrient dynamics at cohort (i.e., all WD same age) versus ecosystem level (i.e., WD of multiple ages): **a** dynamics at the cohort level; **b** an initial WD store of zero; **c** an initial store equal to the steady-state; and **d** an initial store equal to all the dead before and live killed by the disturbance. In the

case of the uptake element there is an input of the element during the decomposition process resulting in a net gain in stores at the cohort level for a period of time; the other elements are lost at rates relative to carbon (i.e., like, faster, or slower)

lower rates of production that have been observed (e.g., Kimetu et al. 2008) might be due as much to the form of addition as its woody nature. Specifically, saw dust and chips are able to interact with the soil to a degree not generally possible for intact pieces of WD, some of which never actually contacts the underlying soil directly. Experiments in which WD was removed are largely related to the effects of whole tree versus stem only harvesting. These studies have generally found that foliage removal associated with whole tree harvest systems is the primary cause of harvest-related productivity reductions (Mann et al. 1988; Olsson et al. 1996; Thiffault et al. 2011; Achat et al. 2015). While this suggests that the nutrients related to WD may not be necessary to maintain forest productivity, the range of WD is often highly restricted because the

majority of tree stems cut are removed regardless (Achat et al. 2015). These experiments therefore do not reflect the variation of WD stores in nature which, based on the Dead:Live ratios of older forests, could be anywhere between 2- and 20-fold. It is therefore possible that there is an impact, but within the narrow range of treatments examined it is not statistically significant. It is also possible, given the slower dynamics of WD, that what many would consider a long-term experiment (i.e., 10 years) is not long enough to observe a response (Walmsley et al. 2009). Longer-term responses are usually determined via modeling, but model responses are dependent on assumptions and data that have generally not been tested in the field for WD. For example, if critical elemental ratios derived from mineral soil or leaf litter

are used, WD would be predicted to immobilize nutrients when they are in fact being released (Hart 1999). Therefore a new round of research into WD-related processes as well as long-term field experiments manipulating WD amounts is needed (Thiffault et al. 2011). Although the recent increase in tree mortality is admittedly alarming, it also provides an opportunity to compare disturbed forest recovery with and without the presence of WD (Wei et al. 2020). However, manipulative experiments need to do more than quantify response variables: to be interpreted one needs to conduct process studies so that the mechanisms behind the responses can be documented.

Conclusion

WD is increasingly being acknowledged as an important past and present influence on biogeochemical and ecological functioning of forested ecosystems. If the anticipated increases in tree mortality related to changes in climate and disturbance occur, then better understanding of the when, where, why, and how of WD's influence will be required to fully assess impacts. It should be borne in mind that key properties of WD including size, rigidity, position relative to the soil, and heterogeneity within and among WD pieces strongly influences function. In addition, it needs to be recognized that WD is a material always in transition; many of its properties that influence function significantly change with time. Given that that WD behavior changes with scale and organizational level (e.g., tissues versus cohorts versus stands versus landscape) it will be necessary to integrate these findings for full understanding of WD's influence. Many WD-related processes, such as the release or accumulation of elements, involve cascades. It is therefore important to embrace the heterogeneity driving this phenomenon if mechanistic understanding is to improve. It will also be important to expand our functional understanding of decomposers by recognizing the distinctions between soil- and WD-related organisms as well as better matching genotypic potential and phenotypic expression with the various WD substrates that are created by mortality. Gaining this new understanding will involve new observations and measurements of processes in a wider range of forest systems in which WD occurs. To successfully apply this newly gained knowledge it must be coupled with the temporal,

spatial and statistical structure of controlling influences (e.g., size, position, species/functional groups, and climate). There is also a need for longer term studies and experiments that are fully coupled to process and modeling studies. Here is to the next 35 years of WD-related discoveries!

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Data availability The models used to generate the figures and conduct analyzes are available upon request to the author.

Compliance with ethical standards

Conflict of interest There are no conflicts of interest or competing interests related to this manuscript.

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