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# Relationships between the stocking levels of live trees and dead tree attributes in forests of the United States

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ABSTRACT

There has been little examination of the relationship between the stocking of live trees in forests and the associated attributes of dead tree resources which could inform large-scale efforts to estimate and manage deadwood resources. The goal of this study was to examine the relationships between the stocking of standing live trees and attributes of standing dead and downed dead trees using a national inventory of forests in the United States. Results indicated that from the lowest to the highest class of live tree relative stand density, the mean biomass/ha of live trees increased over 2000% while standing dead and downed dead trees biomass/ha increased 295 and 75%, respectively. Correlations between downed deadwood biomass and stand/site attributes increased as live tree stocking increased. The size/density attributes of standing and downed deadwood exhibited no relationship with standing live stocking possibly due to the confounding factors of decay and breakage. This study proposes a conceptual deadwood stocking model with standing live tree stocking as an axis along which deadwood accretion factors (e.g., disturbance, self-thinning, and senescence) and depletion factors (e.g., decay, harvest, and stagnation) ultimately determine deadwood stocking.

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## 1. Introduction

Estimates of forest detritus are critical to numerous scientific fields such as carbon accounting (Woodall et al., 2008), wildlife habitat assessment (for examples see Maser et al., 1979; Harmon et al., 1986; Bull et al., 1997), and fuel loading estimation (Van Wagner, 1968; Rollins et al., 2004; Lutes et al., 2006; Woodall and Monleon, 2008). Detritus provides a diversity (stages of decay, size classes, and species) of habitat for fauna ranging from large mammals to invertebrates (Maser et al., 1979; Harmon et al., 1986; Bull et al., 1997). Plants use the microclimate of moisture, shade, and nutrients provided by deadwood to establish and regenerate (Harmon et al., 1986). Due to the possibility of dwindling deadwood habitat for native species and increasing fuel loadings across the United States, comprehensive large-scale inventories of downed deadwood (DDW) have been established for habitat assessments/wildlife conservation efforts and fire hazard mitigation efforts (for examples see Marshall et al., 2000; Ohmann and Waddell, 2002; Tietje et al., 2002; Rollins et al., 2004; Woodall and Monleon, 2008). Worldwide, there has been increased effort during past years to inventory deadwood resources to address greenhouse gas offset accounting and biodiversity concerns (Kukuev et al., 1997; Woldendorp et al., 2004; Woodall et al., in press). Beginning in 2001, the U.S. began implementation of a nationwide inventory of DDW on a subset of inventory plots that inventory standing live and dead trees. An impetus exists to not only predict deadwood attributes for all national inventory plots, but also to assess opportunities to assess deadwood stocking and carbon stock flux (Woodall et al., 2008).

To date, efforts to model DDW attributes have been focused at large scales using remotely sensed information and gradient models (e.g., Rollins et al., 2004) and at small scales by relating DDW to stand/site attributes (e.g., Pyle and Brown, 1999; Rubino and McCarthy, 2003; Idol et al., 2001; McCarthy and Bailey, 1994). Siitonen et al. (2000) found that the total of standing and down deadwood in boreal forests of Finland corresponded with increasing site productivity. Additionally, Spetich and Guldin (1999) found that increasing volume per acre of standing dead trees corresponded with increasing site productivity in sawtimber-sized hardwood stands of natural origin. In contrast, Norden et al. (2004) found no correlation between DDW volume and basal area in temperate broadleaved forests suggesting that stand age and management, which also affect basal area, may preclude the use of basal area as a predictive variable. Despite the development of models to estimate relationships between down woody fuels and stand/site attributes, there remains a sizeable knowledge gap in understanding fundamental relationships between forest detritus and basic stand attributes such as live tree stocking.

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The size–density relationships of live trees have been widely used to estimate forest stand stocking (e.g., biomass per unit area) (for examples see Reineke, 1933; Krajicek et al., 1961; Gingrich, 1967; Drew and Flewelling, 1979; Woodall et al., 2005). Stand Density Index (SDI), based on size/density and self-thinning relationships (Reineke, 1933; Long, 1985), is one such live tree stocking index that can be utilized at a national scale (Woodall et al., 2006). Self-thinning is based on the premise that as mean plant size per unit area increases, the number of individuals per unit area decreases (Enquist et al., 1998). An inherent component of the self-thinning process is density induced tree mortality. The forest detritus of standing dead and DDW must originate from the mortality of live trees. Results from Sturtevant et al. (1997) suggested that quantitative size–density diagrams may be a means to estimate DDW resources. Sturtevant et al. (1997), Harmon et al. (1986), and Spies et al. (1988) have all proposed a conceptual two phase DDW accretion model composed of an initial phase of residual decay of pre-disturbance/disturbance generated DDW followed by a residual accumulation of DDW from the regenerating stand. Downed deadwood stocking and prediction models may be refined through the inclusion of standing live and standing dead tree stocking indices which have not been explored at a continental scale. How are the attributes of detritus (e.g., biomass) in any given forest stand related to the stocking of live trees? Does the size/density attributes of live trees inform the stocking of DDW resources? The goal of this study is to examine the relationship between the stocking levels of live trees and the attributes of dead trees in forests of the United States with specific objectives:

(1) to examine trends in standing live, standing dead, and DDW biomass by classes of live tree stocking (current stand density index/maximum potential stand density index),
(2) to examine size/density attributes of standing live, standing dead, and DDW by classes of live tree stocking,
(3) and to suggest a conceptual stocking model for deadwood resources based on study results.

## 2. Methods

### 2.1. Field data collection

The Forest Inventory and Analysis (FIA) program of the USDA Forest Service is responsible for inventorying the forests of the U.S., including both standing trees and DDW on permanent sample plots established across the United States (Bechtold and Patterson, 2005). Sample plots are established at an intensity of approximately 1 plot per 2400 ha. If the plot lies in a forested area, field crews visit the site and measure tree and site variables ranging from tree sizes to forest types. FIA standing live/dead tree inventory plots consist of four 7.32-m fixed radius subplots for a total plot area of approximately 0.07 ha. All standing trees greater than 12.25 cm diameter at breast height (dbh) are inventoried on the plot, while trees less than 12.25 cm dbh are measured on a 2.07-m fixed radius microplot on each subplot.

DDW sampling methods on FIA plots are detailed by Woodall and Monleon (2008). DDW with a transect diameter (diameter at point of intersection with a sampling transect) greater than 7.60 cm are sampled on each of three 7.32-m horizontal distance transects radiating from each FIA subplot center at 30, 150, and 270°. DDW pieces of this size are termed coarse woody debris (CWD). Data collected for every CWD piece includes transect diameter, length, small-end diameter, large-end diameter, decay class, and species. Fine woody debris (FWD) are DDW pieces with a transect diameter less than 7.60 cm and are sampled on the 150° transect on each subplot. Fine woody debris with transect diameters less than 0.61 and 0.62–2.54 cm were tallied separately on a 1.83-m slope distance transect (4.27–6.09 m on the 150° transect). Fine woody debris with transect diameters of 2.55–7.59 cm were tallied on a 3.05-m slope-distance transect (4.27–7.32 m on the 150° transect). For the purposes of this study, DDW is defined as CWD biomass plus FWD biomass.

### 2.2. Data

FIA inventoried the majority of U.S. states between 2003 and 2006 for standing and down tree attributes on 4220 permanent inventory plots (Fig. 1). The associated field data is available for download at the following site: http://fiatools.fs.fed.us/fiadb-downloads/datamart.html.

Three climatic variables were correlated with stand-level variables in this study: 30-year mean annual precipitation (PRECIP), 30-year mean annual maximum temperature (TMAX), and 30-year mean annual minimum temperature (TMIN). Data for PRECIP, TMAX, and TMIN were obtained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) dataset (4-km grid cell size; PRISM Group, 2004). Each of these three variables is represented by a 30-year climate normal. As such, annual precipitation is the mean annual total precipitation (mm) from 1971 to 2000. TMAX and TMIN are the mean daily temperature (°C) extremes for that period.

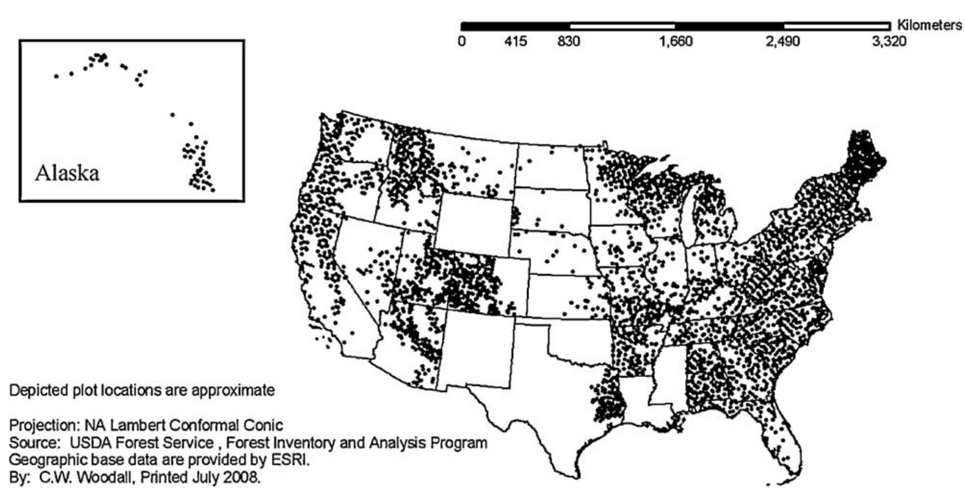


**Fig. 1.** Approximate plot locations across the United States, 2003–2006.

**Table 1**
Mean biomass (tonnes $ha^{-1}$) and associated standard errors for standing live/dead and downed dead woody materials in forests of the United States by classes of relative density, 2003–2006.

| Relative density | Downed, dead woody material | Std. error | Standing dead | Std. error | Standing live | Std. error |
|---|---|---|---|---|---|---|
| 0.0–0.1 | 13.62 | 0.90 | 4.29 | 0.70 | 10.19 | 0.40 |
| 0.1–0.2 | 12.81 | 0.76 | 3.71 | 0.34 | 30.08 | 0.67 |
| 0.2–0.3 | 14.08 | 0.74 | 4.97 | 0.40 | 53.22 | 1.18 |
| 0.3–0.4 | 16.28 | 0.81 | 7.15 | 0.50 | 78.50 | 1.48 |
| 0.4–0.5 | 16.82 | 0.70 | 8.59 | 0.57 | 111.12 | 2.17 |
| 0.5–0.6 | 16.98 | 0.88 | 8.82 | 0.61 | 132.02 | 2.43 |
| 0.6–0.7 | 17.86 | 1.28 | 12.74 | 1.96 | 163.54 | 4.69 |
| 0.7–0.8 | 13.63 | 0.81 | 7.48 | 0.71 | 168.33 | 5.87 |
| 0.8–0.9 | 21.88 | 3.42 | 16.47 | 2.64 | 212.85 | 11.70 |
| 0.9–1.0 | 23.77 | 2.25 | 16.94 | 3.50 | 222.22 | 21.27 |

### 2.3. Analysis

For every inventory plot, the biomass/ha of standing live and dead trees was determined using procedures detailed by Bechtold and Patterson (2005). Plot-level estimates of DDW were estimated using procedures detailed by Woodall and Monleon (2008, Section 3.1). In order to remove extreme outliers due to evident measurement/data management errors, DDW observations were removed if their value exceeded their median plus 25 times the interquartile range for all classes of FWD and CWD (small FWD $< 8.41$, medium FWD $< 35.43$, large FWD $< 127.22$, CWD $< 250.51$; tonnes $ha^{-1}$, respectively) for a total of 14 out of 4220 observations.

In this study, the stocking of live trees was estimated by relative density (RD). The relative density (RD) of live trees on every plot was determined using Stand Density Index (SDI). SDI was first proposed by Reineke (1933) as a stand density assessment tool based on size–density relationships observed in fully stocked pure or nearly pure stands. A metric version of SDI is defined as the equivalent trees per hectare at a quadratic mean diameter of 25 cm and is formulated as:

$$\mathrm{SDI} = \mathrm{tph}\left(\frac{\mathrm{DBH_q}}{25}\right)^{1.6} \quad (1)$$

where SDI is the stand density index, tph is the number of trees per hectare, and $DBH_q$ is the quadratic mean diameter (cm) at breast height (1.4 m) (Long, 1985). SDI has been widely used in even-aged stands because it is independent of species composition (Curtis, 1970). The SDI of even-aged monocultures is typically compared to an empirically observed, species-specific maximum SDI for determining the stand's relative density. Maximum SDI ($SDI_{max}$) may be defined as the maximum density (tph) that can exist for a given mean tree size (25 cm, dbh) in a self-thinning population (Long, 1996). To determine RD, the SDI of any particular stand is compared to the maximum SDI characteristic of the stand's species composition. Woodall et al. (2005) proposed a methodology that estimates the maximum SDI for any stand based on the mean specific gravity of all trees in a stand to estimate its unique maximum SDI. The higher a species' specific gravity, the more elastic its bole, the more foliage that can be supported in its crown, and the less trees per unit area needed to support a site-limited amount of leaf area (Dean and Baldwin, 1996). By using the summation method (Shaw, 2000) to determine the current density of a stand and the Woodall et al. (2005) model to predict a maximum SDI, the RD of all study plots was determined (current SDI/maximum SDI).

Mean biomass and associated standard errors (tonnes $ha^{-1}$) of standing live, standing dead, and DDW were determined by RD classes. Next, slopes of standing live, standing dead, and DDW size class distributions were estimated by class of RD by fitting the following model (Eq. (2)) using simple linear regression:

$$E(\mathrm{PC}) = b_0 + b_1(\mathrm{MP}) + e \quad (2)$$

where $E(\cdot)$ is the statistical expectation, PC is the number of DDW, standing dead, or standing live pieces per ha, MP is the midpoint of each size class (cm), $b_x$ are the coefficients to be estimated, and $e$ is the random error term. It should be noted that for standing live and standing dead trees the MP's were the d.b.h. classes, while for DDW the MP's were transect diameter classes of CWD.

A conceptual model was proposed for approximating the biomass stocking of both DDW and standing dead in forest stands formulated as:

$$\mathrm{Dead_S} = \frac{\mathrm{Dead_B}}{\mathrm{Live_B}}\left(\frac{1}{\mathrm{Live_{RD}}}\right) \quad (3)$$

where $Dead_S$ is the biomass stocking (ratio) of either standing dead or DDW, $Dead_B$ is the biomass/ha of either standing dead or DDW, $Live_B$ is the biomass/ha of all standing live trees, and $Live_{RD}$ is the relative density of standing live trees.

## 3. Results

The mean biomass/ha of standing live trees increased as the RD of standing live trees increased (Table 1). From an RD of less than 0.10 to over 0.90, the mean live tree biomass (tonnes $ha^{-1}$) increased nearly 2080%, while standing dead tree and DDW increased approximately 295% and 75%, respectively (Table 1). When individual values are examined, there is tremendous variation in levels of standing dead and DDW biomass/ha across values of live tree RD (Fig. 2). The biomass/ha of downed deadwood appears to reach higher levels than that of standing deadwood.

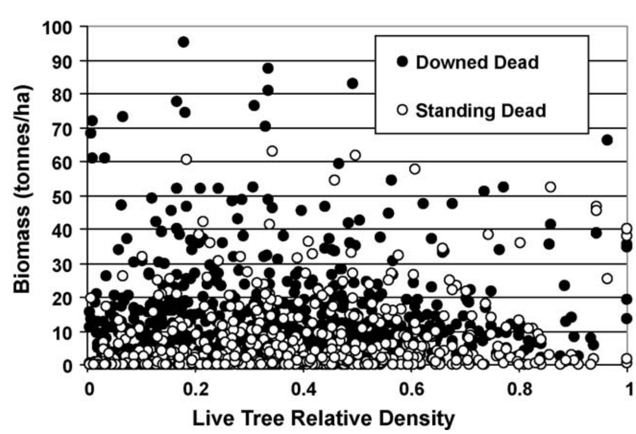


**Fig. 2.** Standing dead and downed dead tree biomass/ha versus live tree relative density in forests of the United States.

**Table 2**
Pearson's correlation coefficients between estimates of downed dead woody material (biomass $ha^{-1}$) and other stand/site attributes in forests of the United States by classes of relative density, 2003–2006.

| Relative density | Standing live biomass | Standing dead biomass | 30-year mean maximum temperature | 30-year mean minimum temperature | 30-year mean annual precipitation | Stand age |
|---|---|---|---|---|---|---|
| 0.0–0.1 | 0.19 | 0.21 | −0.11 | *−0.07* | 0.14 | *−0.03* |
| 0.1–0.2 | 0.29 | 0.20 | −0.19 | −0.12 | 0.15 | *0.02* |
| 0.2–0.3 | 0.20 | 0.21 | −0.24 | −0.18 | 0.12 | *0.02* |
| 0.3–0.4 | 0.21 | 0.32 | −0.21 | −0.14 | 0.13 | *0.01* |
| 0.4–0.5 | 0.24 | 0.25 | −0.23 | −0.21 | *0.07* | 0.13 |
| 0.5–0.6 | 0.25 | 0.27 | −0.25 | −0.21 | 0.17 | 0.27 |
| 0.6–0.7 | 0.39 | 0.36 | −0.23 | −0.22 | 0.04 | 0.21 |
| 0.7–0.8 | 0.25 | 0.36 | −0.23 | −0.19 | *0.15* | 0.24 |
| 0.8–0.9 | 0.68 | 0.65 | −0.26 | *−0.20* | *0.17* | 0.56 |
| 0.9–1.0 | 0.61 | 0.56 | −0.14 | *0.01* | 0.42 | 0.55 |

Italicized coefficients have $p$-values > 0.05.

**Table 3**
Slopes of individual piece size distributions by classes of live tree relative density (all $p$-values < 0.001).

| Relative density | Coarse woody debris | | | | Standing dead | | | | Standing live | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | Std. error | $r^2$ | df | Slope | Std. error | $r^2$ | df | Slope | Std. error | $r^2$ | df |
| 0.0(0.1 | −15.43 | 0.92 | 0.12 | 2103 | −2.47 | 0.26 | 0.09 | 886 | −3.42 | 0.15 | 0.20 | 2103 |
| 0.1(0.2 | −13.87 | 0.65 | 0.14 | 2751 | −2.26 | 0.17 | 0.10 | 1547 | −9.58 | 0.29 | 0.28 | 2751 |
| 0.2(0.3 | −14.66 | 0.67 | 0.17 | 2351 | −2.23 | 0.17 | 0.11 | 1488 | −16.22 | 0.46 | 0.34 | 2351 |
| 0.3(0.4 | −16.00 | 0.61 | 0.21 | 2619 | −2.15 | 0.12 | 0.15 | 1911 | −21.16 | 0.54 | 0.37 | 2619 |
| 0.4(0.5 | −17.93 | 0.64 | 0.25 | 2431 | −2.60 | 0.14 | 0.15 | 1945 | −25.09 | 0.66 | 0.37 | 2431 |
| 0.5(0.6 | −16.38 | 0.67 | 0.23 | 1967 | −2.74 | 0.15 | 0.17 | 1577 | −33.81 | 0.91 | 0.41 | 1967 |
| 0.6(0.7 | −17.22 | 0.83 | 0.26 | 1251 | −2.88 | 0.16 | 0.23 | 1075 | −37.04 | 1.29 | 0.39 | 1251 |
| 0.7(0.8 | −18.83 | 1.09 | 0.31 | 663 | −3.08 | 0.24 | 0.22 | 591 | −45.19 | 2.13 | 0.41 | 663 |
| 0.8(0.9 | −20.29 | 1.96 | 0.24 | 331 | −3.42 | 0.47 | 0.14 | 307 | −52.93 | 3.52 | 0.41 | 331 |
| 0.9(1.0 | −16.90 | 1.61 | 0.24 | 347 | −2.41 | 0.37 | 0.12 | 302 | −58.77 | 4.57 | 0.32 | 347 |

Using the same RD classes, correlations were determined between DDW and a selection of stand/site attributes (Table 2). Generally, as a stand's standing live tree stocking increased so did stand/site correlations with DDW. For RDs between 0.00 and 0.10, no correlation coefficient exceeded 0.25. In contrast, for RDs exceeding 0.80, the majority of correlation coefficients exceeded 0.40. For example, stand age only had a correlation coefficient with DDW of −0.03 ($p$-value > 0.05) when relative density was below 0.10. When a plot's RD was between 0.80 and 0.90, the same correlation had a coefficient of 0.55 ($p$-value < 0.001).

It has often been observed that as a stand approaches a maximum stocking threshold its live tree size–density slope decreases as there are fewer numbers of larger-sized live trees. This study found the same result (Table 3). From the lowest RD to the highest RD class, the size–density slope of standing live-trees decreased from −3.42 to −58.77. The size–density slopes for standing dead trees and DDW by classes of RD did not vary. The slope for standing dead trees ranged between −2.15 and −3.42, while the slope for DDW ranged between −13.87 and −20.29. There is stark contrast in the size–density slopes of standing live, standing dead, and DDW between lightly stocked (RD < 0.1) and highly stocked (RD > 0.9) forest stands (Fig. 3a and b). When a stand is lightly stocked DDW had the steepest size/density slope, while when stands were heavily stocked standing live trees had the steepest size/density slope.

This study's postulated deadwood stocking model was applied to both standing dead and DDW for all study plots. The distribution of DDW stocking by classes of live tree RD indicated that the highest DDW stocking was found at the extremes of low and high live tree stocking (Fig. 4a). For standing deadwood, the highest stocking was found when standing live tree RD was the highest. At both of these extremes of standing live tree stocking, there was tremendous variation in deadwood stocking as indicated by box plot whiskers.

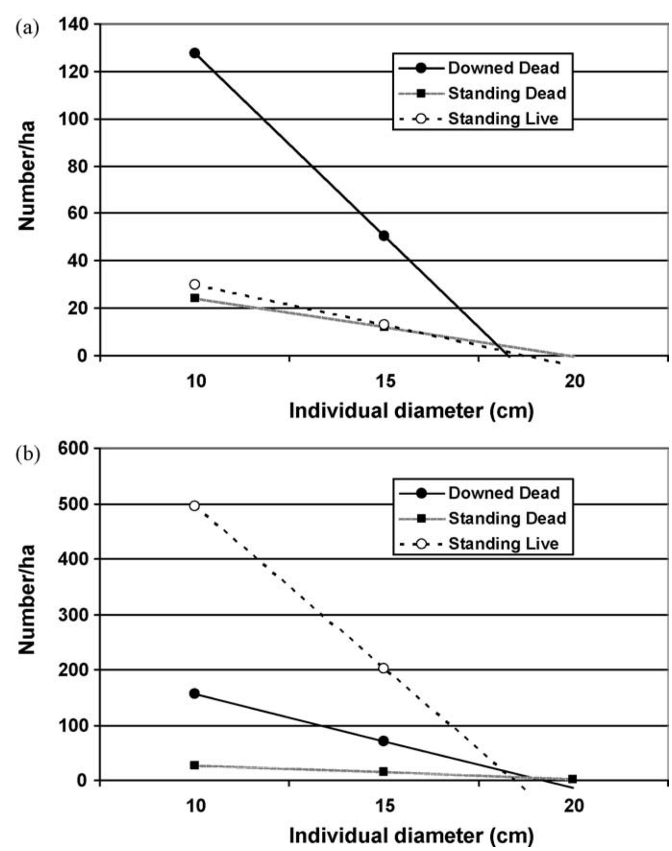


**Fig. 3.** Size/density slopes for downed dead, standing dead, and standing live trees for (a) low live tree relative density (0.0–0.1) and (b) high live tree relative density (0.9 +) forest stands, United States.

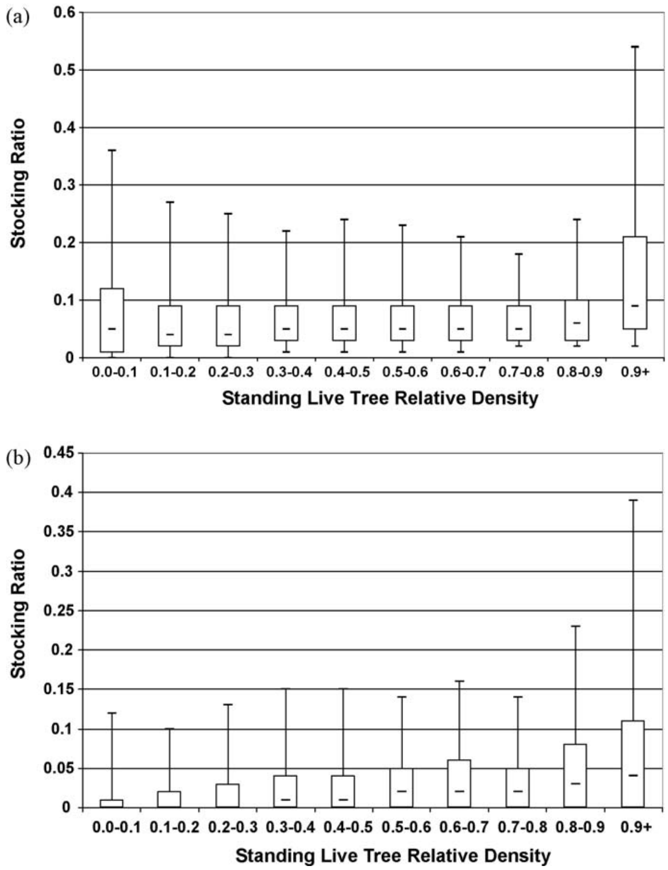


**Fig. 4.** Boxplots of stocking (current deadwood biomass divided by maximum potential deadwood biomass) of (a) downed dead and (b) standing deadwood by classes of standing live tree relative density, United States.

## 4. Discussion

The relationship between the size and number of living plants in populations are a critical component to estimating their associated growth/mortality dynamics (Drew and Flewelling, 1979). It stands to reason that the very same size–density and stocking attributes of living trees may inform understanding of deadwood accretion/depletion dynamics. Because forest detritus originates from forest biomass mortality (Sollins, 1982; Spies et al., 1988; Sturtevant et al., 1997; Bond-Lamberty and Gower, 2008), relationships between live and dead forest biomass should be apparent at some level. This study found that forest stands live biomass changes substantially across classes of RD, but standing dead and DDW biomass levels do not appear to change to such a degree. A great proportion of forests across the U.S. have a RD between 0.2 and 0.8 (>75%; Woodall et al., 2006), our study found DDW ranging between 13.63 and 16.98 tonnes ha$^{-1}$ for those RDs. In contrast, standing live biomass ranged from 53.22 to 212.85 tonnes ha$^{-1}$ for that RD range. In absolute terms, the quantity of living biomass or level of RD does not dictate the amounts of forest detritus. Rather, RD appears to help guide correlation with a host of stand/site attributes. Correlations between living biomass and deadwood biomass only emerged in stands with RDs (live tree stocking) exceeding 0.75. Deadwood resource predictions may only be possible when stands are experiencing self-thinning. Bond-Lamberty and Gower (2008) found a related phenomena in that tree mortality was only a significant contributor of deadwood in older stands . . . ones more likely to be highly stocked. When stands are under-stocked with a low number of small-sized trees, deadwood resources may be unpredictable. Either the stand was recently clear-cut with residue removal/burning or the stand was blown down with creation of substantial deadwood biomass. In stands at the maximum size–density limit, there has been a lack of stochastic disturbance events (e.g., harvesting or blowdowns) for a long period of time allowing for deadwood accretion from self-thinning mortality and branch-shedding. In stands such as these, deadwood resources may be contingent on stand/site attributes (e.g., moisture availability, site productivity, and stand age). These results mirror those found at smaller scales by Sturtevant et al. (1997).

This study found that a stand's standing live tree size–density slope decreased from −3 to −58 across classes of RD (ranging from 0.0 to 1.0). No strong trends in size–density slopes across classes of RD were found for CWD or standing dead trees. This finding highlights the point that decay/breakage will adjust the size–density relationships of deadwood pieces that originated from live tree self-thinning processes. If a highly stocked self-thinning stand of trees is leveled by a blowdown (Woodall and Nagel, 2007), one would not expect the size–density relationships of the resulting deadwood pieces to match that of the former living trees over time. The decay of deadwood pieces tends to rapidly decay small wood pieces reducing log taper (Woodall and Westfall, 2008) and breaking deadwood pieces into more uniform sizes (Beets et al., 2008; Radtke et al., 2009). The homogenization of deadwood piece size by decay/breakage processes appears to confound the size–density relationships of deadwood pieces. Lee et al. (1997) and Lee (1998) found that the negative exponential size distribution of standing dead trees tended to decrease in terms of slope as stands aged. In this study, standing dead trees had no discernible trends in size–density slopes across classes of RD. Once a tree is dead and standing, a certain minimum structural support is required in order to maintain its vertical stature. Smaller diameter standing dead trees will topple over more rapidly along with top breakage (Passovoy and Fule, 2006), thus eliminating smaller-sized standing deadwood pieces and flattening the size–density slope. Coarse woody debris pieces may tend to have more smaller-sized pieces lying horizontal coupled with continuous branch shedding during stand development (Oliver and Larson, 1996), thus a steeper size/density slope as found in this study. These results resemble those by Fridman and Walheim (2000) that found that the size–density slope of DDW is more negative than that of standing dead trees. Whereas, size–density attributes can form a biological basis for live tree stocking indices (e.g., SDI), the same attributes of deadwood may provide little foundation for understanding their accretion/depletion dynamics due to the effects of decomposition and breakage. Given the sometimes rapid decay of deadwood pieces (Herrmann and Prescott, 2008; Bond-Lamberty and Gower, 2008; Passovoy and Fule, 2006) relative to other stand processes; the current size–density attributes of deadwood in any stand may be spurious to informing long-term deadwood dynamics.

How might a deadwood stocking index be constructed if stocking is defined at the maximum amount of deadwood possible in any given forest stand? This study proposed a deadwood stocking index explicitly linked to standing live stocking. Results from our study indicated that deadwood stocking was highest in stands with either very low or very high stocking of live trees (Fig. 5). The lowest levels of deadwood stocking were in stands with moderate levels of live tree stocking. Similar trends in deadwood abundance along gradients of stand development have been documented in western U.S. forests by Ohmann and Waddell (2002). Based on our study's observations, we propose a deadwood stocking conundrum for stands with moderate live tree stocking which have not had recent disturbance or density-induced mortality. Are such stands understocked with deadwood? The only way for deadwood stocking to increase is for disturbance (e.g.,

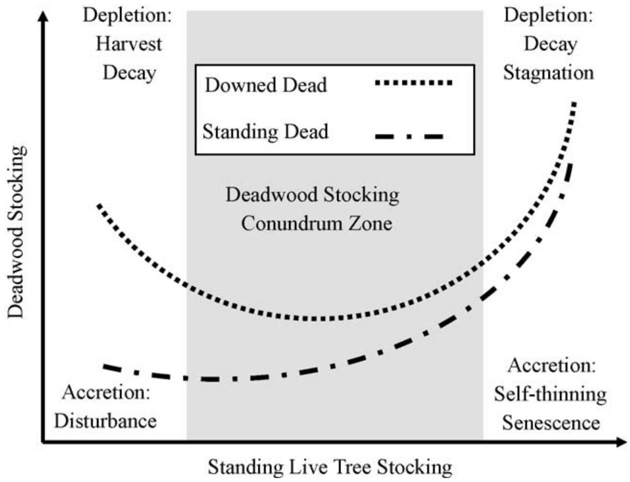


**Fig. 5.** Conceptual diagram of relationship between the stocking of standing live trees and deadwood with highlighted area of stocking conundrum and sources of accretion/depletion.

harvest or blowdowns) or self-thinning to induce tree mortality. In other words, a stand's live tree stocking needs to shift to either low or high levels in order to increase deadwood stocking. Possibly these dynamics need to be viewed in a different light where the deadwood stocking in stands with moderate live tree stocking is assumed to be relatively high with the tails of the live tree RD distribution affected by accretion/depletion processes. The only way for deadwood stocking to increase is at the tails of the distribution through mortality processes. While deadwood stocking can be the greatest when stand stocking is at extremes (low or high), the phenomena of harvest, decay, and stagnation serve as factors that reduce deadwood stocking. In stands with low live tree stocking, the highest deadwood stocking will be achieved when disturbance has killed all live trees whereby harvest and decay will serve to reduce deadwood stocking. In contrast, in stands with high live tree stocking deadwood stocking will be maximized when there is self-thinning and senescence whereby decay and stand stagnation will reduce deadwood stocking. There appears to be no simple deadwood stocking formulation due to the inherent complexity of all the stand, site, and management factors that drive deadwood dynamics. Elucidation of site-specific deadwood trends may not be possible until more intensive studies are conducted within stands of varying forest types, disturbance regimes, stages of stand development, and site productivity.

## 5. Conclusions

Relationships between the stocking of standing live trees and standing/down dead trees provide a framework for understanding and estimating deadwood resources in forests across the United States. For stands that are highly stocked in terms of the live tree size–density indices, deadwood resources may be correlated with stand and site attributes (e.g., stand age and precipitation). Although size–density attributes of standing live trees forms a biological basis for live tree stocking indices, the size–density attributes of standing and downed dead trees provides little biological basis for construction of stocking indices due to the confounding factors of breakage and decay. This study proposed a deadwood stocking index explicitly linked to live tree stocking with the assumption that the maximum deadwood biomass on any given site is directly related to the maximum live tree biomass. In order to compensate for a deadwood stocking conundrum in moderately stocked stands, we further suggest an alteration of our stocking index to acknowledge the effects that harvest, decay, natural disturbance, stagnation, and self-thinning have on deadwood accretion.

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