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Tamm Review

Quantifying carbon stores and decomposition in dead wood: A review

Matthew B. Russell [a,*], Shawn Fraver [b], Tuomas Aakala [c], Jeffrey H. Gove [d], Christopher W. Woodall [e], Anthony W. D'Amato [f], Mark J. Ducey [g]

[a] Department of Forest Resources, University of Minnesota, St. Paul, MN, USA
[b] School of Forest Resources, University of Maine, Orono, ME, USA
[c] Department of Forest Sciences, University of Helsinki, Helsinki, Finland
[d] USDA Forest Service, Northern Research Station, Durham, NH, USA
[e] USDA Forest Service, Northern Research Station, St. Paul, MN, USA
[f] Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA
[g] Department of Natural Resources, University of New Hampshire, Durham, NH, USA

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ABSTRACT

The amount and dynamics of forest dead wood (both standing and downed) has been quantified by a variety of approaches throughout the forest science and ecology literature. Differences in the sampling and quantification of dead wood can lead to differences in our understanding of forests and their role in the sequestration and emissions of CO_2, as well as in developing appropriate strategies for achieving dead wood-related objectives, including biodiversity protection, and procurement of forest bioenergy feedstocks. A thorough understanding of the various methods available for quantifying dead wood stores and decomposition is critical for comparing studies and drawing valid conclusions. General assessments of forest dead wood are conducted by numerous countries as a part of their national forest inventories, while detailed experiments that employ field-based and modeling methods to understand woody debris patterns and processes have greatly advanced our understanding of dead wood dynamics. We review methods for quantifying dead wood in forest ecosystems, with an emphasis on biomass and carbon attributes. These methods encompass various sampling protocols for inventorying standing dead trees and downed woody debris, and an assortment of approaches for forecasting wood decomposition through time. Recent research has provided insight on dead wood attributes related to biomass and carbon content, through the use of structural reduction factors and robust modeling approaches, both of which have improved our understanding of dead wood dynamics. Our review, while emphasizing temperate forests, identifies key research needs and knowledge which at present impede our ability to accurately characterize dead wood populations. In sum, we synthesize the current literature on the measurement and dynamics of forest dead wood carbon stores and decomposition as a baseline for researchers and natural resource managers concerned about forest dead wood patterns and processes.

Contents

* Corresponding author.
E-mail address: russellm@umn.edu (M.B. Russell).

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1. Introduction

Forest ecosystem management has become an important global strategy for mitigating future climate change effects (Ryan et al., 2010; Malmsheimer et al., 2011; McKinley et al., 2011). Societal demands and trends in land use, in combination with future global change scenarios, may reduce the amount of carbon (C) stored in forests and associated wood products (Joyce et al., 2014). However, substantial knowledge gaps exist regarding the C implications of various forest management activities, given the complex interplay between C emissions and sequestration in forest ecosystems (Malmsheimer et al., 2011; McKinley et al., 2011). Further complicating the assessment of forest ecosystem C stores and fluxes is the diversity of constituent pools, ranging from standing live trees to soil organic C. Tree mortality, canopy damage, and pruning create woody detritus, a critical component of natural forests. We focus here on detritus in the form of aboveground coarse woody debris (Harmon et al., 1986) because it represents a critical stage in the C cycle as live biomass transitions to other pools, such as to the atmosphere or soil organic material, through the process of decomposition.

Aboveground coarse woody debris includes standing dead trees (SDTs), downed woody debris (DWD), and stumps (Fig. 1), forming an important C pool with varying turnover rates. Less is known about the amount of downed dead wood that is buried, but this population can accumulate over centuries given the reduced decomposition when wood is found belowground (Moroni et al., 2015). The DWD pool alone accounts for approximately 20% of total ecosystem C in old-growth (Harmon et al., 1990) and secondary (Bradford et al., 2009) forests, and it is increasingly being considered for use in bioenergy production (Schlamadinger et al., 1995; Sathre and Gustavsson, 2011; Zanchi et al., 2012). At local scales, forest management guidelines and forest certification programs may require maintaining or increasing the abundance of woody debris (e.g., Sustainable Forestry Initiative, 2015). From a global perspective, estimates of woody debris biomass and C are needed for countries that report greenhouse gas emissions from land use, land-use change, and forestry sectors to the United Nations Framework Convention on Climate Change (e.g., Woodall et al., 2012a). In addition to being a dynamic C pool, woody debris is a determinant of fire behavior (Arno, 2000), a component of biodiversity (Martinuzzi et al., 2009; Stokland et al., 2012), and an important substrate for regeneration of many tree species (Bolton and D'Amato, 2011). Thus, quantifying and forecasting the amount and characteristics of woody debris is important to determining current and future forest structure, function, and composition. Accordingly, the annual number of scientific publications on woody debris has numbered around 200 in recent years compared to less than 20 publications per year in the mid-1980s and early 1990s (Fig. 2).

Our review provides a synopsis of the available methods for quantifying woody debris C stores and decomposition and for forecasting dead wood attributes as a part of model simulations. While we focus on methods for quantifying dead wood as a part of national forest inventories (NFIs) from primarily temperate forests, we also emphasize how experiments have furthered the scientific development of dead wood modeling efforts. Common abbreviations used throughout the text may be found in Table 1. With an emphasis on C stores and fluxes, two main sections are presented. The first discusses common sampling techniques for inventorying

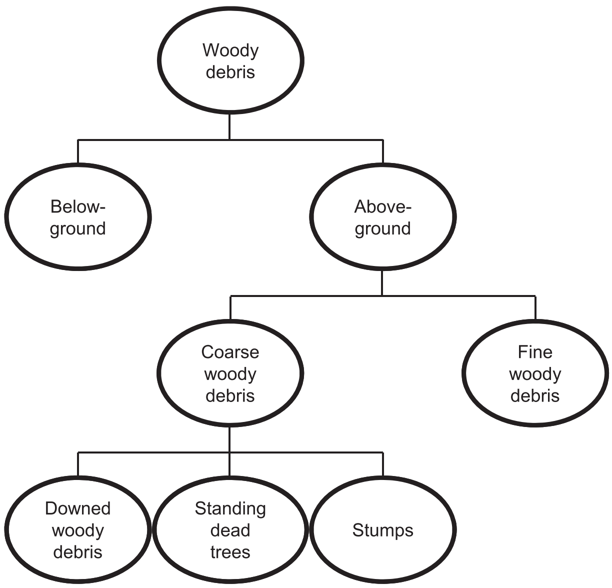

Fig. 1. Overview of woody debris pools (adapted from Harmon and Sexton (1996)).

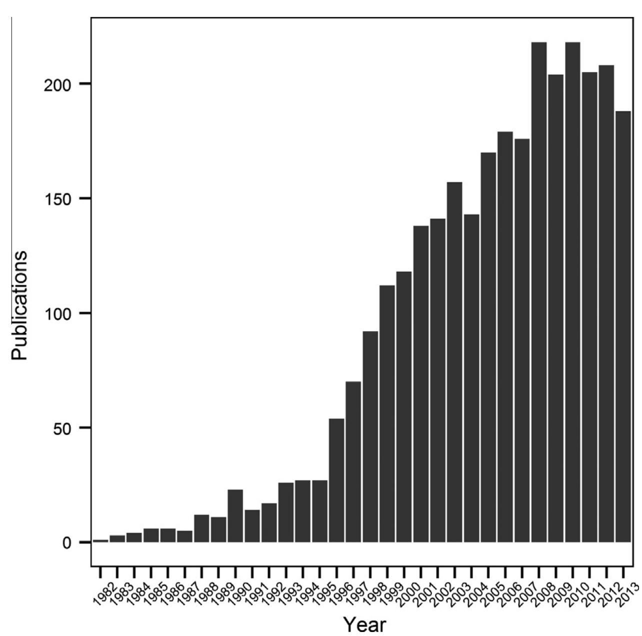

Fig. 2. Number of publications on woody debris, by publication year (accessed 25 November 2014 from the Scopus database, www.scopus.com).

SDTs and DWD populations and methods used to quantify their volume, biomass, and C attributes. A sensitivity analysis using data compiled from the United States' NFI is presented as a case study to highlight the importance of selecting the appropriate metrics to quantify C stores and fluxes. The second section emphasizes the differences between field-based and modeling methods for understanding C flux, with an emphasis on its role within forest dynamics. The particulars of how forest simulation models address woody debris dynamics (with an emphasis on empirical model designs) are subsequently discussed. We conclude by highlighting information gaps and research needs. This assessment will aid forest and conservation managers who seek to restore and maintain target woody debris populations, and it can inform policy related to the role of forests in sequestering and storing atmospheric C.

Table 1
Abbreviations used throughout this review (units, if applicable, in parentheses).

Abbreviation	Description
A_{LARGE}	Cross-sectional area at largest-diameter end of piece of downed woody debris
A_{SMALL}	Cross-sectional area at smallest-diameter end of piece of downed woody debris
C	Carbon
C_{CONC}	Carbon concentration
CHS	Critical height sampling
DBH	Diameter at breast height (cm)
DC	Decay class
DCRF	Decay class reduction factor
DEF	Dukes Experimental Forest
DRS	Diameter relascope sampling
DT	Downed woody debris piece diameter (m) at point of intersection
DWD	Downed woody debris
DWD_C	Carbon of downed woody debris piece (kg)
DWD_{VOL}	Volume of downed woody debris piece (m^3)
FIA	Forest Inventory and Analysis Program of the United States
FFE	Fire and Fuels Extension to the Forest Vegetation Simulator
HLS	Horizontal line sampling
HPS	Horizontal point sampling
IPCC	Intergovernmental Panel on Climate Change
L	Transect length (m) used in line intersect sampling
LEN	Downed woody debris piece length (m)
LIS	Line intersect sampling
MHLS	Modified horizontal line sampling
NFI	National forest inventory
PEF	Penobscot Experimental Forest
PRS	Point relascope sampling
SDT	Standing dead tree
SRF	Structural reduction factor
TRS	Transect relascope sampling
VOL	Volume of downed woody debris (m^3 ha^{-1})
WD	Wood density (kg m^{-3})

2. Quantifying woody debris stores

2.1. Strategies for estimating carbon in woody debris

Despite the structural importance of coarse woody debris, its attributes have not traditionally been the focus of forest inventories (Kenning et al., 2005; Ritter and Saborowski, 2014). Ståhl et al. (2001) review several methods for sampling woody debris; however, additional field verifications and novel methodologies have emerged since their original assessment. A number of sampling strategies can be used for characterizing SDT and DWD volume, biomass, and C, each with strengths and weaknesses (Table 2). In this section, we review the methodology for determining C content of a woody stem to be used in the sampling methods that follow.

In the most general case, the cross-sectional area and concentration of C and wood density both vary along the length of a woody stem. The volume of a stem can be determined by knowledge of its average cross-sectional area and either height (in the case of SDTs) or length (in the case of DWD), while conversion of volume to C content requires knowing wood density and C concentration. Due to the impracticality of determining C concentration along the length of a stem in most inventories, C mass is typically calculated as 50% of wood mass (IPCC, 2003), although species-specific values exist for some regions (e.g., Lamlom and Savidge, 2003). Subsequent calculation of gross SDT or DWD volume requires information such as the state of decay and structural reduction of woody debris. In the context of forest inventories, the two main methods for stem volume estimation are from models based on empirical measurements or using various Monte Carlo-based methods to estimate volume directly from simpler measurements. Monte Carlo-based methods provide a unified

Table 2
Overview of key sampling methods for standing dead trees (SDT) and downed woody debris (DWD) biomass and carbon.

Method	Description	Pros	Cons	Citation (s)
Standing dead trees				
Fixed-area sampling	Sample all SDTs within a fixed area	Practical to implement in the field; efficient for tracking mortality if plots are remeasured	May not be as efficient as other methods for predicting attributes other than SDTs per unit area	Ståhl et al. (2001)
n-tree	Sample the closest *n* SDTs from a sample point	Cost-effective for rapid inventory; can set a limit for the maximum search distance	May underestimate the number of SDTs when *n* is low; does not display design-unbiasedness	Moore (1954), Cottam and Curtis (1956) and Kenning et al. (2005)
Strip sampling	Sample SDTs in predetermined strips	Practical to implement in the field; analogous to fixed-area samples; efficient for sampling rare SDTs (e.g., a certain species, quality)	Need to account for DWD if they are partially within the plot; planning the location of strips is needed (e.g., parallel to environmental gradients)	Stehman and Salzer (2000)
Airborne laser scanning	Relate height distribution derived from airborne laser scanning to vertical structure of vegetation to characterize SDTs	Detecting SDTs can be accomplished using area- or single-tree based techniques; can be effective across large areas	SDT quality (e.g., decay stage) is difficult to measure; quantifying biomass and C remains largely untested	Pesonen et al. (2008), Bater et al. (2009) and Maltamo et al. (2014)
Downed woody debris				
Fixed-area sampling	Sample all DWD within a fixed area	Practical to implement in the field	Need to account for DWD if they are partially within the plot	Ståhl et al. (2001) and Gove and Van Deusen (2011)
Line-intersect sampling	Sample DWD along a transect line	Wide application in national forest inventories and for estimating forest fuel loads; 50 years of methodological development	Calculations of population-level summaries can be complex	Warren and Olsen (1964), Van Wagner (1968), Brown (1974) and Woodall and Monleon (2008)
Strip sampling	Sample DWD in predetermined strips	Practical to implement in the field; analogous to fixed-area samples	Need to account for DWD if they are partially within the plot; planning the location of strips is needed (e.g., parallel to environmental gradients)	Stehman and Salzer (2000)
Point relascope sampling	Employ a wide-angled relascope and sample all DWD whose lengths completely fill the relascope	Theory is based on angle gauge sampling, a common sampling regime in forest resource inventories	Potential for field bias in thick understories or dense slash fields	Gove et al. (1999, 2001) and Ståhl et al. (2001)
Transect relascope sampling	Sample DWD along a transect using a relascope	Produces lower standard error for cost relative to fixed-area plots and line-intersect samples; less sensitive to the orientation of DWD than line-intersect sampling	Likely need to subsample logs for volume; Largely untested for examining biomass and C	Ståhl (1998)
Airborne laser scanning	Relate height distribution derived from airborne laser scanning to vertical structure of vegetation to characterize DWD	Estimates of DWD volume may outperform estimates derived from field measurements of live trees; can be effective across large areas	DWD quality (e.g., decay stage) is difficult to measure; single-tree detection techniques are problematic; quantifying biomass and C remains largely untested	Pesonen et al. (2008) and Maltamo et al. (2014)
Perpendicular distance sampling	Measure the perpendicular distance to DWD and compare to cross-sectional area of the log at the point of measurement	Samples DWD with probability proportional to volume; can set a limiting distance for sampling DWD (Gove et al., 2012)	Potential for field bias in thick understories or dense slash fields	Williams and Gove (2003), Williams et al. (2005), Ducey et al. (2008), Valentine et al. (2008) and Gove et al. (2013)
Critical length sampling	Sum the critical lengths of DWD sampled with a relascope or wedge prism	Can be combined with critical height sampling for rapid estimation of both live and dead tree volume	Field performance on irregularly-shaped DWD pieces is uncertain. Experience with this technique in the field is not widespread	Ståhl et al. (2010)
Diameter relascope sampling	DWD is measured if the angle extended through the midpoint diameter is greater than a critical relascope angle; conducted by doing “prism sweeps”	Greater statistical power compared to fixed area plots and line intercept sampling	Efficiency can vary when DWD diameter and length differ substantially; Difficulty in measuring DWD obscured by trees, undergrowth, and litter	Bebber and Thomas (2003)
Line intersect distance sampling	Combines aspects of perpendicular distance sampling with line intercept sampling	More precise estimates of DWD volume than line intercept sampling	Requires more time in the field than line intercept sampling; may not be efficient if DWD frequency is the primary variable of interest	Affleck (2008, 2010)

theory for integrating both line and point samples (Valentine et al., 2001). Model-based estimators of volume have found large acceptance and coverage in the literature, and are discussed more in §2.2.2. Monte Carlo methods can be classified as those that result from a given sampling protocol, or those that can be applied independently to any first-stage sampling method via a second stage subsample (e.g., crude Monte Carlo sampling and importance sampling; Gregoire and Valentine, 2008; their Chap. 4). Monte Carlo methods provide one or more unbiased selection points along the stem if additional measurements are desired (e.g., wood density) and are more easily accomplished on DWD than on SDTs.

2.2. Sampling methods for woody debris

A variety of sampling methods are available to estimate C in forests. Field sampling methods that are augmented for the estimation of wood volume can be optimized for the estimation of C (Van Deusen and Roesch, 2011). In general, these are unequal probability methods that sample proportional to some auxiliary variable that is closely correlated with volume or (even better) observed volume. A number of methods are available in the former category, but very few in the latter are available for both SDTs and DWD. The choice in NFIs, however, is seldom based on optimization for a single attribute such as C due to the complexity and range of forest measurements desired. In such cases, sampling methods that perform well for a wider variety of attributes are often preferred. Design parameters include those that influence the size and shape of the inclusion zone (e.g., plot radius, line length, and relascope angle) and also may include minimum size specifications for standing and downed material. Such parameters are specific to the objectives of the inventory. Varying the size of the inclusion zone for a given sampling method is an effective method for adjusting the number of individuals included on a particular sample point (e.g., for line-based methods, the sample point is assumed at the center of the line segment), but comes with an increase in sampling effort, directly influencing the cost of the survey. For search-based methods, which form the majority of methods, larger inclusion areas can also lead to implementation bias through lack of detection of all stems on a given point.

2.2.1. Standing dead trees

Fixed-area plots are perhaps the simplest and most general method for sampling forest attributes (Gregoire and Valentine, 2008; their Chap. 7). The geometric arrangement of the physical plot itself can be readily modified to fit the sampling objectives, using either rectangular or circular designs. Fixed-area plots select individuals with probability proportional to frequency, a protocol which serves well if the interest is in estimating the number of pieces per unit area. However, fixed-area plots are not the most efficient for the volume or C content of SDTs. The relative rarity of SDTs in many systems also poses challenges, as plots designed for conventional live-tree inventories will often contain zero SDTs and may have a high sampling variance. However, narrow rectangular plots (often termed strips or belt transects) can be efficient for inventorying rare features of standing dead wood biomass and C (e.g., SDTs of a specific size, quality, or species) because of the increased inclusion area in such designs, coupled with a relatively simple and rapid search on each side of the center line of the plot or transect.

Fixed-area plots are the dominant method used to sample SDTs in ecological studies and NFIs (Woodall et al., 2009). Estimates of various components of change important for NFIs are facilitated under fixed areal designs. Such a framework is efficient in the field given that live trees are likely be sampled within the same plot as SDTs. Particularly if plots are monumented and revisited in the future (i.e., permanent sample plots), the use of fixed-area plots is attractive because their measurements provide insight into SDT dynamics (e.g., fall rates, change in decay stage, loss in height), which are easily calculated under such designs. Plot size and minimum threshold tree diameter are two key considerations when planning inventories because of the direct influence of these criteria in assessing the abundance of SDTs. For example, Woodall et al. (2012a) observed that nearly 45% of plots in the US NFI contained no SDTs (considering a 0.07-ha area and a minimum tree diameter threshold of 12.7 cm), ultimately hampering modeling efforts of SDT biomass and C from such inventories. Additional analyses suggest that SDTs sampled using small fixed-area plots may be difficult to use when modeling the presence and abundance of SDTs because a sizeable number of plots may contain zero observations of standing dead wood, i.e., the problem of zero inflation (Eskelson et al., 2009; Woodall et al., 2012a; Woodall and MacFarlane, 2012; Russell, 2015).

Angle gauge sampling at points (also termed Bitterlich, prism, or horizontal point sampling [HPS]; Bitterlich, 1948; Grosenbaugh, 1952, 1958) has arguably become one of the most widely used methods for inventorying live trees. The attraction for C inventories is the selection of SDTs with probability proportional to basal area, which is correlated with stem volume and C content. In such designs, more sampling effort is concentrated on higher-volume stems. When sampling for SDTs, horizontal line sampling (HLS), which uses an angle gauge along a line, might be more expedient since it enlarges the inclusion area for each tree through the line length. Enlarging the inclusion zone can also be done by modifying the gauge or prism factor in point sampling. However, the larger the inclusion zone on the point, the higher the probability of missing trees that are further away from the point center because each tree's respective plot radius increases accordingly. The HLS method allows one to expand the inclusion zone by employing a longer line length, while maintaining a reasonable perpendicular distance from the line in which trees are selected via a reasonable gauge angle, thus limiting the possibility of non-detection. The two methods have been combined into a hybrid method known as modified horizontal line sampling (MHLS), which was specifically developed for sampling SDTs and other rare features like cavity trees (Ducey et al., 2002). The MHLS approach combines the attributes of both point and line sampling with an angle gauge while requiring little extra effort over a pure HLS inventory and was found to be time-efficient in field performance (Kenning et al., 2005). Finally, Ducey (2009) introduced an extension to generalized horizontal point sampling (Zöhrer, 1978, 1979), a method based on angle gauge sampling that allows the selection of stems with probability approximately proportional to biomass. This approach introduces some complexity, which could lead to field errors despite its theoretical advantages. The approach is relatively untested for SDT inventories but could prove useful in appropriate situations.

Both fixed-area plot sampling and angle gauge sampling for SDTs typically rely on a volume model in order to convert field data to C content. Second stage subsampling using independent Monte Carlo methods are an option, but a design-unbiased alternative exists for volume estimation under both HPS and HLS that is an intrinsic part of the sampling protocol. Critical height sampling (CHS; Kitamura, 1962; Iles, 1979) can be used to select a random subsample point along the stem that is determined based on the location of the first-stage HPS sample point. A simple augmentation to CHS in the form of antithetic importance sampling both reduces the variance of the original CHS estimator, and repositions the subsample point to one that is more easily measured from the HPS point location (Lynch and Gove, 2014). Lynch (2014) extended this work to HLS, and these extensions could also be applied to create a design-unbiased subsampling protocol for volume under MHLS. Horizontal point sampling has been adopted in NFIs, and was used in the United States' NFI program using a 10-point cluster design beginning in the 1960s (LaBau et al., 2007; pp. 24–25). This design was modified in 1995 to favor a four-point fixed-area cluster design (LaBau et al., 2007; p. 45), which was subsequently annualized.

Several additional promising methods of inventorying SDTs have recently been introduced and have been applied in specific forest types. One method, termed n-tree sampling, is conducted by measuring the closest n trees to a plot center (Moore, 1954; Cottam and Curtis, 1956). Kenning et al. (2005) report success in using n-tree sampling to measure SDT abundance (e.g., count per ha) but found inconsistent results when investigating basal area. The n-tree method would seemingly provide similar inconsistencies if SDT biomass is of interest. In general, n-tree methods are fast but lack a guaranteed unbiased estimating equation. Given their present state of development, such methods seem most useful for rapid assessments where unbiasedness is not absolutely required.

2.2.2. Downed woody debris

Fixed-area plots are also widely used for sampling DWD. As with SDTs, plots or strips of various dimensions may be used. Portions of DWD that cross the plot boundary present a challenge when using fixed-area plots, as a decision must be made to determine which pieces or portions of pieces must be inventoried. Gove and Van Deusen (2011) recently reviewed three protocols for sampling DWD on circular plots. With the first protocol, a selection point is determined on the piece as one of the design parameters—if that point falls within the plot, the entire piece is sampled, including portions extending beyond the plot boundary. Generally the selection point is chosen as the largest end of the log, hence the protocol is termed the "stand-up" method since it would be analogous to standing the stem up inside the plot and sampling it as if it were a SDT. This protocol ignores portions of DWD that are rooted outside the plot but fell within the plot boundary, the assumption being that the non-measured volume from such pieces is balanced by the "extra" volume measured on pieces originating within but extending beyond the plot boundary. A second protocol, termed the "chainsaw" method, includes only those sections of DWD that are inside the plot, as if one took a chainsaw around the plot circumference. This protocol is unbiased for volume, but not for density. A solution was found employing the "sausage" protocol which allows for sampling an entire piece of DWD if any part of it falls within the plot (Gove and Van Deusen, 2011). This protocol selects pieces with probability approximately proportional to length rather than frequency, so it would be preferred when the target variable is related to volume, and it requires estimating equations that differ from the usual fixed-area plot equations. These latter two protocols have no analogy for SDTs, though they are compatible with SDT fixed-area plot designs. Fixed-area plots are used in several European NFIs, however, there is a lack of reporting on the exact protocol used by these countries (Woodall et al., 2009; Gove and Van Deusen, 2011), which hinders the assessment of the method for depicting biomass and C stocks. Fixed-area designs require either a volume model (to convert field-measured dimensions to stem volume) or a second stage Monte Carlo subsample for the estimation of volume as there currently is no intrinsic Monte Carlo protocol.

Another widely used method of sampling DWD is line intersect sampling (LIS), introduced to forestry by Warren and Olsen (1964) as a method for sampling logging residue with probability proportional to length. The LIS method was further developed to rapidly quantify forest fuel loads to assess fire risk (Van Wagner, 1968; Brown, 1974). The LIS method has an intrinsic Monte Carlo version of the estimator due to the random intersection point of the log and line segment, requiring only the measurement of cross-sectional area to estimate volume. The theory of LIS has been rigorously studied by Kaiser (1983) and de Vries (1986; their Chap. 13), with recent exposition, including use of multiple line segment designs, found in Gregoire and Valentine (2008; their Chap. 9). An important consideration here is the length of transects sampled, as longer transects yield more precise estimates, and longer transects are required in areas with sparse DWD pieces (Pickford and Hazard, 1978; Woldendorp et al., 2004). Another important consideration is the arrangement of multiple transects, as a number of reasonable options have been suggested (Van Wagner, 1968; Woldendorp et al., 2004). Line intersect sampling is dominant throughout North American NFIs (Woodall et al., 2009), largely because of its time efficiency, given that a minimum of one diameter measurement is required on the subset of DWD pieces intersected by the transect line. For the US NFI, detailed documentation exists for computing volume, biomass, and/or C using line intersect samples (e.g., Waddell, 2002; Woodall and Monleon, 2008; Domke et al., 2013; Woodall et al., 2013). Such work that details the methods associated with calculating population-level estimates of DWD have no doubt promoted the implementation of line intersects samples in forest C accounting.

Several methods that use an angle gauge (or relascope) have recently been developed that are similar to the techniques used for standing trees. Ståhl (1998) developed transect relascope sampling (TRS) as an extension to LIS to include DWD off the line segment, thus augmenting the usual LIS count in woodlands with sparse DWD. The TRS method selects pieces with probability proportional to length (similar to LIS and the fixed-area sausage protocol) and has performed well in both field and simulation studies (Ståhl, 1998; Pesonen et al., 2009). Building on Ståhl's work, Gove et al. (1999) developed a point-based version termed point relascope sampling (PRS) that samples DWD with probability proportional to length-squared. The PRS method has been tested against various other methods for measuring DWD attributes in northern hardwoods (Jordan et al., 2004), mixed-species stands in the northeastern US (Brissette et al., 2003), and in commercial forests of central Finland (Pesonen et al., 2009), where it was generally found to be more time efficient than competing methods such as LIS and fixed-area plots (using a stand-up protocol) for volume estimation. Both methods use a wide-angled relascope for sampling DWD when evaluating the length of the piece. A design-unbiased extension to PRS was developed by Gove et al. (2005) providing an intrinsic Monte Carlo-based estimator for volume. An alternative method termed diameter relascope sampling (DRS; Bebber and Thomas, 2003) uses a prism to select DWD based on midpoint diameter with implicit volume model based on Huber's formula (e.g., Fraver et al., 2007). In independent simulation studies, both Bebber and Thomas (2003) and Williams and Gove (2003) found little difference in the performance of DRS and PRS for estimation of volume. Ståhl et al. (2010) proposed an additional method that uses a prism to determine a critical length on a DWD piece, defined as the length between points on the stem that are exactly borderline when evaluated by a prism from the sample point. This method is related to both DRS and to CHS of standing trees.

Valentine et al. (2008) proposed perpendicular distance sampling (PDS; Williams and Gove, 2003) as the most appropriate method for C estimation in DWD, because PDS selects stems with probability proportional to volume. Under PDS framework, a design-unbiased estimate of volume is recovered using a simple tally of the "in" stems on the point. The PDS sampling technique has consistently performed well in simulation studies of volume estimation (Williams and Gove, 2003; Ståhl et al., 2010; Gove et al., 2012). Originally, PDS was envisioned as a method for estimation of DWD volume, but it was subsequently extended to other attributes (Williams et al., 2005; Ducey et al., 2008). Similar to the techniques discussed above, PDS is a search-based method. Depending on several design parameters, search distances can potentially be large when using PDS, which may subsequently contribute to non-detection bias (Williams and Gove, 2003). Distance-limited PDS was introduced to overcome this potential problem by limiting the maximum search distance in field application of PDS to one that is reasonable for the understory conditions in the survey (Ducey et al., 2013; Gove et al., 2013). In all variants of PDS, a Monte Carlo sampling point is intrinsic in the design, which is based on the perpendicular intersection distance with the stem. A related method, termed distance-limited sampling, samples DWD pieces with probability proportional to length, is simple to implement in the field, and has an intrinsic Monte Carlo estimator (Gove et al., 2012).

2.2.3. Airborne laser scanning

A promising and rapidly developing method for quantifying woody debris volumes is the use of airborne laser scanning (e.g., LiDAR). In their assessment of the current state of the method, Maltamo et al. (2014) reported that the accuracy of studies that implement airborne laser scanning for woody debris populations varied considerably. Bater et al. (2009) observed a moderate relationship (Pearson correlation of 0.61) between the proportion of

Table 3
Sampling of key decay class criterion implemented in various woody debris studies.

Country/region	Citation	Type[a]	Number of classes	Limbs/ branches/ twigs present	Bark cover	Wood color	Shape of SDT top	Sapwood condition	Heartwood condition	Wood hardness	Snapped/ nonsnapped	Height	Structural integrity	Texture of rotten portions	Portion on ground	Shape	Covered with vegetation	Invading roots	Moss and fungi present
United States	USDA Forest Service (2012)	SDT	5	x	x	x	x	x	x										
United States	USDA Forest Service (2011)	DWD	5	x	x	x							x	x				x	
Quebec, Canada	Aakala et al. (2007)	SDT	5	x						x	x	x							
Northern Finland/ Northwest Russia	Lännenpää et al.(2008) and Aakala (2010)	SDT	5					x				x							
Northern Finland/ Northwest Russia	Lännenpää et al.(2008) and Aakala (2010)	DWD	6	x												x	x		
Ontario, Canada	Anderson and Rice (1993) and Vanderwel et al. (2006)	SDT	5	x	x		x					x							
North-central Sweden	Söderström (1988) and Kruys et al. (2002)	SDT, DWD	8		x					x						x			
West Carpathians, Poland	Holeksa et al. (2008)	SDT, DWD	8		x					x						x			
Canada	Canadian Forest Service (2008)	DWD	5	x	x								x	x	x	x			
Southeast Norway	Storaunet and Rolstad (2002)	SDT, DWD	5 and 8	x	x			x		x						x			
Eastern United States	Pyle and Brown (1998) and Radtke et al. (2009)	DWD	5		x	x							x			x			
Tasmania, Australia	Grove et al. (2009)	DWD	5	x	x	x							x					x	x
Central Panama	Larjavaara and Muller-Landau (2010)	DWD	5	x	x								x						
Moscow Region, Russia	Temnuhin (1996)	DWD	5	x	x	x							x				x		x
Newfoundland and Nova Scotia	Campbell and Laroque (2007)	SDT, DWD	5	x	x								x			x	x		x
Central Germany	Müller-Using and Bartsch (2009)	DWD	4	x									x			x			
Jura Mountains, Switzerland	Bütler et al. (2007)	DWD	5	x	x	x								x	x	x			

[a] Standing dead tree (SDT); downed woody debris (DWD).

SDTs observed within an area and a LiDAR-derived estimate of the coefficient of variation of canopy height. Eskelson et al. (2012) found little success in quantifying SDTs in various stage of decomposition, which they attributed to disregarding canopy height variability in their analysis.

For DWD, Pesonen et al. (2008) observed that volume estimates derived from airborne laser scanning produced adequate estimates of DWD volume. Such techniques may provide insight into coarse woody debris inputs resulting from disturbance, such as detecting the presence of windthrown trees (Nystrom et al., 2014). Airborne laser scanning techniques may be used in concert with traditional woody debris inventory techniques, as Pesonen et al. (2009) demonstrate in central Finland.

A particular need for remote sensing-based approaches is the development of methods that account for additional woody debris attributes such as species, wood density, decay stage, or nesting cavity presence. Although volume is a common woody debris metric, an assessment of the decay stage is needed for accurate assessments of woody debris biomass and C using airborne laser scanning techniques. The degree to which remote sensing information is integrated with field-based and/or biophysical information can strengthen the usefulness of these data. For example, Eskelson et al. (2012) used Landsat-derived predictors with climate variables and field-based observations of topography and stand attributes from forest inventory plots to compare modeling strategies for estimating the abundance of SDTs. Metrics that describe vertical canopy structure and its associated variability may be essential to refine estimates of SDT biomass and C by size and/or decay class (Bater et al., 2009; Martinuzzi et al., 2009; Eskelson et al., 2012). For DWD, area-based techniques and associated measurements of DWD cover should be pursued, as single-tree detection techniques are problematic (Maltamo et al., 2014).

2.3. Quantifying woody debris attributes

2.3.1. Decay class

Although subjectively assigned in most studies, there is perhaps no more useful measure that reflects the decomposition stage of woody debris than its decay class (DC). These DCs are used in data summaries and analyses to gauge the reduction in volume, biomass, C, and density of highly-decomposed wood, as these four metrics diminish as decomposition advances (Harmon et al., 1986; Fraver et al., 2013). The use of DC systems has a long history of implementation in woody debris studies (e.g., Ingles, 1933; Sernander, 1936; McCullough, 1948). A very large number of published DC systems exist, and to date no standard system has been agreed upon. In the US, there may be a convergence on the five-class system that grew out of work by Maser et al. (1979) and Sollins (1982), in addition to Cline et al. (1980) who addressed SDT decomposition. The US NFI uses a five-class system for DWD (Woodall and Monleon, 2008).

Decay classes are assigned in the field based on tactile and visual criteria, many of which are correlated with wood density. Increasingly, criteria for designating DCs have become more diverse depending on the criteria of interest (Table 3). Tactile criteria may include surface hardness; the ease with which branch stubs pull out; the distance a sharp object can penetrate the log; the ability of the piece to hold weight; and the difficulty with which bark can be removed. Visual criteria may include color; the amount of bark remaining; the presence of leaves, fine twigs, and branches; colonization by plants; the presence of invading roots, crevices, and fragmentation; and cross-sectional shape (round for fresh pieces vs elliptical for highly decomposed pieces). This latter visual criteria is especially important, as it provides one method for estimating the volume that has been lost through decomposition (Fraver et al., 2013).

These criteria may also be related to time since death (Storaunet and Rolstad, 2002; Fast et al., 2008; Angers et al., 2012). For instance, Storaunet (2004) concluded that for *Picea abies* (L.) Karst SDTs the use of branch orders as criteria for classifying SDTs into DCs explained the majority of variance in time since death, and the inclusion of further morphological attributes, such as size or bark cover, led to only minor improvements.

Many studies employ separate DC criteria for SDTs and DWD (e.g., Lännenpää et al., 2008; Aakala, 2010; USDA Forest Service, 2011, 2012), but some use a single DC system for both (e.g., Storaunet and Rolstad, 2002; Holeksa et al., 2008). In addition, the differences in how decomposition progresses between DWD of hardwoods and conifers has led to the application of different criteria to assign DCs depending on species (Pyle and Brown, 1998; Fraver et al., 2002). Angers et al. (2012) point out that an additional problem of current DC systems is the lack of specificity with regard to species and their broad use across a range of ecosystems, which is especially problematic in the tropics, with high tree species diversity (Chambers et al., 2000; Larjavaara and Muller-Landau, 2010). A further shortcoming of the DC system, especially in large-scale inventories such as NFIs, is the repeatability of the classification (Larjavaara and Muller-Landau, 2010), given the subjectivity in assigning classes (Brown, 2002). Toward this end, Larjavaara and Muller-Landau (2010) developed and advocate for a method based on a dynamic penetrometer, the use of which reduced error inherent in subjective estimates. An assumption of the penetrometer is that decay is present from the outside of the log and it is not sensitive to measuring internal decay. For fine woody debris, the assessment of decay class is problematic (Fasth et al., 2010) given their ephemeral nature, small size, and limited approaches available to quantify these C stocks. Most efforts to estimate the C attributes of fine material assume a single decay class reduction factor (e.g., Woodall and Monleon, 2008) or simply separate between decomposed and non-decomposed dead wood (Klockow et al., 2013).

2.3.2. Volume

Similar to live trees, accurate calculation of volume in SDTs depends on measurements of the cross-sectional area at various points along the stem and understanding its degree of taper. Although definitions vary, SDTs are typically defined as those trees with a diameter at breast height (DBH) and height greater than specified thresholds with a lean angle less than 45° measured from vertical. As volume had traditionally been the standard metric for determining the merchantable product in live trees, assessment of volume in SDTs has focused primarily on the bole portion. The geometric shapes of SDTs mimic those of live trees, where lower sections display a neiloid shape, middle portions display a parabolic shape, and top sections display a conic shape (Avery and Burkhart, 2002). Less attention has been given to computing the volume in branches, stumps, and bark. Key measurements needed to compute SDT volumes are diameter (e.g., at stump, breast height, and/or top), height, and DC. Measurement of diameters at stump and breast height are relatively straightforward, however top diameters are not as easily obtained. Top diameters can be directly measured on short SDTs (e.g., <2 m), can be visually estimated, or can be measured using a dendrometer such as optical calipers or a relascope. Although there is a tendency for underestimation of the top diameters of SDTs when visually estimated (Harmon and Sexton, 1996), field crews may be able to locate the tops of broken stems and "indirectly" measure the diameter at breakage. Increased use of optical dendrometers in forest inventories should lead to improved SDT top diameter measurements.

With measurements of DBH and height along with a regional equation for the species of interest, a taper equation is commonly used to estimate SDT volume (e.g., Aakala et al., 2008; Russell et al.,

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2012). By estimating volume integrals, employing taper equations allows one to account for volume reductions in SDTs that experienced breakage, without requiring a measurement of diameter at breakage (Aakala et al., 2008). To accomplish this task, measurement of SDT height at breakage is needed. Most taper equations also require intact height, which could be measured in the field using the fallen tops of the snags or estimated through the use of allometric models. Taper equations are generally available for the primary species in forested regions (e.g., Sharma and Zhang, 2004; Westfall and Scott, 2010; Li et al., 2012). Hence, volume can be estimated for any SDT with stem breakage and the same equation can similarly be used for determining the volume for live trees. If taper equations are not available, SDT volume can be determined assuming the frustum of a cone, neiloid, or paraboloid (Harmon and Sexton, 1996) or conic-paraboloid (Fraver et al., 2007) or by employing a general power function based on SDT diameter as in the case of Sweden (Jönsson et al., 2009). The primary concern in using taper equations for dead wood is that their form is likely based on that of live trees. Refinements for implementing taper equations for SDTs include (1) more accurate assessment of live tree versus dead wood differences in volume, particularly for SDTs with frayed breakages and/or intact branches, and (2) determination of the presence/absence of bark in the calculation of SDT volume, particularly as bark ranges from 4% to 26% of total stem volume, tapers along the length of the bole (Maguire and Hann, 1990) and varies by species (Woodall et al., 2011; their electronic appendix REF_SPECIES.xlsx).

Obtaining volume in DWD pieces is somewhat more straightforward than SDTs primarily because of the ease of measuring diameters and lengths of individual pieces, assuming one of several available geometric forms (Fraver et al., 2007). Woody debris with a diameter less than the specified threshold is typically categorized as fine woody debris. Key measurements for determining volume are diameters (at the small- and large-end, midpoint, and/or transect intercept), total length, and DC. Length is an important attribute particularly if managers are interested in a complete assessment of stand structural diversity and habitat requirements for specific organisms (Marshall and Davis, 2002).

Assuming one measures small- and large-end diameters and length, the conic paraboloid form yields DWD volume for individual pieces (Fraver et al., 2007). The conic paraboloid from is shown by:

$$\mathrm{DWD}_{\mathrm{VOL}} = \frac{\mathrm{LEN}}{12}\left(5A_{\mathrm{LARGE}} + 5A_{\mathrm{SMALL}} + 2\sqrt{A_{\mathrm{LARGE}}A_{\mathrm{SMALL}}}\right) \quad (1)$$

where LEN is DWD piece length and A_{LARGE} and A_{SMALL} are the cross-sectional areas at the largest- and smallest-diameter ends of the DWD piece, respectively. Fraver et al. (2007) compared various formulae for determining DWD volume for three species in north-central Sweden and concluded that a conic paraboloid equation form exhibited the lowest bias and greatest accuracy when compared to traditional forms (e.g., Smalian, conical frustrum) that also require small- and large-end diameters and length. However, not all dead wood inventories require end diameters, particularly in line-intersect samples (Woodall et al., 2008), which provide an area-based volume estimate solely from a subsample of diameters at transect intersection. To combat the problems of nonmeasured end-diameters and length, Woodall et al. (2008) present equations to predict small- and large-end diameter in addition to length using diameter measured at transect, DC, and ecological province. The accuracy of such models in determining DWD dimensional attributes (e.g., Woodall et al., 2008 observed R-squared values in excess of 0.60) allows forest resource managers to weigh the advantages of predicting DWD dimensional attributes using static equations with the time and effort required to make detailed measurements on DWD pieces.

Area-based estimates of DWD volume from the LIS can be obtained from the following formula:

$$\mathrm{VOL} = \left(\pi^2 \sum \mathrm{DT}^2/8L\right) \times 10{,}000 \quad (2)$$

where VOL is the volume ($\mathrm{m}^3\ \mathrm{ha}^{-1}$), DT is the DWD piece diameter (m) at point of intersection, and L is the total transect length (m; Van Wagner, 1968).

Although the degree of hollowness is rarely measured on dead wood (particularly for SDTs) due to difficulties in determining internal decay, it would diminish woody debris volume as well as reduce DWD residence time (Hale and Pastor, 1998). Volume in the stumps of SDTs may be estimated using DBH-based models, as in Raile (1982), Westfall (2010) and Söderberg et al. (2014).

2.3.2.1. Structural reduction. Determining woody debris mass loss through decomposition requires linking wood density with volume reduction. That is, the use of wood density alone underestimates biomass loss because it fails to consider volume loss as decomposition progresses (Harmon et al., 1987; Næsset, 1999; Zell et al., 2009; Fraver et al., 2013). Nevertheless, density reduction is often used as a surrogate for mass loss: from 37 wood-decomposition studies reviewed by Laiho and Prescott (2004; their Table 4), only five investigated the mass loss of woody debris while most studies focused on density reductions. Hence, structural reduction factors (SRFs) are needed to fully account for woody debris volume loss.

Structural loss in SDTs (e.g., the loss of tops and branches, peeling of bark) is almost always considered as part of the qualitative assessment of DC (e.g., Cline et al., 1980; Tyrrell and Crow, 1994; Duvall and Grigal, 1999; Aakala et al., 2007; USDA Forest Service, 2012; and others). Of particular importance in calculating the volume of SDTs (and ultimately their biomass and C content) is the computation of SRFs not only by DC but also by tree component (i.e., tops and bark). Theoretically, if SDT height is measured as part of an inventory, an accurate assessment of bole volume should result, given it would account for the breakage and/or snapping of SDTs. However, as most inventory protocols neglect measurement of SDT height and top diameters, approaches that account for volume loss are needed. Not surprisingly, incorporating SRFs for SDTs lends to substantial decreases in SDT biomass. For example, after taking into account both SRFs and DC reduction factors, Domke et al. (2011) reported that the proportion of biomass in tops and branches was 19% and 11% higher for *Populus tremuloides* Michx. and *Pseudotsuga menziesii* (Mirb.) Franco, respectively, for SDTs in DC 1 versus DC 5.

Also termed collapse ratios (Fraver et al., 2007, 2013), SRFs for DWD are a measure of the volume of DWD remaining, mathematically stated as the cross-sectional height of a DWD piece divided by its width. This ratio, which defines the elliptical cross-sectional shape of well-decomposed logs, results from the log's gradual collapse under the force of gravity, due to internal voids and structural degradation (Fraver et al., 2013). Whereas SRFs for SDTs relate to structural loss in various tree components, SRFs for DWD are required because log width (long-axis diameter parallel with the forest floor) but not log height (short-axis diameter perpendicular to the forest floor) is recorded using calipers during typical field inventories. Using only the log width over-estimates the volume of well decayed DWD (i.e., DC 4 and 5). Interestingly, reported values for DWD SRFs seem to vary little globally. For example, SRFs for DC 5 logs of *Pseudotsuga menziesii* in the US Pacific Northwest (0.43; Means et al., 1985; Spies et al., 1988) are similar to those of several conifer and hardwood species examined in the US Lake States (0.42 and 0.41; Fraver and Palik, 2012; Fraver et al., 2013) and to *Picea abies* in the Czech Republic (0.50; Svoboda et al., 2010; Fig. 3). Similarly, using a DC system employing eight classes on *Picea abies*, *Pinus sylvestris* L., and

Fig. 3. Structural reduction factors by species for downed woody debris compiled throughout the literature for studies that implement a five-stage decay class system. Error bar for Fraver et al. (2013) study denotes one standard deviation.

Betula pubescens Ehrh. logs in north-central Sweden, Fraver et al. (2007) observed mean SRFs of 0.81, 0.63, and 0.38 for DC 6, 7, and 8, respectively (analogous to DC 3, 4, and 5 in a five-class system). Hence, given the variety of species and agents of decomposition influencing structural reduction in DWD globally, reported values for SRFs are consistent and strongly related to stage of decomposition (Means et al., 1985; Spies et al., 1988; Fraver et al., 2007, 2013; Svoboda et al., 2010).

2.3.3. Biomass

2.3.3.1. Wood density. To convert field-measured volumes to mass (and ultimately C), we must begin with a knowledge of wood density (WD; typically expressed as dry mass/fresh volume) of our woody debris samples (i.e., mass = density × volume). Researchers often estimate the density of woody debris from field-collected samples to develop density-depletion curves (e.g., Lambert et al., 1980; Foster and Lang, 1982; Krankina and Harmon, 1995; Duvall and Grigal, 1999; Laiho and Prescott, 1999; Næsset, 1999; Fraver et al., 2013; and others). Initial, non-decayed densities can be obtained for individual species from sources such as the USDA Forest Service's Wood Handbook (Forest Products Laboratory, 1999; Zanne et al., 2009). However, given that wood density generally decreases as decomposition advances, DC- and species-specific density reduction factors are essential, which may be obtained from published sources (e.g., Harmon et al., 2008). Species and DC explain greater than 80% of the variability associated with wood density (Seedre et al., 2013); hence, many studies present WD not only by species but also by DC and woody debris position (e.g., Duvall and Grigal, 1999; Fraver et al., 2002; Paletto and Tosi, 2010; Seedre et al., 2013).

2.3.3.2. Decay class reduction. The ratio of the density of a decomposed piece of woody debris to that of a non-decomposed piece may be termed a DC reduction factor (DCRF). In particular the development of DCRFs have the ability to reduce uncertainty in predicting woody debris biomass and C stocks using field data (Harmon et al., 2008, 2011b). For example, Harmon et al. (2011b) synthesized woody debris density data from the northern hemisphere to estimate DCRFs for woody debris in various stages of decay.

Such DCRFs are occasionally available for individual species; however, researchers are often limited by few observations of species in each DC. Hence, DCRFs are often presented according to position (SDT or DWD) and general species group (conifer or hardwood) of woody debris (Waddell, 2002; Harmon et al., 2008, 2011b). For a given DC, DCRFs for DWD will typically be less than those for SDTs given differences in decomposition agents for downed versus standing debris (Harmon et al., 2011b). In terms of biomass and C accounting, DCRFs are a critical consideration when quantifying dead wood pools, as they may substantially overestimate SDT stocks if ignored (Harmon et al., 2011b). When coupled with SRFs, these factors could result in reductions of SDT biomass by as much as 50% (Domke et al., 2011).

2.3.4. Carbon

The C concentration (C_{CONC}) of woody debris is rarely measured as a part of strategic forest inventories. Therefore, a preliminary assumption is that C represents 50% of biomass (obtained from woody debris volume; IPCC, 2003; Woodall and Monleon, 2008; Heath et al., 2009; Smith et al., 2013). Mäkinen et al. (2006) concluded that C concentration during decomposition remained close to the generic 50%. Lamlom and Savidge (2003) concluded that C concentration varied substantially within individual trees and among species. Weggler et al. (2012) observed that default values for C concentration overestimated woody debris C by 31% when compared to species-specific values for common species occurring in Switzerland. Harmon et al. (2013) showed that C concentration varies for wood versus bark and that it changes throughout the decomposition process. Assuming identical C concentration values for both bark and wood may result in an inaccurate portrayal of woody debris C stores, particularly if one is interested in their decomposition dynamics (Shorohova and Kapitsa, 2014). Incorporating C_{CONC} values by DC, position (i.e., SDT versus DWD), and species (when available for the region of interest) can help to reduce the uncertainty of C attributes. Improvements in volume-biomass-C conversion factors, through detailed field and laboratory measurements, could help to refine the C accounting framework for woody debris.

2.3.5. Measurement error

Accurate measurements of dead wood dimensions and their associated attributes are needed to reliably determine forest carbon stocks. Measurement errors on SDTs and DWD can propagate when scaled to estimate stand, landscape, and national populations. The effect of measurement errors on population estimates has been examined in live trees, e.g., a 10% bias in the measurement in tree diameter at breast height can lead to a 25% error in stand basal error (Gertner and Dzialowy, 1984). Such examinations on the sensitivity of measurement errors in dead wood have focused on data quality control techniques. Using a metric of DWD taper and relative size, Woodall and Westfall (2008) identified 3% of all DWD measurements across the United States as potential outliers. An analysis of DWD quality assurance indicated poor to moderate repeatability of DWD measurements, but these inconsistencies had little impact on plot-level estimates of forest fuels (Westfall and Woodall, 2007). The choice of model functional form similarly impacts the volume, biomass, and carbon content of forest dead wood. For example, Fraver et al. (2007) observed as much as a 17% bias when computing the volume of DWD depending on which equation was implemented. Ensuring data quality protocols when measurements occur in the field, particularly in multi-resource inventories where dead wood are one of many attributes being collected, and justification on the use of selected model forms can allow one to understand and control the influence of measurement errors on dead wood populations.

2.4. Case study: Quantifying woody debris in the US national forest inventory

The US Department of Agriculture-Forest Service's Forest Inventory and Analysis (FIA) program is responsible for inventorying forest resources across the US, including live trees, SDTs, and DWD. Permanent sample plots are established across the US using a three phase inventory (Bechtold and Patterson, 2005). During the inventory's first phase, sample plot locations are established at an intensity of approximately one plot per 2400 ha. If the plot lies partially or wholly within a forested area, field personnel visit the site and establish a second phase inventory plot where all standing trees (live and dead) and site attributes are measured. During FIA's third phase, a subset of plots (approximately one of every 16 phase two plots) is sampled for downed woody materials including DWD. All data were obtained from the FIA data access website (USDA Forest Service, 2014).

Sensitivity analyses are effective tools for quantifying forest attributes through their ability to reveal which parameters cause the greatest fluctuation in predictions when perturbed (Weiskittel et al., 2011). Given that estimating woody debris is dependent on multiple inputs (e.g., WD, SRF, DCRF, C_{CONC}), we performed a sensitivity analysis to examine which factors have a stronger influence on SDT_C and DWD_C predictions using recent FIA data collected across the United States. Although some FIA plots have been remeasured once or twice, we restrict our analysis to using only the most recent measurement of an FIA plot (generally within the past five to ten years) and emphasize the sensitivity of the input variables (i.e., not their uncertainty).

2.4.1. Data

Standing dead trees are defined in the FIA program as stems ⩾12.7 cm DBH, and they are collected on four circular subplots with a 7.2-m radius spaced 36.6 m apart. This main plot totals 0.07 ha in area. Nearly 493,000 SDTs were available for analysis, upon which 43% and 57% of SDT observations were made on conifer and hardwood species, respectively (Supplemental Material 1).

Gross volume for SDTs was initially calculated using regional volume equations, then converted to sound volume after taking into account merchantable stem reductions (Woodall et al., 2011). To compute bole biomass, sound volume was multiplied by species-specific initial wood density (Miles and Smith, 2009). To compute the biomass of additional SDT structures (e.g., tops and bark), the component ratio method (Woodall et al., 2011) was implemented to calculate the biomass of these structures based on tree component proportions presented in Jenkins et al. (2003). The DCRFs for SDTs were obtained from Harmon et al. (2011b; their Table 6). Standing dead tree SRFs were obtained from Domke et al. (2011; their Table 2) for tops/branches and bark by DC (there were no SRFs for boles and stumps). Carbon concentrations for SDTs were obtained from Harmon et al. (2013; their Table 3). To summarize, SDT_C was estimated by:

$$SDT_C = SDT_{BIO} * DCRF_{SDTkn} * SRF_{SDT} * C\text{-}CONC_{SDTkn} \quad (3)$$

where SDT_{BIO} is the sum of biomass in the bole, tops, bark, and stumps, $DCRF_{SDTkn}$ is the decay class reduction factor of a given species group n (i.e., conifer versus hardwood) in a DC k, SRF_{SDT} is the mean structural reduction factor for the bole, top, bark, and stump, and $C\text{-}CONC_{SDTkn}$ are the C concentrations for a species group n in a DC k. Summary statistics for SDT volume, biomass, and C are presented in Supplemental Material 1.

Downed woody debris is defined in the FIA program as woody debris in forested conditions with a diameter greater than 7.62 cm along a length of at least 0.91 m and a lean angle greater than 45° from vertical (Woodall and Monleon, 2008). Woody pieces are sampled on each of three 7.32-m horizontal distance transects using an LIS design. These transects radiate from each FIA subplot center at azimuths of 30°, 150°, and 270°, totaling 87.8 m for a fully forested inventory plot. Data collected for every DWD piece include location information (i.e. plot, subplot, and transect number) and individual piece attributes (transect, small-end, and large-end diameters, DC, length, and species). Length is defined as the total length of the DWD piece between the small- and large-end diameter measurements. A DC of one indicated the least decomposed (freshly fallen log), while a DC of five is an extremely decomposed log (Sollins, 1982; Waddell 2002; Harmon et al., 2008). For DC 5 pieces, species is not identified, and end diameters are not measured to gain field efficiency. Nearly 368,000 DWD pieces were available for analysis, upon which 86% and 14% of DWD observations were made on conifer and hardwood species, respectively (Supplemental Material 1).

Volume was computed for DWD by assuming a conic–paraboloid form (Fraver et al., 2007; Eq. (1)) using small- and large-end diameters and length. For DC 5 pieces, end diameters were estimated using an equation form that employed DC and diameters as independent variables (Woodall et al., 2008; Russell et al., 2014b). To compute DWD_C, five values were multiplied: (1) the volume of DWD (DWD_{VOL}), (2) WD for an individual species m (Miles and Smith, 2009), (3) the DCRF for DWD of a given species group n in a DC k (Harmon et al., 2011b), (4) the SRF for DC k, specified as 1, 1, 1, 0.800, and 0.412 for DC 1, 2, 3, 4, and 5, respectively (Fraver et al., 2013) to account for the gradual collapse of the log through decomposition, producing an elliptical cross-section, and (5) the C concentrations of a given species group n in a DC k (Harmon et al., 2013). To summarize, DWD_C for an individual piece was estimated by:

$$DWD_C = DWD_{VOL} * WD_m * DCRF_{DWDkn} * SRF_{DWDk} * C - CONC_{DWDkn} \quad (4)$$

Summary statistics for DWD volume, biomass, and C are presented in Supplemental Material 1.

2.4.2. Sensitivity analysis framework

We employed generalized boosted regression models (GBMs) to quantitatively assess model sensitivity when predicting SDT_C and DWD_C (Makler-Pick et al., 2011). A GBM analysis allows one to quantify the sensitivity of variables to model parameters. In our case, we were interested in quantifying how sensitive DWD_C and SDT_C were to parameters such as decay class, structural reduction factors, and wood density. In this machine learning algorithm, regression trees are calculated where each tree is designed to predict the residuals from the preceding tree. Of particular interest in a GBM analysis is the relative influence of each input parameter on model output. Relative influence is based on minimizing a loss function after splitting an input parameter within a regression tree, then averaging across all trees generated in the GBM. The relative influence metric for a specific input variable ranges from 0 (no influence) to 100 (complete influence), and the cumulative sum of relative influence scores totals 100. For assessing SDT_C and DWD_C, input parameters examined were WD, SRF, DCRF, and C_{CONC}.

The GBM method as described in Friedman (2001) was implemented for DWD_C and SDT_C using the 'gbm' package in R (Ridgeway, 2013). Each GBM was run using a squared error (Gaussian) distribution with three-way variable interactions and fivefold cross validation. One thousand regression trees were run in total, upon which half of the data were used for training the GBM.

2.4.3. Sensitivity analysis results and implications

Results show that SDT_C was most sensitive to SRF (59.1%), followed by WD, DCRF, and C concentration (Fig. 4). The dominance of the influence by SRFs was not surprising given the relatively coarse values by DC and tree component that were specified (Domke et al., 2011). An interesting finding resides in comparing the DC classification system with that of the SRFs implemented in the US FIA program: for example, the description for a DC 2 piece states that its top "may be broken" yet an SRF for DC 2 defaults to assuming only 50% of a top's biomass remains (Domke et al., 2011). Future refinements in the specification of structural reduction factors for SDTs should emphasize the use of height and diameter and their compatibility with DC classification systems in addition to quantifying species differences in SRFs to the extent possible. Measurements of SDT morphological attributes (e.g., Angers et al., 2012) should help to inform this research gap as they relate to SDT biomass and C.

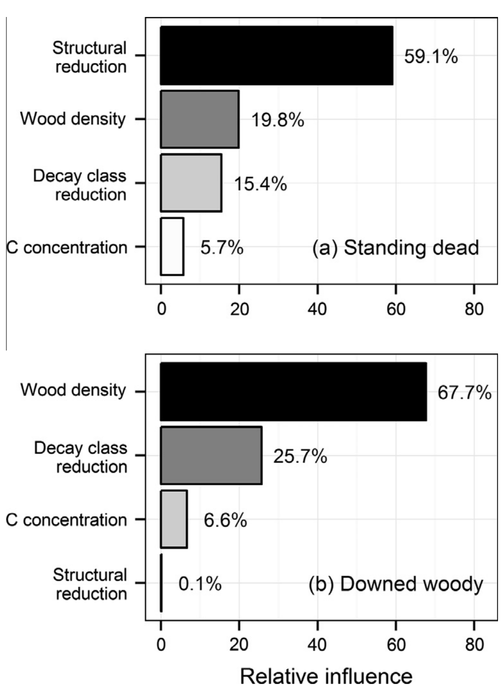

Fig. 4. Results of sensitivity analyses comparing which factors influence total C content of standing dead trees (a) and downed woody debris (b) in the United States' national forest inventory. Relative influence score ranges from 0 (no influence) to 100 (complete influence) using generalized boosted regression models.

In contrast to SDT_C, DWD_C was found to be most sensitive to WD (67.7%), followed by DCRF, C_{CONC}, and SRF. This finding is likely related to the large number of species inventoried in the US NFI, each with a unique initial wood density for DWD (Miles and Smith, 2009). Therefore, in comparing SDT_C and DWD_C estimation strategies, this analysis suggests that species differences may play a larger role in determining the C content of DWD relative to SDTs. This result suggests the need for continued investigation of density depletion as DWD advance in decomposition. The negligible influence of SRFs in depicting DWD_C (e.g., Fraver et al., 2013; Fig. 3) likely speaks to their robustness and stability across the range of species and size classes investigated.

3. Quantifying woody debris carbon flux

3.1. Processes of woody debris carbon flux

Decomposition of woody debris is the result of microbial respiration, physical degradation (i.e., fragmentation and weathering), leaching, and biological transformation. Of these, microbial respiration is considered the main process. For instance, Chambers et al. (2001) estimated that respiration contributed 76% to the loss of C from coarse woody debris. The role of other processes is less well understood, but at least fragmentation is considered important as it continuously exposes more surface area for heterotrophic activity (Bond-Lamberty and Gower, 2008). In a few studies that have attempted to separate these processes, fragmentation and/or leaching have accounted for 10% to 30% of DWD mass loss (Mattson et al., 1987; Chueng and Brown, 1995; Bond-Lamberty and Gower, 2008). Among these, the role of leaching is often considered minor, especially in low-precipitation systems (Mattson et al., 1987; Bond-Lamberty and Gower, 2008). However, leaching is potentially important because it transports dissolved C either into soil pools with short or long residence times, or out of the system (Cornwell et al., 2009), but may contribute little to organic matter inputs into the soil profile (Spears et al., 2003). In ecosystems where termites are present, consumption of dead wood by invertebrates can be of high importance, although the magnitude of this process is not well quantified (Cornwell et al., 2009).

3.2. Field-based methods

Strategies for observing woody debris dynamics in the field involve two primary methods: time series and chronosequence studies. These methods are described by Harmon and Sexton (1996) and Harmon et al. (1999). Time series approaches (i.e., following the same individual woody debris pieces over time) provide a precise estimation of the temporal dynamics of woody debris by examining how various pieces or in some cases cohorts of woody debris advance in decomposition. For example, Alban and Pastor (1993) revisited three species of decomposing logs 11–17 years after felling to determine biomass and nutrient contents. Similarly, Garrett et al. (2012) estimated decomposition rates for branch and root biomass of *Pinus radiata* D. Don using data collected from an initial measurement and a subsequent remeasurement made four years later. The advantages of using a time series method is that the initial conditions of the woody debris piece (e.g., its volume, biomass, C, and nutrient concentrations) can be measured with certainty, site conditions affecting the decomposition process can be held constant (e.g., local climate and soil conditions), and therefore can be easily selected for comparing differences in wood decomposition (e.g., cool versus warm climates; conifer versus hardwood forest types) as affected by biophysical and stand conditions. Upon remeasurement, an accurate assessment of decomposition can be made. Given the long duration of decomposition in woody debris, particularly in colder climates, disadvantages include a considerable investment in time and effort to obtain information. Further, as interest in woody debris studies is fairly recent (i.e., Fig. 2), the required time series needed to assess the temporal dynamics of woody debris are rare or absent for many forest types. Some studies have implemented wooden blocks (e.g., 15-cm in length; Bradford et al., 2014) to determine decomposition pathways using time series methods over shorter time periods (e.g., 13 months). While appropriate for assessing general differences between species, environmental gradients, and fungal colonization patterns, the use of wooden blocks may fail to capture complexities in the decomposition process. These complexities include the influence of bark (e.g., presence/absence), DWD size (both length and diameter), and DWD morphology that can lend to increased variability in decomposition dynamics that may not captured when investigating wooden blocks of a consistent size and limited variability in wood attributes.

Chronosequence studies involve assembling information obtained from a set of woody debris pieces with varying mortality and felling dates spanning lengthy time periods (thereby capturing various sizes and DCs) and subsequently estimating changes in attributes such as volume, density, biomass, and C. Estimates of decomposition derived from chronosequences can be made rapidly and may incorporate the diversity of species and size class distributions of woody debris across an entire forest. However, chronosequence methods also suffer from the inability to accurately estimate initial conditions, fully control site differences affecting decomposition processes, and address concerns in dating the timing of tree death. As emphasized by Harmon and Sexton (1996), inherent to chronosequence studies is the "substitution of space for time" (their page 38). As examples, Lambert et al. (1980) sampled SDTs at various stages of decomposition along transects to estimate changes in mass and nutrients, Ganjegunte et al. (2004) sampled DWD in stands that were thinned one to 13 years previously, and Fraver et al. (2013) located logs with known initial sizes and mortality dates to simultaneously track DWD volume, density, mass, and C dynamics.

The chronosequence approach has several general drawbacks (Johnson and Miyanishi, 2008), but also several that are specifically related to wood decomposition. For instance, Kruys et al. (2002) note that such "snapshot" sampling increases the probability of slowly decomposing DWD to be included in the sample. The usefulness of repeat measurements is well illustrated in the permanent sample plot measurements used by Chambers et al. (2000) in which faster decomposing trees disappeared within the remeasurement interval. As they were originally recorded, Chambers et al. (2000) were able to take this into account, which avoided the underestimation of decomposition rates. Similarly, Storaunet (2006) indicates that sampling in non-equilibrium conditions may either under- or overestimate decomposition rates. As an example, sampling close (in time) to an episodic disturbance would increase the number of fast-decomposing trees included in the advanced stages of decomposition, whereas conducting the same sampling far removed (in time) from the same disturbance would increase the number of slow-decomposing trees included in those stages. As a result, fluctuations in DWD input should be considered when sampling (Storaunet, 2006).

Time series approaches can be implemented that combine field-based and modeling methods to quantify woody debris stores (Harmon et al., 1999). Through resampling chronosequences in the field, the changes in woody debris attributes from one state to the next can be assessed, a method referred to as decomposition vectors (Harmon et al., 2000). Decomposition vectors combine time series with chronosequence methods, providing additional insight into the temporal dynamics of woody debris. The use of decomposition vectors can evaluate the commonly assumed negative exponential model of decomposition and result in a finer temporal resolution when investigating the relationship between DWD inputs and forest disturbances (Harmon et al., 2000). Freschet et al. (2012) extended this method by implementing woody debris relative density (current wood density divided by initial wood density) as an alternative for decay stage.

An additional method used in quantifying decomposition has been to estimate decomposition rates from the ratio between dead wood inputs and stores (e.g., Sollins, 1982; Tyrrell and Crow, 1994). The shortcoming of this method is that it assumes equilibrium conditions, which are not likely met in many forest ecosystems and are difficult to verify (Mackensen et al., 2003; Storaunet, 2006; Aakala, 2011).

Information on dead wood attributes is collected routinely as a part of NFIs and other ecological studies that employ permanent sample plots. For countries that conduct dead wood inventories, nearly all measure both SDTs and DWD and the majority employ a four- or five-class system of decay (Woodall et al., 2009). The resulting data provide the opportunity for remeasurements that would shed much light on woody debris dynamics. As an example, although DWD pieces are not individually tracked in the US FIA program, Woodall et al. (2012b) created an algorithm to "match" DWD pieces measured at two distinct time periods using observations of the location of the piece along a transect and its size. Such an effort yielded subsequent analyses of DWD dynamics including the estimation of DC transition models (Russell et al., 2013) and rates of decomposition and residence times (Russell et al., 2014b) for 36 species occurring in the eastern US.

3.3. Modeling methods

Key factors that influence the decay rate of woody debris are the composition of the decomposer community (Liu et al., 2013; Bradford et al., 2014), environment (e.g., temperature and/or moisture; Russell et al., 2013; Crockatt and Bebber, 2014) and substrate type and quality (Laiho and Prescott, 2004). Successful modeling efforts have incorporated several of these factors in describing woody debris C dynamics. Model validation of woody debris C flux estimates is oftentimes nonexistent and would be inherently difficult given the lack of information available from long-term measurements.

3.3.1. Decay class transition models

The work of Kruys et al. (2002) was groundbreaking in its application of a stage-based matrix model to estimate woody debris decomposition dynamics, termed a DC transition model. As DC is related to C content and can also be used as a surrogate measure for the habitat availability for dead wood-dependent species (Martikainen et al., 2000), modeling woody debris dynamics as transitions between decay classes serves a number of purposes. Unfortunately, different classes are often somewhat arbitrary, or tailored to the needs of specific studies, so their usefulness is also questioned (Bond-Lamberty and Gower, 2008).

In the approach of Kruys et al. (2002), the 5-year probability of woody debris advancing in decomposition was quantified by predicting the transition rates between DCs. Vanderwel et al. (2006) extended this approach by including the probability of an SDT falling when characterizing SDT dynamics. The method has been applied to estimate SDT and DWD dynamics for various species and forest types across the world (e.g., Vanderwel et al., 2006; Holeksa et al., 2008; Aakala, 2010, 2011; Russell et al., 2013).

Central to these transition models is the parameterization of the transition probabilities between DCs, often computed from residence times of woody debris in each class. Different studies have estimated these residence times in various ways. For instance, Kruys et al. (2002) used a Horwitz–Thompson estimator that accounts for the problem that trees that decompose slower (i.e., stay in the dead wood pool longer) have a higher probability of being sampled, while Aakala (2010) used the approach suggested by Huggard (1999) to graphically determine residence times from curves depicting cumulative frequencies in different DCs. In general, these parameterizations face the same constraints as studies of DWD decomposition. That is, repeated measurements from permanent plots are rare, and data for parameterization are often obtained from chronosequences with known limitations.

3.3.2. Transition from standing to downed

There are several additional considerations and concerns with using woody debris dynamics models in the context of understanding C dynamics. In particular, a thorough representation of SDT survival is essential in understanding dead wood pools to concomitantly inform both SDT and DWD C dynamics. As discussed by Tyrrell and Crow (1994), live trees can immediately transition into SDT and/or DWD pools through mortality, while an SDT can (1) collapse and enter the DWD pool, (2) fragment partially where a only a portion of the SDT enters the DWD pool, or (3) can remain an intact SDT during the sampling interval. This distinction is important, as mass loss rates (and associated C fluxes) can differ greatly between DWD and SDTs of similar species and decay class. While standing, SDTs may lose very little density (Johnson and Greene, 1991; Krankina and Harmon, 1995; Aakala, 2010). Central to this is estimating the SDT survival rate (defined as the probability of an SDT to remain standing for a specified duration) and its dynamics as it transitions from standing to downed wood. Half-lives for SDTs, defined as the survival probability equal to 0.5, can be as short as six years as observed in mixed-species forests in central Maine, USA (Garber et al., 2005) but may be as high as 35 years for *Pseudotsuga menziesii* in the US Pacific Northwest (McArdle, 1931). To predict SDT survival, curves that employ a reverse sigmoid function are typically estimated based on the number of years since tree death and censoring (e.g., Garber et al., 2005; Vanderwel et al., 2006; Aakala et al., 2008; Angers et al., 2010). Storaunet and Rolstad (2004) concluded that using years since death is most feasible for estimating SDT survival; however, because the actual time when a tree died and entered the SDT population is often unknown, researchers have turned to using surrogates for time since death, such as DC (Russell and Weiskittel, 2012). Important environmental covariates that influence SDT survival curves include tree species, SDT size, agent of mortality, decay stage, stand age, stand density, and type of forest management (Lee, 1998; Garber et al., 2005; Vanderwel et al., 2006; Aakala et al., 2008; Smith et al., 2009; Angers et al., 2010; Russell and Weiskittel, 2012).

Although a DC transition model can be specified to estimate SDT survival (e.g., Aakala et al., 2008), less is understood on the dynamics of SDT height loss and associated DWD inputs. The loss in height of SDTs has been related to species and whether or not it displays a broken or intact top (Ganey and Vojta, 2005). The probability of height loss was predicted to be highest for larger-diameter SDTs found in stands with frequent forest management activities (Russell and Weiskittel, 2012). If SDT height is collected within forest inventories, equations may be developed that first quantify the probability of height loss, then subsequently estimate the amount of woody debris (e.g., its biomass and C) that transitions into the DWD pool, assuming the SDT lost height over a specified duration.

3.3.3. Modeling density versus mass loss

In studies that quantify DWD dynamics, it is critical to note the differences between mass loss, volume loss, and wood density reduction. Interestingly, most studies that present decomposition rates estimate changes in wood density, which is often used as an inappropriate surrogate for biomass. As an example, Laiho and Prescott (2004; their Table 4) found that only five out of 37 studies addressed mass loss while the majority focused instead on density depletion. The use of density depletion is known to underestimate mass loss because it does not consider log volume loss (change in log shape and size) as decomposition progresses (Harmon et al., 1987; Næsset, 1999; Zell et al., 2009; Fraver et al., 2013). Such findings highlight the need for developing methods to accurately determine current volume and/or improve SRFs (Means et al., 1985; Spies et al., 1988; Fraver and Palik, 2012; Fraver et al., 2013) for the species of interest in depicting woody debris volume, biomass, and C loss. The negative exponential model presented by Olson (1963) is by far the most common model form used to quantify density and mass loss, but this form may not appropriately account for lags in decomposition, water-logged pieces, and/or may be inappropriate for depicting the dynamics of decay-resistant wood (Harmon et al., 2000; Hérault et al., 2010; Freschet et al., 2012; Fraver et al., 2013). Fraver et al. (2013) compared 11 model forms for depicting DWD biomass and C depletion, concluding that a Weibull or rational form provided the best fit to three species in northern Minnesota, USA. The relatively poor performance for the negative exponential model form suggests that the rate and pattern of biomass and C decomposition varies through time (Fraver et al., 2013).

Modelers turn to parsimonious approaches for quantifying dead wood decomposition (Radtke et al., 2009), but recognize that a large number of factors influence biomass and C loss. Forest management practices may reduce SDTs by removing trees deemed to be unacceptable growing stock (Cline et al., 1980; Kenefic and Nyland, 2007). The size of the woody debris piece of interest is commonly specified to represent decomposition potential. Larger diameter SDTs may (Garber et al., 2005; Yamasaki and Leak, 2006) or may not (Vanderwel et al., 2006; Holeksa et al., 2008) show greater survival than their smaller diameter counterparts, or their longevities may be approximately equal (Lee, 1998). Species differences in decomposition rates of woody debris can be considerable (e.g., Laiho and Prescott, 2004; Russell et al., 2014b), with the general consensus that conifer species will decompose more slowly than hardwoods (Weedon et al., 2009; Russell et al., 2014b). For DWD, some studies have found diameter to influence its decomposition rate (Mackensen et al., 2003; Zell et al., 2009) while others have not (Harmon et al., 1987; Radtke et al., 2009). Russell et al. (2013) developed DC transition models using DWD length, assuming it reflected the extent of fragmentation and intactness of DWD pieces. Regional climate variables have been shown to be useful surrogates of SDT abundance (Eskelson et al., 2012; Russell, 2015) and DWD C stocks (Woodall and Liknes, 2008a). Several studies have employed climate information to represent DWD decomposition (Yin, 1999; Mackensen et al., 2003; Radtke et al., 2009; Zell et al., 2009; Russell et al., 2013, 2014b), and future climate scenarios may reduce DWD residence times (Russell et al., 2014a). An analysis of 117 decomposition rates representing 87 individual genera and/or species indicates a significant positive relationship at the 25th, 50th, and 75th percentiles with mean annual temperature obtained from WorldClim (http://www.worldclim.org/bioclim; Table 4; Fig. 5; Supplemental Material 2). This analysis highlights the influence that regional climate plays in estimating the decomposition of woody debris, (e.g., warmer climates indicate faster decomposition compared to cooler climates). The increased variability in decay rates in warmer regions indicates additional factors (e.g., species) may exhibit a larger impact in warmer climates. Although these relationships are generally intuitive, surprisingly little work has explored how future climate conditions may affect this cornerstone of forest ecosystem structure and function (Russell et al., 2014b). Additional examinations that determine which variables influence woody debris decomposition, such as the resident wood decomposition fungal community, microclimate, or disturbance patterns common to a given forest type may help to refine existing models of biomass and C depletion.

3.3.4. Direct measurements of CO_2 flux

Several studies have assessed decomposition rates by direct measurement of CO_2 fluxes from DWD pieces (e.g., Marra and Edmonds, 1996; Chambers et al., 2001; Bond-Lamberty et al., 2003; Jomura et al., 2008; Forrester et al., 2012). It is noteworthy that these direct measurements capture the influence of respiration, but not other processes (i.e., fragmentation or leaching). In addition to predicting annual CO_2 flux from woody debris, such studies have been motivated by the need to better understand CO_2 fluxes from different components of forest ecosystems (e.g., for partitioning CO_2 flux measurements from eddy covariance tower measurements). Jomura et al. (2007) estimated that DWD respiration accounted for 10–16% of total heterotrophic respiration in a secondary temperature broadleaved forest in Japan. Jomura et al. (2008) and Bond-Lamberty and Gower (2008) compared decomposition rates computed from these direct measurements with those obtained from mass loss rates, and both methods provided relatively consistent decomposition rates. Although direct measurements of CO_2 flux from dead wood are tedious to implement, they have the clear advantage over the other methods used in that they allow linking short-term variation in environmental conditions to respiration rates (e.g., Bond-Lamberty et al., 2003; Forrester et al., 2012).

3.4. Woody debris carbon flux and forest stand dynamics

The dynamics of woody debris C pools over the course of forest development is a function of disturbance, demographic processes, and decomposition rates. Stand-level woody debris biomass may follow a U-shaped pattern following stand-replacing disturbance, with initial high biomass reflecting pre-disturbance legacies and subsequent coarse wood inputs dependent on the disturbance (Harmon, 2001). The U-shaped pattern has primarily been reinforced with chronosequence studies of dead wood biomass following fire or forest harvesting (Sturtevant et al., 1997; Harmon, 2001). However, the universality of this pattern for natural forests at a specified spatial scale (e.g., stand level) is questionable for regions and forest types where the return interval for stand-replacing disturbances is several times greater than the average longevity of canopy trees. Through an analysis of chronosequence studies, Harmon (2009) showed that temporal patterns may also exhibit a reverse-J, S-shaped, or mixed shaped curves. Instead, a general equilibrium between dead wood inputs and decomposition may be expected for these systems, perhaps resulting in relatively constant dead wood abundance over time (Jenny et al., 1949; Tyrrell and Crow, 1994; Aakala, 2011). However, periodic non-stand-replacing disturbances create pulses in dead wood abundance that disrupt this general equilibrium (Fraver et al., 2002; D'Amato et al., 2008; Vanderwel et al., 2008; Aakala, 2011; Jönsson et al., 2011).

Despite theoretical expectations for patterns of woody debris C dynamics over the course of stand development, prediction of these dynamics is often quite challenging, particularly over large geographic regions where an assortment of stand successional stages, management and disturbance histories, climate, and other drivers of decomposition are operating (Woodall and Westfall, 2009). To some degree, the input of recent tree mortality to the dead wood pool should be predictable when forest stands are experiencing self-thinning (Sturtevant et al., 1997; Westfall and Woodall, 2007). However, the complexities associated with SDT fall rates and associated decomposition/fragmentation of dead

Table 4
Parameters for estimating decay rates for downed woody debris density and/or mass using regression at three corresponding percentiles[a].

Parameter	Percentile	Estimate	SE	*p*-value
α_0	25th	−4.18956	0.22208	0.00000
	50th	−3.95090	0.14902	0.00000
	75th	−3.50965	0.14316	0.00000
α_1	25th	0.07429	0.01241	0.00000
	50th	0.08474	0.00943	0.00000
	75th	0.09703	0.00778	0.00000

[a] Model: $k = \exp(\alpha_0 + \alpha_1 \text{MAT})$, where k is the annual decay rate parameter, MAT is the mean annual temperature (°C), and α_i's are parameters estimated using quantile regression techniques.

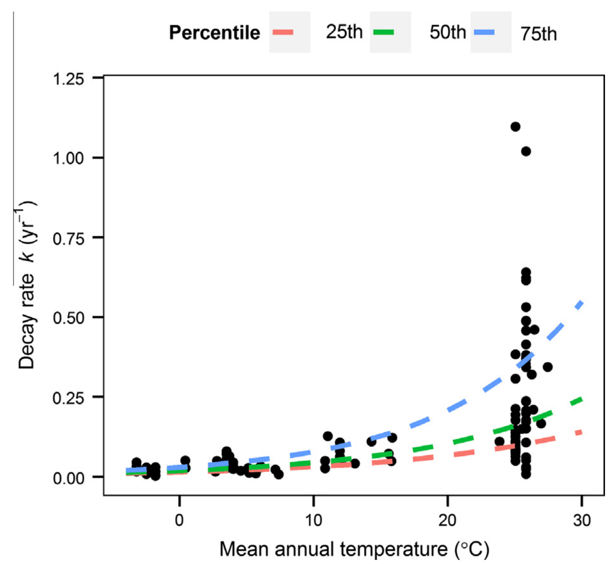

Fig. 5. Decay rates (k) reported for downed woody debris density and/or mass at three corresponding percentiles. Parameter estimates can be found in Table 4. For a list of studies included in this figure, see Supplemental Material 2.

wood obscures causalities between self-thinning processes and dead wood abundance. Furthermore, most forest stands are not experiencing high levels of self-thinning mortality. Instead, most forest stands have stocking levels where mortality and associated input to the dead wood C pool are difficult to predict (Woodall, 2010). Most studies regarding dead wood C flux in the context of stand attributes have been conducted at small scales over short periods of time (e.g., Wang et al., 2002; Gough et al., 2007; Jönsson et al., 2011). A large knowledge gap identified in dead wood C dynamics is that due to variation of heterotrophic respiration (Harmon et al., 2011a) or combustion over the course of stand development.

3.5. Forecasting woody debris

Modeling the dynamics of woody debris populations requires knowledge of decomposition rates, breakage, and fall of SDTs followed by the decomposition rate of DWD. Initially, the creation of SDTs relies on an accurate assessment of stand and/or individual tree mortality, a process that remains poorly understood. Background mortality rates (i.e., mortality not associated with disturbance pulses) are sparsely documented and according to a number of recent studies, are changing due to anthropogenic environmental changes (van Mantgem et al., 2009). Rare and highly episodic mortality events are difficult to predict (Weiskittel et al., 2011). Vanderwel et al. (2006) simulated SDT decomposition and longevity and found that SDTs with smaller diameters in stands with recent harvesting activity would fall with greater likelihood. Woody material lost in SDT volume through height loss will transition to DWD biomass. The decomposition of DWD biomass and C can then be simulated through the use of DC transition models (e.g., Aakala, 2010, 2011; Russell et al., 2013) and/or depletion curves (e.g., Laiho and Prescott, 1999; Harmon et al., 2000; Fraver et al., 2013). Complete decomposition of DWD may be specified as the number of years in which pieces reach their residence time (e.g., Alban and Pastor, 1993; Mackensen and Bauhus, 2003; Hérault et al., 2010; Russell et al., 2014b), upon which DWD has undergone complete heterotrophic respiration and/or transitioned into subsequent C pools (i.e., soil organic matter), termed the "limit value" by Mackensen et al. (2003).

Although the emphasis here is on the empirical modeling of woody debris, simulation models operating at other scales also forecast woody debris dynamics. For example, the process-based CenW model (Kirschbaum, 1999) quantifies woody debris decomposition separately for branches, stems, and coarse dead roots while varying rates based on temperature, moisture level in the relevant soil layer (the litter layer in the case for DWD), and the lignin concentration of wood. Dynamic global vegetation models characterize woody debris decomposition by assigning grid cells to one of several plant functional types (e.g., boreal evergreen, tropical broad-leaved). For example, woody debris in the LPJ model (Sitch et al., 2003) decomposes on a monthly time step (driven similarly by moisture and temperature) by either entering directly into the atmosphere as CO_2 or transitioning into intermediate- and/or slower-decomposing soil organic matter pools.

3.5.1. Case study: The Fire and Fuels Extension to the Forest Vegetation Simulator

As an example, the Fire and Fuels Extension (FFE; Reinhardt and Crookston, 2003; Rebain et al., 2010) of the Forest Vegetation Simulator (Crookston and Dixon, 2005), an empirical forest growth and yield model widely used throughout North America. The FFE model performs computations consistent with the Intergovernmental Panel on Climate Change's (IPCC) good practice guidelines (IPCC, 2003) for C accounting. As the primary use of FFE is in forest fuel modeling (e.g., Noonan-Wright et al., 2014) and simulating forest C (e.g., Hoover and Rebain, 2011), dead wood components are simulated using a variety of model subroutines. To initialize a model simulation, individual tree attributes can be input for live trees (e.g., tree DBH and height), while SDT and DWD information can be specified using forest inventory data. Alternatively, default values can be used for dead wood populations. Estimates for dead wood will subsequently fluctuate to represent DWD decomposition as well as DWD additions, such as SDT fall and harvest residues (Hoover and Rebain, 2011).

The loss in height of SDTs within FFE assumes a fixed proportion of height lost annually, with some differences in rates between species and hard versus soft SDTs. The decomposition in biomass of SDTs is dependent on SDT diameter and species, while the rate of SDT fall is greater in stands where fire has occurred. Annual decomposition of DWD is simulated using species-specific mass decomposition rates which can be specified by DWD size class, decay rate class, and hard versus soft woody debris (Rebain et al., 2010).

Because the FFE model framework within the Forest Vegetation Simulator permits user-specified options to adapt model output to a region or forest type of interest, several keywords are available to specify parameters relating to dead wood dynamics. Of particular interest to those addressing C stocks and fluxes of woody debris are to set different mass loss rates of DWD for various size classes (FUELDCAY) and to change the rate of SDT height loss (SNAGBRK) and fall (SNAGFALL). Tree mortality is estimated at the end of each cycle length (e.g., every 10 years) resulting in an increase in the abundance and amount of SDTs. As fire is a primary concern in western North America, the majority of the equations inherent to FFE have been developed with western species, but there are differences depending on the geographic variant chosen (Rebain et al., 2010).

To examine the influence of decomposition rates in empirical models of woody debris dynamics, we compared trajectories of DWD C in FFE using data from two experimental forests in the northern US and two scenarios of decomposition rates. Forest inventory data (live tree DBH measurements) from the Dukes Experimental Forest (DEF), comprised of northern hardwood species and located in the Upper Peninsula of Michigan (46°21′ N, 87°10′ W) and the Penobscot Experimental Forest (PEF), comprised of primarily mixed-conifer species in central Maine (44°52′ N, 68°38′ W), were simulated using the Lake States and Northeast variants of the Forest Vegetation Simulator, respectively. Data from stands that had never been harvested previously were used in this analysis: for the DEF this resulted in information from 38 plots collected in 2008 (Gronewold et al., 2010) while for the PEF 19 plots were used that were collected in 2009 (Brissette et al., 2012). Default DWD C stocks for pieces >7.6 cm provided by FFE were simulated for 100 years using two mass loss rates. Default FFE annual loss rates (negative exponential decay constants, k) for the DEF were 0.06 (DWD 7.6–30.5 cm) and 0.02 (DWD > 30.5 cm) while the decay rate from Russell et al. (2014b) was used for hardwood species of all size classes (0.050). For the PEF, FFE annual loss rates were 0.07 (DWD 7.6–15.2 cm) and 0.03 (DWD > 15.2 cm) while the decay rate from Russell et al. (2014b) was used for conifer species of all size classes (0.028).

Slightly different trends were observed for the DEF and PEF when analyzing estimates of DWD C (Fig. 6). For the DEF, DWD C stocks for both decay rate scenarios were initially 9.2 Mg C ha^{-1}, increased in concert until approximately year 70, then diverged slightly where DWD C using Russell et al. (2014b) decay rates appeared to reach an asymptote while DWD C using FFE parameters continued to increase. Carbon stocks were initially 17.6 Mg ha^{-1} for PEF DWD, with C stocks estimated using Russell et al. (2014b) decay rates consistently 40% higher than FFE output through 100 years.

Findings highlight that using even slightly different rates of decomposition results in large differences when forecasting DWD C stocks. Specifically for the PEF, FFE designates *Picea spp., Pinus spp., Tsuga spp.* (i.e., the common species occurring in this forest) as non-resistant to decomposition, while empirical estimates derived from US FIA data (e.g., Russell et al., 2014b), indicating that conifer wood displays a longer residence time, may reflect differences in how FFE is parameterized. In contrast, the DEF displays large dead wood pieces (as in Gronewold et al., 2010), hence, mass loss rates for hardwood species developed in Russell et al. (2014b) could potentially overestimate decomposition for large hardwood pieces occurring in this forest. Ultimately, the continued development and refinement of the empirical equations representing SDT and DWD dynamics is critical to models aimed at quantifying biomass and C stores in dead wood.

4. Research needs

Recent findings spanning the disciplines of forest ecology, biogeosciences, and forest biometrics and modeling have highlighted several research needs and information gaps that became evident through this synthesis. To further the knowledge base on forest dead wood patterns and processes, expanded efforts in the topics listed below will promote the accurate quantification of dead wood C stocks and a reliable representation of their decomposition dynamics through time.

4.1. Continue efforts in monitoring and evaluating wood density, decay class, and structural reduction factors

The finding that SDT and DWD C were highly sensitive to wood density values (i.e., Fig. 4) underscores the importance of this issue. Important too is the continual refinement of individual wood density values that are often applied to all dead wood pieces for an individual species or species group, such as in national forest inventories. Measurement and refinement of wood density values at local scales can aid in quantifying related dead wood parameters such as decay class and structural reduction factors to improve the accuracy of dead wood biomass and C pools.

4.2. Assess the pros and cons of the various field protocols for sampling forest dead wood

In the context of field protocols within national forest inventories and biomass and C accounting for National Greenhouse Gas Inventories (e.g., US EPA, 2014), consideration should be given to sampling protocols that are accurate, efficient, and do not require excessive field research (e.g., new parameters for wood density and decay class and structural reduction factors), and can be implemented by field crews with minimal formal training. In the context of national forest inventories, dead wood is one of several attributes being measured as a part of such multi-resource forest inventories. Hence, the implementation of novel methods for sampling dead wood may be limited. However, the use of auxiliary information may supplement standard dead wood inventory plots by incorporating existing remote sensing data products and/or climate information to present new research opportunities.

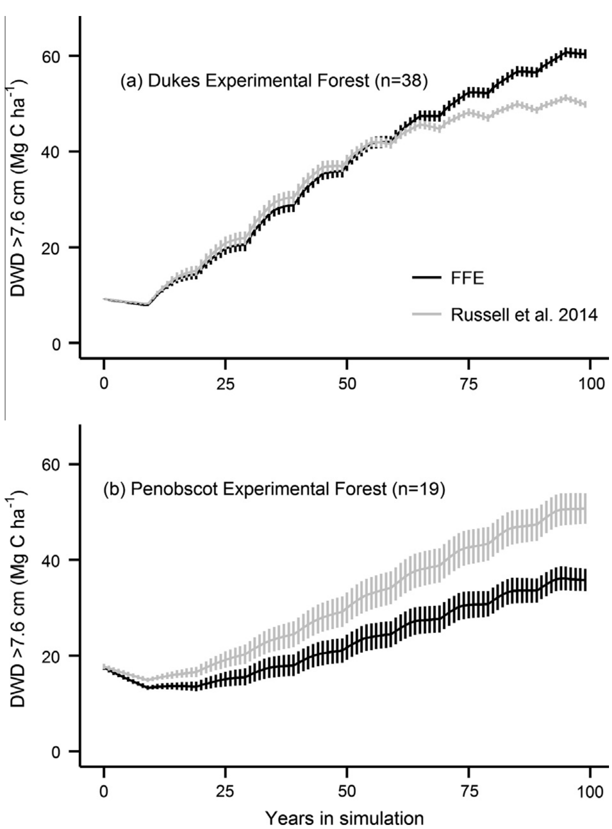

Fig. 6. Comparison of downed woody debris (DWD) carbon stocks using default decay rates in the Fire and Fuels Extension (FFE) to the Forest Vegetation Simulator versus those presented in Russell et al. (2014b). Error bars indicate one standard error.

4.3. Expand research on emerging remote sensing technologies, particularly LiDAR, for estimating the quantity and quality of forest dead wood

Current approaches that have evaluated the robustness of LiDAR to quantify dead wood vary considerably (Maltamo et al., 2014). Applications employing new sensors and novel processing techniques should continue to be evaluated as a tool for determining woody debris biomass and C stocks. Of particular concern is their need to account for dead wood quality (e.g., stage of decomposition and structural losses). Comparisons between ground-based and airborne LiDAR for depicting woody debris abundance and quality should be assessed, particularly in the context of area-based (e.g., plot or stand level) and single-tree detection methods (Maltamo et al., 2014). Should relationships between site-level attributes and dead wood attributes be developed and refined, the application of LiDAR is particularly appealing to help inform the role of dead wood in forest management planning.

4.4. Further our understanding on the role that structural reduction factors play in determining standing dead tree volume, biomass, and C

As these structural reduction factors were the most sensitive component in determining the amount of C in SDTs (Fig. 4), parameters chosen for this value contribute largely to the variation in biomass and C. Generic structural reduction factors for SDTs such as those presented in Domke et al. (2011) may provide a baseline for estimating structural losses that reflect decay stage. Measurement of morphological attributes of SDTs (e.g., bark cover and wood penetrability; Angers et al., 2012) may help to better refine volume, biomass and C content of SDTs. Although the SRFs proposed for DWD appear to be consistent, at least within the northern temperate and boreal systems where they have been developed, further work is needed to test their applicability in other regions, particularly moist tropical and arid regions.

4.5. Refine and adapt modeling tools that concomitantly estimate the biomass and C content of live and dead trees

Equations that facilitate the estimation of biomass and C for both live and dead trees should be compatible in an accounting framework. As an example, SDT volume can be constrained through an understanding of the stem volume of a live tree with equivalent dimensions and growing conditions. The implementation of refined taper equations that incorporate SDT measurements in addition to live trees will result in improved estimates that reflect the unique forms of SDTs (e.g., stem breakages, branch loss, and bark sloughing). Improved taper relationships for DWD can be related to stage of decay, thereby reducing measurement errors in field surveys (Woodall and Westfall, 2008).

4.6. Promote and implement the results from emerging science on dead wood C flux in the areas of bioenergy and forest C accounting

As the greenhouse gas benefits from using forest-derived biomass for energy continue to be examined (e.g., Miner et al., 2014), ecological studies that examine flux patterns and fate of logging residue have the ability to provide tremendous insight into these emerging issues. As an example, Wang et al. (2013) examined the performance of the CENTURY ecosystem model to improve fine woody debris dynamics within the framework of the bioenergy sector. Incorporating results of dead wood C flux analyses as parameters in such simulation models will provide guidance to decision makers within the bioenergy sectors.

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4.7. Develop an increased understanding of local- and regional-scale factors that influence decomposition rates of dead wood

Fungal colonization and termite biomass can account for nearly three-quarters of the variability in wood decomposition on the local scale (Bradford et al., 2014). Factors driving variability on regional scales often employ climate as the main driver of dead wood decomposition across contrasting forest types (Russell et al., 2014a). It is essential to understand and quantify the relative importance of these factors across scales. This understanding would not only improve C modeling, but would allow us to assess temporal changes in DWD as they relate to tree regeneration (e.g., nurse logs), forest fuel loads and fire risk, and substrate suitability for dead wood-dependent organisms.

4.8. Further our understanding of decomposition differences across tropical, temperate, and boreal biomes

As the majority of dead wood research has been conducted across temperate forests (as emphasized here), research needs in this biome can be compared to tropical and boreal ones. Tropical systems may be more concerned with more rapid turnover rates and a diversity of species, while longer residence times and a potential for buried dead wood stocks (e.g., Moroni et al., 2015) are inherent to dead wood in boreal forests. The examination of temperate systems when analyzing the decomposition of dead wood is ideal given these forests display both of these attributes. The shift in downed woody debris C stocks being greater than fine woody debris stocks occurs at mid-latitudes in US forests (Woodall and Liknes, 2008b) which can reflect a change in forests with rapid decomposition and decay with continual fine woody inputs to forests with abundant downed woody debris with and longer residence time. Hence, understanding these patterns above and beyond using climate alone will help to refine decomposition differences as one transitions from tropical to boreal biomes.

4.9. Refine conceptual models of stand-level dead wood abundance through time

The accumulation and fate of dead wood throughout stand development is an expansive area where refinements can be sought. Serving as a baseline, the U-shaped pattern of total dead wood biomass following stand-replacing disturbance may not be appropriate in forests with few stand-replacing disturbances or with longer return intervals. Understanding the role of spatial scale (i.e., stand to landscape scales) on the temporal patterns of dead wood accumulation and decomposition will aid in defining such conceptual models. Competing theories may be sought that examine these trends in dead wood abundance related to time since disturbance or indices of forest developmental stage (e.g., Lorimer and Halpin, 2014), which may serve more useful in examining dead wood dynamics in multi-aged forests.

4.10. Explore the finer-scale components controlling the fate of carbon through the latter stages of decomposition

While modeling efforts tend to simplify the process of decomposition by examining mass loss through time (e.g., with the negative exponential model form), it is important to understand the nuances that govern dead wood decomposition, particularly the late transition stage where DWD enters subsequent C pools. McFee and Stone (1966) presented early work on this topic regarding the transfer of decomposing wood into the humus layer, but much remains to be explored for similar processes. For example, our understanding of the proportion of dead wood that is released to atmosphere, leached, passed up the food chain by decomposers and consumers, or incorporated into soil organic layers remains to be quantified for many of the world's forests. Similarly, this understanding would increase our ability to partition C fluxes measured from flux towers to different ecosystem components.

5. Conclusions

This synthesis highlights current approaches for quantifying woody debris C stores and fluxes ranging from detailed experiments conducted within specific forest types to broad protocols implemented at national scales. Several examples from the recent literature suggest that there is no universal approach to determining the total amount woody debris and its patterns of decomposition, but rather several approaches serve this purpose. Biomass and carbon fluxes have been examined to a lesser degree, with numerous modeling approaches outweighing field-based experiments that document the decomposition of forest dead wood. Although it is difficult to attribute differences in stocks and fluxes that result from various measurement techniques, generally each method determines the amount and flux of woody debris in a comprehensive and sound manner.

The uncertainties surrounding biomass and C stock estimates across many of the world's forests remain to be evaluated. Recent advances in sampling methods that measure woody debris in proportion to their size (i.e., volume or biomass) encourages efficient and robust field protocols that generate data needed for broader-scale assessments. Despite the fact that numerous approaches are available for determining C stocks based on inventory information, the potential for using information collected from the measurement of all ecosystem pools (e.g., live and dead trees) is encouraging given the importance of broad concerns on forest C sequestration and emission patterns.

Many of the issues presented here are hindered by the unknowns that future global change scenarios may present in terms of altering forest disturbances, mortality, and decomposition rates across the world's diverse forest types. Future dead wood biomass and C stocks will need to be continually monitored at national scales to serve as a baseline for informing managers interested in understanding implications in biodiversity maintenance, forest productivity and bioenergy production, and fire ecology. As a result, managers may need to strategically manage for forest dead wood while understanding the implications that uncertain future scenarios can play in modifying forest dead wood populations. Understanding the relationships that local and regional factors play in woody debris stocks and fluxes is essential to maintaining the forest structure and ecological services that woody debris provides.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.04.033.

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