Standing Dead Trees in a Northeastern Deciduous Forest:

Decay Patterns and Biomass impacts

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ABSTRACT

Mortality in forests is an essential process for a healthy ecosystem. However, the decomposition of standing dead trees is largely ignored, or deemed inconsequential. Due to the nature of disturbance by drought and pests, mass tree mortality events will result in an increase in standing dead trees. Furthermore, it is critical to investigate decomposition patterns and their influence on standing dead biomass. This study investigated the patterns of density loss in terms of species (*Acer sacchrum, Fagus grandifolia, and Betula alleghaniensis* and *Fraxinus americana*) and position on a tree (upper or lower) to determine if Hubbard Brook Experimental Forest accurately estimates standing dead biomass. I found the volume and density of 32 standing dead individuals through varied decay stages to test for patterns and to compare biomass estimations between methods. This study found no evidence that patterns of density loss exist between the four studied species or that patterns of density loss differ between upper and lower position of tree. However, through the more accurate estimation of density for standing dead individuals, this study found that Hubbard Brook Experimental Forest estimates biomass by underestimating tree density by 29% and overestimating tree volume by 39%. This study contributes to the literature of decomposition processes for tree species *Acer sacchrum, Betula alleghaniensis, Fagus grandifolia*, and *Fraxinus Americana*, as well as decomposition patterns of trees in a low elevation, Northeastern broadleaf-deciduous forest. Additionally, this study provides Hubbard Brook Experimental Forest incentive to re-evaluate their techniques for estimating standing dead biomass.

KEYWORDS

decomposition, degradation, Hubbard Brook Experimental Forest, carbon, monitoring protocol

INTRODUCTION

Mortality in forests is an essential process for a healthy ecosystem. When a tree dies, its decomposition provides an abundance of resources including light, carbon, nutrients, moisture, and habitat (Franklin et al. 1982, Harmon et al. 1986). The flow of trees from the live to dead wood pools is highly influential on wildlife resource availability, carbon cycling, and nutrient cycling in an ecosystem. Moreover, a dead tree that remains standing influences its ecosystem in ways that a downed tree does not. Standing dead trees undergo decomposition more slowly than downed dead wood from lack of soil contact and moisture (Harmon et al. 1986; 2011). Yet similar to downed wood, as a standing dead tree decays it releases carbon to the atmosphere the carbon released through decomposition is balanced by the growth of new vegetation (Harmon et al.1986; Fahey et al. 2004).

However, carbon balances in forests can be offset by mass mortality events. Worldwide, forests are experiencing mass mortality from heat-induced factors including drought and pests, as well as other direct anthropogenic causes like air pollution and ozone (Allen et al. 2010, Bytnerowicz et al. 2007). Furthermore, the human caused spread of invasive pathogens and pests has also generated mass tree mortality. From 2003-2017 the Emerald Ash Borer, a native beetle to China, caused mortality in 20-100 million Ash Trees (*Fraxinus Americana*) in the Midwest and East coast of the United States (Poland, 2007; Herms and McCullough 2013). Similar catastrophes have occurred in the Eastern US with American Chestnut (*Castanea dentata*) and American elm (*Ulmus americana)* from invasive pathogens.

Due to the nature of disturbance by drought and pests, these mass tree mortality events will result in an increase in standing dead trees (Franklin et al.1982; Bentz et al.2010). For many forests experiencing extreme mortality, the majority of aboveground carbon may be stored in standing dead trees (Hagemann et al. 2010). Subsequently, respiration from tree decomposition will cause the forest to act as net source for carbon (Kurz et al.2008). Yet, limited knowledge around how standing dead trees decompose exists in the literature, and as such standing dead tress have only begun to recently be considered when estimating biomass in forests.

The biomass of standing dead trees has typically been estimated as a function of live tree carbon, however this fails to correctly evaluate the changing density and carbon concentrations in a standing dead tree as it decomposes (Harmon et al.2008; 2013). By accounting for density loss through decay, biomass estimates on standing dead aspen and Douglas-fir decreased from previous estimates by 50% and 36% respectively (Domke et al. 2011). Quantifying patterns of density loss in different species and taxa is critical for accurately estimating biomass in a future with increasing mass tree mortality.

Generally, when a standing dead tree progresses through decay its volume decreases through degradation and its wood density decreases through decomposition. Degradation occurs when the tree loses limbs, breaks its top, and eventually falls over. Degradation is a process that occurs because decomposition weakens the structural integrity of the tree (Aakala et al. 2008). Decomposition is a process orchestrated by a number of organismal activities within the wood. Fungus, insects and bacteria digest the nutrients in the tree at different stages of decay and in return, release carbon (Graham and Cromack 1982, Harmon et al. 1986). The pattern in which this process occurs is less straightforward. Taxonomic group, position on bole, species, size, and initial conditions all influence decay in a standing dead tree (Harmon et al. 2013, 2011). Different fungal communities digest the wood in softwoods and hardwoods, leading to differential density loss (Harmon et al. 2013). Due to differing gradients of decay in live trees, upper and lower portions of trees may decay at different rates (Bowyer et al. 2007). For example, lower portions of trees can decay at higher rates than upper portions due to higher contact with soil moisture and organisms (Boddy et al. 2001; Harmon et al. 1986). However, in some instances, upper portions can decay at higher rates than lower portions, as this pattern is consistent with live tree density gradients and size-decay patterns (Cousins et al. 2015; Bowyer et al. 2001). Larger trees are considered to decay at lower rates than smaller trees due to their low surface area to volume ratios (Raphael and Morrison 1987; Cousins et al. 2015) and that they have high amounts of heartwood (Vanderwel et al. 2006). Species driven patterns of decay are difficult to discern from environmental factors influencing decay. For example, snag decay extent may be more indicative of mass loss patterns in downed wood than species (Vanderwel et al. 2006), however species traits like bark chemistry can cause differing density loss patterns between species of downed dead wood (Johnson et al. 2014). In terms of standing dead trees, species traits are considered to make species differentially resistant to degradation and decomposition (Aakala et al. 2017; Cousins et al. 2015; Chambers et al. 2000). However, this is in contrast to other studies (Harmon et al. 1986).

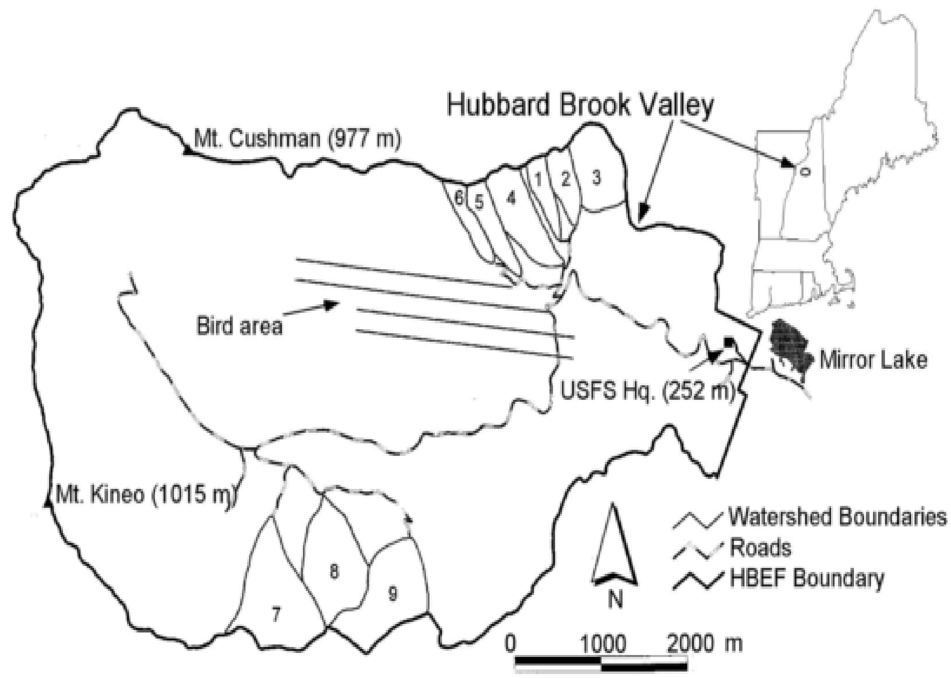
Although, the role of standing dead trees in ecosystems is vital for understanding wildlife and biomass, monitoring is only a recent development. In 1999, the US Forest Service included standing dead trees in the Forest Inventory Analysis (FIA) Program (Woodall et al. 2009). The purpose of adding standing dead trees into the inventory was to account for their nutrients, carbon, and habitat (Woodall et al. 2013). The FIA uses a five-category system to classify extent of decay in a standing dead tree, which directly accounts for both wildlife habitat and carbon. In 1981, Hubbard Brook Experimental Forest (HBEF) began inventorying mid-elevation tree health every two years. HBEF uses a two-category system to classify extent of decay and to qualify carbon in standing dead trees (Siccama et al. 2007; Whittaker et al. 1974). Due to the different approach of accounting for carbon in standing dead trees, Hubbard Brook Experimental Forest can serve as an excellent laboratory to assess the effectiveness of quantifying decay with a five-category system used for both wildlife and carbon accounting. Moreover, these monitoring programs are key to understanding standing dead decay and the role in forest habitat and biomass.

The objective of this study is to estimate patterns of standing dead tree decay in four dominant hardwoods in terms of species (*Acer sacchrum, Fagus grandifolia, and Betula alleghaniensis* and *Fraxinus americana*) and position on a tree (upper or lower). This study aims to investigate if patterns of decay in terms of species and position change standing dead biomass estimations for Hubbard Brook Experimental Forest as well as assessing the effectiveness of using a more descriptive classification system (FIA) to describe decay. I hypothesize (a) species traits will drive density loss to follow the pattern birch > maple > beech > ash; (b) position will influence density and follow the pattern upper > lower; (c) the HBEF standing dead biomass estimations are an overestimation of forest biomass.

METHODS

Study site

This study was conducted at Hubbard Brook Experimental Forest (HBEF) (43°56'30.7"N 71°46'51.3"W) located in the southern White mountains in central New Hampshire, USA (Map 1). Although the forest is most famous for six monitored watersheds, where the hydrological inputs and outputs are precisely gauged, this study takes place in the vegetative plots established within the bird monitoring and study area. In 1981 permanent vegetative plots were created within the bird area, referred to as the "bird lines." The bird lines consist of four 2.5km long transects that run NW to SE. Each bird line consists of about 100 plots 25 m by 10 m wide. In total the plots represent approximately 2.5km^2 of second-growth, mid-elevation, Northeastern deciduous broadleaf forest. The dominate tree species in the bird lines are *Acer sacchrum* (sugar maple), *Fagus grandifolia* (American beech), *Betula alleghaniensis* (yellow birch). These three species approximately form 84% of the canopy (Siccama et al.2007).



Map 1. Hubbard Brook watershed and forest boundaries. This map depicts the bird lines and nine experimental watersheds along with the two highest peaks within the watersheds. Adpated from (Siccama et al. 2007).

Monitoring of bird lines and tree sampling

Since 1981 trees within the bird line plots are inventoried every two years under the same protocol. Every tree in the plots > 10cm in diameter at breast height (DBH) has a recorded vigor. HB Vigor is categorized as 1 (healthy), 2 (less-healthy), 3 (sick), 4 (standing dead with branches), 5 (standing dead with no branches), and 6 (downed dead tree). Additionally, in each inventory session any tree that has reached DBH > 10 is added as a new recruit.

Identification of sample trees

Although inventorying the bird lines for general tree vigor, I identified trees with certain characteristics appropriate for this study of tree decay. To avoid felling standing dead trees I chose sample trees that had a HB vigor of 4 or 5 (standing dead) in 2015 and a vigor of 6 (downed) in 2017. Under this method, I assumed that the difference in decay caused by falling within the two-year inventory period is negligible for this study. Once all possible sample trees were identified, I chose additional criteria based on size classes (12-17 cm, 17-25 cm, and 25-55 cm) and species to have a representative spread of trees. As such, when I use the term standing dead tree I am describing the trees in this study.

Sample tree assessments

Field sampling included both qualitative and quantitative assessment of the standing dead trees. Qualitative assessments included assessing decay using FIA decay class 1-5 for the entire tree, within-tree density class categorization DC1, DC2, or DC3 when sampling the heartwood and sapwood of the tree as described later, and a percentage of bark cover (Table 1). Quantitative assessments included measuring appropriate dimensional data for volumetric estimation.

Table 1. Summary of qualitative descriptions for whole-tree and within-tree decay classes. Whole-tree decay classes are adopted from the FIA classification system and are labeled 1-5 below. Within tree density classes are adopted from Cousins et al. (2015) and are labeled as DC1, DC2, and DC3.

Decay Classification	Description
1	Limbs and branches all present, top pointed, all bark remaining, sapwood intact, heartwood sound hard original color.
2	Few limbs and no fine branches present, top may be broken, bark variable, sapwood sloughing, heartwood sound at base incipient decay in outer edge of upper bole, hard, light to reddish brown.
3	Branches absent with only limb stubs, top broken, bark variable, sapwood sloughing, heartwood with incipient decay at base, advanced decay throughout upper bole, fibrous to cubical, soft, dark, reddish brown.

4	Branches absent with few or no stubs, top broken, bark variable, sapwood sloughing, heartwood with advanced decay at base, sloughing from upper bole, fibrous to cubical, soft, dark, reddish brown.
5	No limbs or branches, top broken , bark less than 20%, sapwood gone, heartwood sloughing, cubical, soft, dark brown, or fibrous, very soft, dark reddish brown, encased in hardened shell.
DC1	Very hard, intact wood, usually light in color, a sharp knife penetrates by only 1-2 cm.
DC2	Softer wood, variable in color, intermediate between DC1 and DC3, a sharp knife penetrates up to 5-6 cm.
DC3	Very punky wood, dark in color, a sharp knife penetrates wood with essentially no resistance.

Whole-tree sampling

To estimate volume of each standing dead tree, I measured multiple diameters and lengths. I measured diameter of each tree at the base above the root flare, DBH, 2m, and the tip of the tree. I divided each tree into lower and upper sections, with length of the lower section consistently at 2m and length of the upper section equaling the difference between the total length and lower length of the tree. To include branches in the volume estimates, I measured any branches present by following the same method of measuring diameter at the base and tip as well as a single length of the branch. I recorded bark thickness for branches and upper and lower sections with a caliper three times and then took the average to estimate.

Within-tree sampling

I took cross sections of every tree in the midpoint of the lower and upper sections to conduct a qualitative assessment of within-tree density class DC1-DC3 using transects and to collect samples for each class present. I cut trees with either a chainsaw or crosscut saw to generate a clean face to be able to accurately read transects on the cross section. I generated three transects separated by 120 degrees, with placement of the first transect occurring randomly. I measured each transect from the center of the cross section outward and denoted of each length with the qualitative estimation of within-tree density class DC1-DC3. I measured length of each class with a ruler. Finally, I collected any within-tree density classes present within the tree and on the transects to be analyzed for a quantitative density.

Density estimation

Within- tree density estimation

I estimated the true density of all within-tree density classes DC1-DC3 found in both upper and lower sections for every sampled tree using the equation $D = \frac{mass}{volume}$. Density calculation methods were adapted from Cousins et al. (2015). I used water displacement as the method to estimate volume for every sample of wood, bark, or branch. This estimation technique involves submerging the sample and measuring the mass of displaced water. Additionally, 10% of all samples were re-measured to test for accuracy. I calculated mass by drying all samples of wood, bark and branch at 105 degrees C until measured to a constant weight $\pm$ 0.1g.

Biomass and whole-tree density estimation

Biomass is the mass of carbon per area. In this study I assume that density is a proxy for decomposition, and thus for amount of carbon. To calculate standing dead biomass for the stem, I used the within-tree density class DC1-DC3 estimated densities, the area of DC1, DC2, and DC3 per upper/lower section, and the volume of upper and lower wood. In addition, I generated a "live biomass" estimate for all the tree samples in order to check for accuracy.

Using the volumetric data from the field, I calculated the volume of each lower and upper section per tree using the equation for a frustum, $V = \frac{\pi h}{3}\left({R_{base}}^2 + R_{base}R_{top} + {R_{top}}^2\right)$ (Battles et al. 2014). I estimated the area of within-tree densities DC1, DC2, and DC3 per tree using the associated lengths on the transects (Figure1a/b). For area, I used the equation for a circle with transect lengths as the radius or the length of a within-tree density class as the radius. If lengths were not equal, I averaged them to find a single radius. For within-tree areas that were not in the shape of a circle, I used the area of the entire cross section of upper or lower and subtracted the area of the density class closest to the center. I assumed that each density class area was a perfect circle or a portion of a perfect circle, which resulted in underestimation of true density class area.

To apply DC1, DC2, and DC3 areas to the entire lower or upper section volumes, I calculated a proportion to represent estimated volume of each within-tree density class per upper or lower section and tree (Figure 1c).

I generated density-specific volumes in which different density values found for each DC1, DC2, DC3 could be applied to the volume of DC1, DC2, and DC3. I assumed that density would be consistent throughout the entire section of tree. Therefore, to calculate standing dead biomass, the volumes of each within-tree density class DC1-DC3 were multiplied by respective actual densities. Finally, I estimated total biomass of each standing dead tree by adding the biomasses of each within-tree density class DC1, DC2, and DC3 per section, and then combining the lower, upper, and branch sections of the standing dead tree.

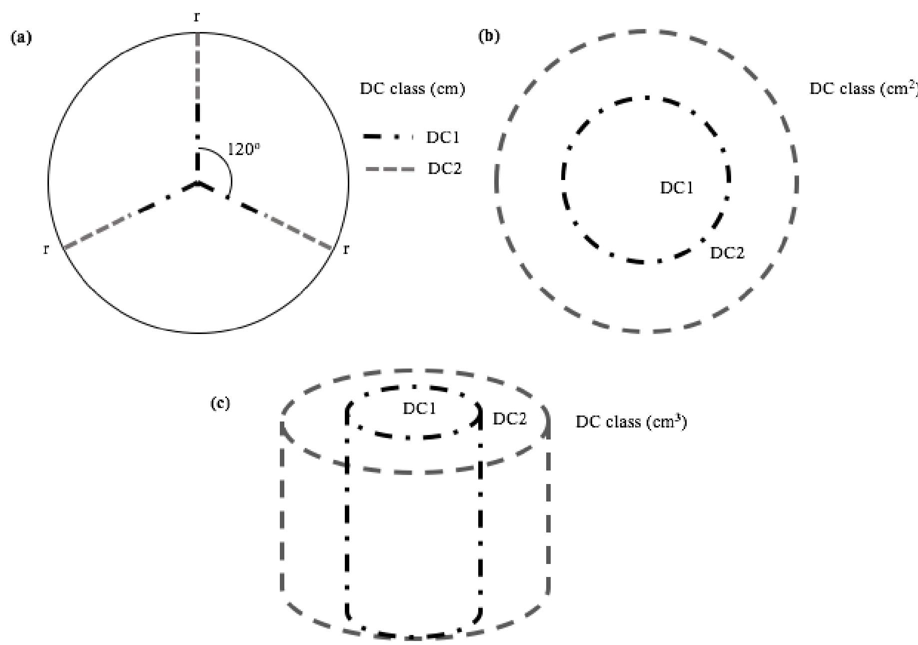


Figure 1. Estimating volume of within-tree density classes from transect lengths. (a) represents a cross section of a tree with different lengths of DC1 and DC2 on three transects, (b) represents a cross section of a tree with estimated area of DC1 and DC2, calculated from (a), and (c) represents a portion of tree (upper or lower) with estimated volume of DC1 and DC2, calculated from (b).

Hubbard Brook Biomass Estimations

I adapted biomass calculations used by Hubbard Brook Experimental Forest for standing dead biomass from Battles et al. (2014). Which uses density reduction factors for HB Vigor 4 (0.7283) and 5 (0.5683) on species-specific live tree density adapted from decay rates of trees in a southern temperate deciduous forest (Onega and Eickmeier, 1991; Arthur et al. 1992). Volume reduction factors are proportions of live tree volumes specific to HB vigor 4 and 5. These reduced factors are then used to estimate standing dead biomass.

Analysis

Analysis of the data will use R-studio Version 1.0.136 (2016) to determine if significant differences in the means of the independent variable tree density occurs between species, tree portion, and standing dead biomass. To determine if differences in means existed between density by upper and lower portion of stem, I used a paired T-test. To determine if differences in means existed between the four species in this study, I conducted a one-way analysis of variance for density. To understand whether my calculation of standing dead biomass was more accurate than Hubbard Brook's estimations I used a paired T-test to compare the means of biomass. Additionally, in this study, I will report standard errors opposed to standard deviations because I find standard error to be more useful in understanding the statistical significance of patterns in decay.

RESULTS

Hubbard Brook bird line tree demographics

The forest on the birdlines at HBEF is codominated by *Acer sacchrum* (Sugar maple), *Fagus grandifolia* (American beech), and *Betula alleghaniensis* (Yellow birch), and has a smaller population of *Fraxinus americana* (American ash). These four species compromise 84% of the canopy. The total number of trees in the bird line plots for the 2017 inventory was 5506, where the four species in this study totaled 3785 live trees and 800 standing dead trees. On average, the total ratio of live trees to dead trees is 5:1 with standing dead trees contributing to 17% of the entire studied tree species population (Table 2).

Table 2. Live and dead trees at Hubbard Brook. Bird line vegetation plot demographics by species.

Species	Live trees 2017	Standing dead 2017	Totals 2017	Population Ratio Live:Dead	% standing dead for whole pop.
Sugar maple	1215	199	1414	6:1	4.3%
Yellow birch	1719	395	2114	4:1	8.6%
American beech	766	203	969	4:1	4.4%
American ash	88	6	94	15:1	0.1%
Total	3785	800	4584	5:1	17%

Standing dead trees sampled

This study sampled 32 standing dead trees. The opportunistic sampling method favored trees in decay classes 3-5; with only 4 trees in decay classes 1-2 and 28 trees in decay classes 3-5. Additionally, sampling favored trees in HB vigor class 5, with 23 trees with code 5 and 9 with code 4 (Table 3). However, due to sampling trees within a specifically chosen range of DBH's, the amount of trees within each size class is fairly equal. The opportunistic sampling method limited my ability to collect samples for each species by each decay class (Table 3). For within tree density classes DC1, DC2 and DC3 I estimated a total of 181 samples for density.

Table 3. Distribution of sampled trees. Standing dead tree characteristics by species, FIA decay class, and HB Vigor class.

Species	FIA decay class(n)					HB vigor class(n)		Total
	1	2	3	4	5	4	5	
Sugar maple	0	0	4	5	1	3	7	10
Yellow birch	0	1	0	4	3	1	7	8
American beech	2	1	4	3	1	4	7	11
American ash	0	0	1	2	0	1	2	3
All species	2	2	9	14	5	9	23	32

Within-tree density patterns

Stem wood placed in density classes DC1, DC2 and DC3 differed in mean density (ANOVA, 171.3, $p < 0.0001$). DC1 had a 57% higher density than DC2 and an 83% higher density than DC3, where DC2 had a 61% higher density than DC3 (Table 4). By grouping DC1-DC3 by species, no significant differences existed between density and species. I measured each within-tree density at the same density for each FIA decay class (Figure 2). Furthermore, abundance of within-tree density class followed an expected pattern: DC1 decreasing through FIA decay class, DC3 increasing through FIA decay class and DC2 acting as an intermediate (Figure 3). These results imply that my sampling was consistent.

Table 4. Within-tree density summary. Mean density was calculated using the density equation. All within-tree density classes are significantly different from each other (P=2e-16) and decreased in density from DC1-DC3.

Within tree density class	Mean density (g/cm3)	n
DC1	0.48 (0.02)	51
DC2	0.20 (0.02)	39
DC3	0.08 (0.005)	24

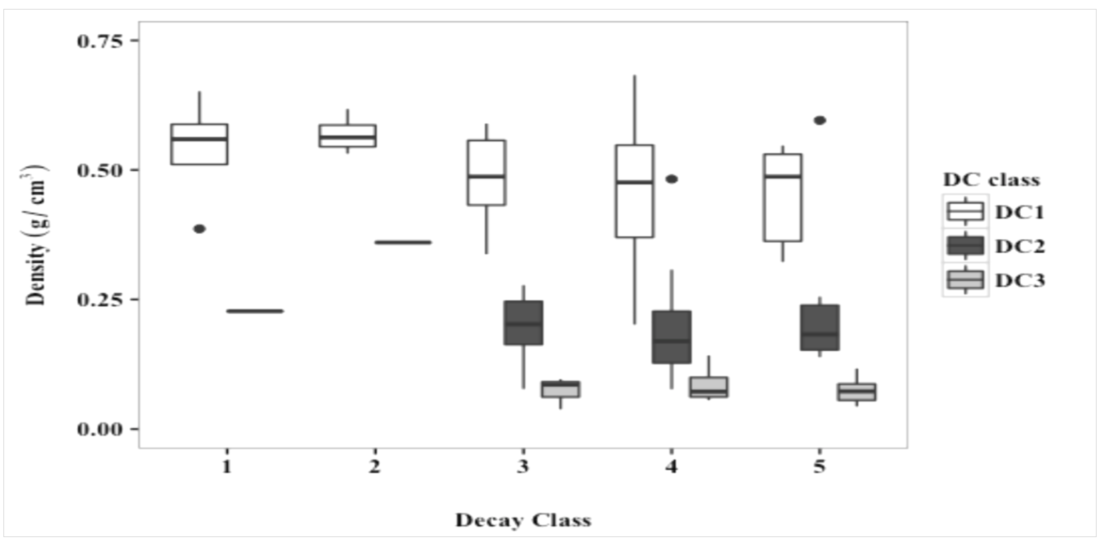


Figure 2. Densities of within tree DC1, DC2 and DC3 by FIA decay class 1-5. I found significant differences between DC1, DC2, and DC3 ($p < 0.0001$) using a one-way ANOVA. As shown, no differences exist between each density class DC by FIA class, however overall density decreases by FIA decay class. Boxes represent 50% quartile range, whiskers represent 25% upper and lower quartile range.

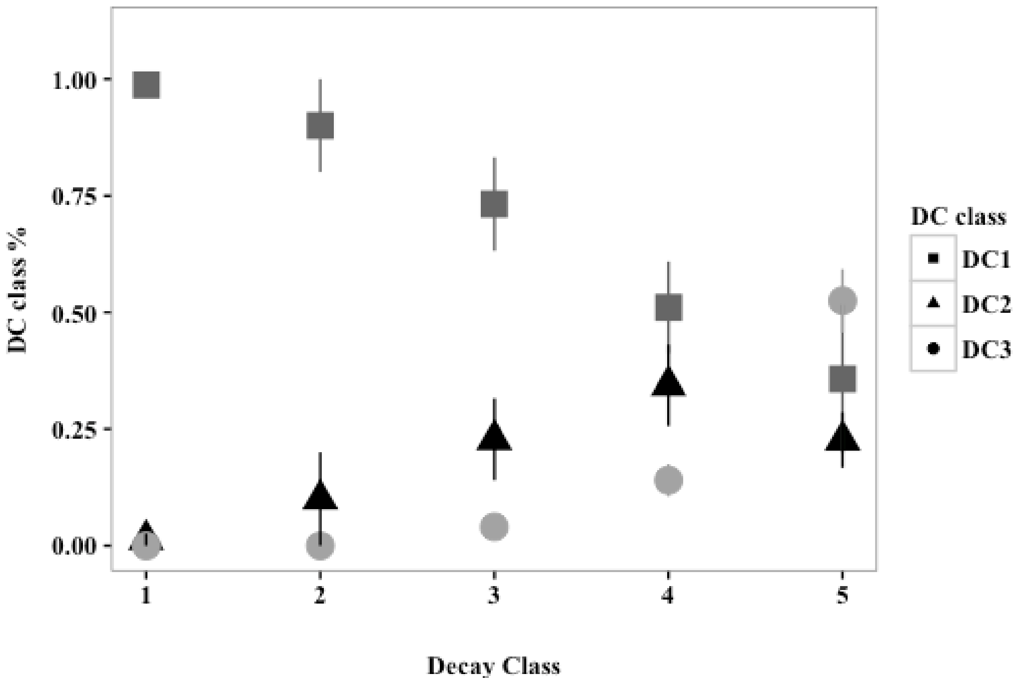


Figure 3. Percent of DC1, DC2, and DC3 by FIA Decay class. DC1 (square) decreases through increasing FIA class, DC2 (triangle) increases through FIA class 4, and then declines by 5. DC3 (circle) remains at zero percent for FIA decay classes 1 and 2, and increases from class 3-5. Points represent mean percentage; lines represent standard error around the mean.

Whole-tree density patterns

For all tree species, standing dead stem wood for each FIA decay class 1-5 had similar mean densities, meaning that there were no notable species differences in decomposition. All species declined in density as they progressed through increasing FIA decay class (Figure 4a) (ANOVA, $F = 5.407$, $p = 0.00249$). However, the differences between decay class 5-1 and 5-2, drove the significance (Tukey HSD). Using a mean live wood density of 0.55 g/cm^3 for all species, extent of decay is illustrated by the large difference of dead to live ratios between decay class 1 (0.98) and decay class 5 (0.41) (Table 5). As such, stem wood in FIA decay class 1 had 1.8% lower density than live wood and stem wood in FIA decay class 5 had 58.2% lower density than live wood. For the HB Vigor classification system, significant loses of density occurred between classes 4 and 5 (one-way ANOVA, $F = 21.23$, $p < 0.0001$) (Figure 4b). HB Vigor 4 had density 40% higher than HB Vigor 5. This is reflected in the dead to live ratios for 4 (0.90) and 5 (0.54) (Table 5).

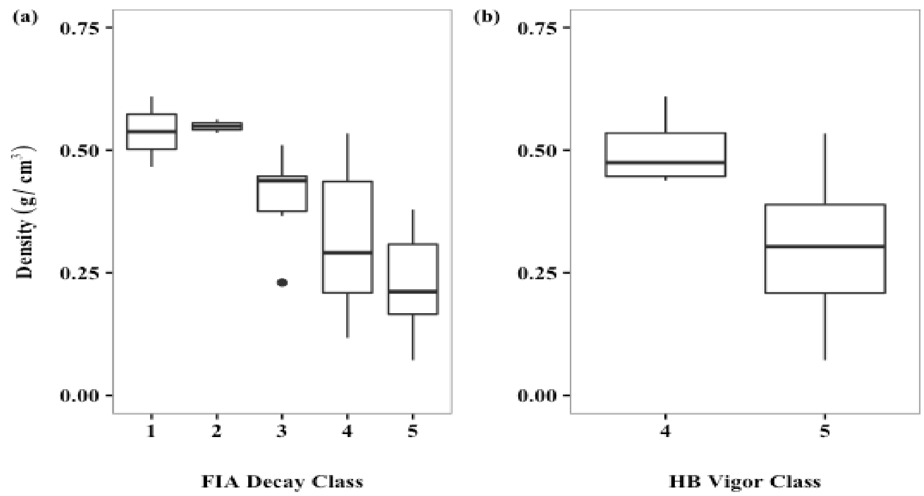


Figure 4. Quantified density ranges for both the Forest Service (FIA) and Hubbard Brook (HB) decay qualification systems for all tree species combined. (a) significant differences in density between decay class 5-1 and 5-2 drove the significance for the ANOVA between density and decay class ($p < 0.01$). (b) I found significant differences between density for HB Vigor 4 and 5. For both plots the boxes represents the 50% quartile, and whiskers represent 25% upper and lower quartiles for the data.

Table 5. Density by FIA decay class and HB Vigor Class. FIA decay classes are denoted with "F" wood, where HB vigor classes are denoted with "HB" characterizes bark. Standard errors are reported in parenthesis; n represents sample size.

Decay Class	Mean density (g/cm^3)	n	Dead:Live ratio
1F	0.54 (0.07)	2	0.98
2F	0.55 (0.01)	2	1.00
3F	0.41 (0.03)	9	0.75
4F	0.31 (0.04)	14	0.56
5F	0.23 (0.05)	5	0.42
4H	0.50 (0.02)	9	0.90
5H	0.30 (0.03)	23	0.54

Influence of tree characteristics on density

Role of upper and lower bole position on density loss

The position of the bole had no influence on the extent of decay within the tree. Upper portions of the tree across all decay classes and species had densities 6.6% higher than for lower portions in the same decay class (Table 6). However, this did not generate significant density patterns by upper and lower stem (Paired T-test).

Table 6. Summary of densities for lower and upper portion of trees. I used a two sample paired T-test to compare means between lower and upper portion of trees.

Position	Mean density (g/cm^3)	n
Lower	0.34 (0.03)	32
Upper	0.37 (0.03)	32

Role of species on density loss

Sugar maple, Yellow birch, American beech, and American ash did not have unique densities by FIA decay class or HB Vigor class. All species had densities within the range 0.28-0.41 g/cm^3 (Table 7).

Table 7. Summary of densities for tree species. I used a oneway ANOVA to compare mean densities between species of standing dead tree and found no significant differences in density.

Species	Mean density g/cm^3	n
Sugar maple	0.37 (0.05)	10
Yellow birch	0.28 (0.05)	8
American beech	0.41 (0.04)	11
American ash	0.32 (0.08)	3

Comparison between biomass estimation methods

The standing dead biomass estimates I calculated for all 32 trees were similar to the biomass estimates for the same trees using Hubbard Brook standing dead biomass methods. However, in comparing HB standing dead density to the standing dead density that this study calculates, I found that Hubbard Brook underestimates standing dead density by 29% (Table 8). Hubbard Brook Estimates of mean density was significantly higher than the density measured in this study (Paired

T-test, df=31, p = 0.0001) (Figure 5). HB volume estimations are significantly higher than this study's estimations (Paired T-test, df = 31, P = 0.00164) (Figure 4), and overestimates volume by 39% (Table 8).

Table 8. Differences by calculating method. Summary of mean volumes, total mass, and total tree density between Hubbard Brook and this study. Ratio of estimates between Hubbard Brook and this study (ZK) in the last column.

Calculating method	Mean Volume (m^3)	Mean density (g/cm^3)	Mean Biomass (kg)
This Study	0.334 (0.06)	0.27 (0.02)	126.97 (22.45)
Hubbard Brook	0.551 (0.11)	0.38 (0.03)	133.94 (33.7)
Percent difference (HB-ZK / HB)	39%	29%	5%

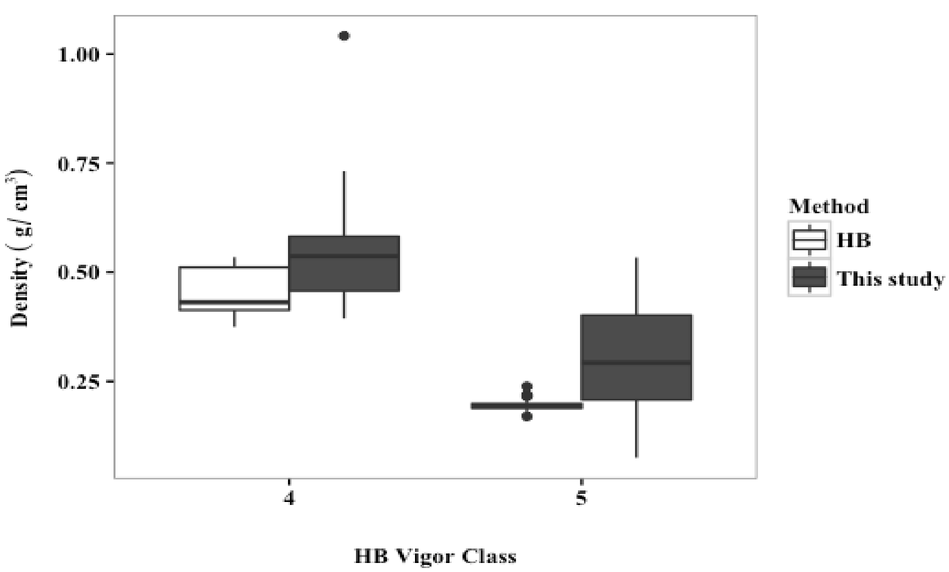


Figure 5. Comparison between density by HB vigor and method. "HB" refer to densities calculated by Hubbard Brook Experimental Forest and "This study" refers to densities calculated in this study. Hubbard brook uses significantly lower tree densities than this study for estimating biomass (p = 0.001). For both plots the boxes represents the 50% quartile, and whiskers represent 25% upper and lower quartiles for the data.

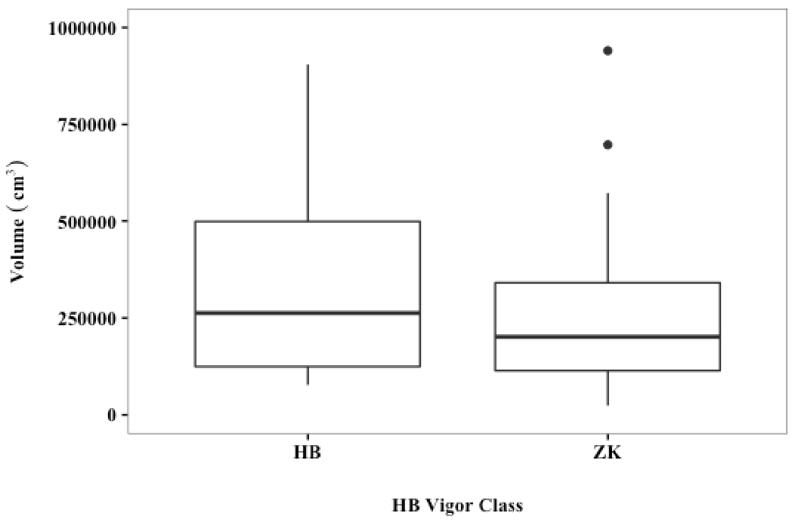


Figure 6. Comparison between volume by method. "HB" refers to volumes calculated by Hubbard Brook Experimental Forest and "This study" refers to volumes calculated in this study. Hubbard brook uses significantly higher tree volumes than this study for estimating biomass ($p < 0.01$). For both plots the boxes represents the 50% quartile, and whiskers represent 25% upper and lower quartiles for the data.

DISCUSSION

A standing dead tree is an ecological unit that undergoes dynamic processes just like any ecosystem (Franklin et al.1960, Graham 1925). The process of decay is varied and intricately dependent upon a number of variables such as microorganism communities, temperature, precipitation, wildlife use, and how the tree died. With this in mind, the individual standing dead tree is highly variable in the decomposition process and intrinsically, no two trees decay the exact same way. There is diversity in decay that is nearly impossible to quantify. However, it is possible investigate the patterns of decay and use these patterns to estimate biomass for forests. This study found evidence to support that estimating within-tree patterns of density can more accurately describe standing dead tree decay by the two decay classification systems (FIA and HB). However, this study found no supporting evidence that the roles of species and tree position drive patterns of density within standing dead trees. Another goal of this study was to test how accurately Hubbard Brook Experimental Forest (HBEF) estimates standing dead biomass, by comparing the HBEF standing dead biomass estimates from the refined within-tree densities of this study. While standing dead biomass estimates calculated by HBEF are accurate in relation to this study's calculations, HBEF standing dead biomass estimates are accurate for the wrong reasons.

Whole-tree and within-tree density loss patterns

This study successfully quantified patterns of density for a standing dead tree from a qualitative assessment. My findings emphasize that standing dead trees lose density predictably through both FIA decay class and HB Vigor class. To estimate patterns of density loss, this study first estimated within-tree density. The qualification of within-tree density classes DC1, DC2, and DC3 translated quantitatively into specific densities. This method of estimating density within a tree has been successfully implemented in other studies (Harmon et al. 2011, 2013; Cousins et al. 2015). However, the pattern in which DC1, DC2, and DC3 occur across decay classes has often been ignored. Each within-tree decay class had a very distinct range of densities. However, with increasing FIA decay class the equivalent within-tree densities did not lose density. This provides evidence that differing abundances of DC1, DC2, and DC3 drive whole-tree density, not their decrease in density as a class. The relative abundances of differing within-tree decay classes may be more useful in quantifying whole tree density than using singular densities for each FIA decay class. Furthermore, monitoring abundance may be useful in connecting protocols for carbon accounting and wildlife habitat. For example, as cavity-nesting birds prefer snags with pockets of high decayed wood (Raphael and Morrison 1984) monitoring for abundances of DC3 may illuminate that a tree in a higher decay class can serve as wildlife habitat.

By using within-tree density, this study was successful in quantifying whole-tree density. Moreover, as standing dead trees move through FIA decay classes 1 through 5 and HB Vigor classes 4 to 5, they incrementally loose wood density. A tree in FIA decay class 5 of this study has about 42% of its original live density. This pattern of density loss is consistent with the lower range of dead to live ratios found in other studies (Cousins et al. 2015; Harmon et al. 2011).

For this study, a tree in HB Vigor class 4 has about 90% of its original live density and a tree in class 5 has about 54% of its live density. The HBEF dead to live ratios for both classes are 73% and 56% respectively. Whereas this studies ratio for HB vigor class 5 is only slightly lower than than the ratio used at HBEF to estimate density reductions for standing dead trees (Onega and Eickmeier 1991; Battles et al. 2014), density reduction for HB Vigor class 4 is 18% lower (73%)

than my findings. This difference illuminates specifically that HBEF is underestimating the density in standing dead trees residing in HB Vigor class 4. Yet, my findings on overall whole-tree and within-tree density patterns suggest that the FIA and HB classification systems are useful tools in qualifying density loss in standing dead trees.

Influence of tree characteristics on density loss: species and position

I expected species to be a driver in differences of decay patterns between individuals based on differential wood characteristics and fungal/insect communities, however I found no evidence to support this claim. Previous studies on the same species, have found examples of species differences in decay in downed trees (Johnson et al. 2015) in which birch decayed the most quickly, beech decayed the slowest and maple decayed intermediately. However, in investigating standing dead decay, species characteristics and environmental factors are often difficult to disentangle. Decay differences have been found to exist between taxa due to the presence of different wood rot fungi (Cousins et al. 2015; Harmon et al. 2013), yet there is contradicting evidence between species driven decay differences (Harmon et al. 1986; Aakala et al,. 2008, 2017). To control for macro-environmental influences such as temperature and precipitation, we sampled trees at the same elevation and forest. Therefore, my result that species does influence density loss provides evidence to support that micro-environmental factors such as decomposing agents and micro-climate are the primary drivers in density loss patterns found between standing dead trees.

This study found that bole position had no influence on extent of decay within a tree. This is contradictory to other findings that claim bottom-deterioration gradients in decay due to organismal accessibility to the lower bole from direct contact to the soil (Harmon et al. 1986). It is also contradictory to findings that claim a top-deterioration gradient in trees due to consistencies to live tree density patterns (Cousins et al. 2015; Bowyer et al. 2001). Top deterioration is thought to aid in the process of lowering tree center of gravity to prevent the tree from falling over. This was seen in *Picea spp*. and *Abies spp.* in the Canadian Northeast, where the *Abies spp.* decayed more quickly from the top, thus transitioning more slowly to the downed wood pool and falling over as an intact tree (Aakala et al.2017). Additionally, soil moisture exposure may be less influential than previously thought on decaying lower portions of trees more quickly than upper portions, based on findings in Liu et al. (2013) that claim temperature and moisture explained less than half of the variation in wood decay in a sub-tropical forest. Therefore, illuminating the critical role of decomposing agents in the decay processes and their varying preferences and methods for decomposing wood. However, this study found no evidence to support the hypothesis that the density of upper and lower portion of trees is different. This may be a result of the extreme environment of the Northeast broadleaf deciduous forest. Decay rates for Hubbard Brook Experimental Forest are quite high (Arthur, 1991). Furthermore, standing dead trees may have less distinct patterns of density loss between upper and lower tree portions because decay rates are so rapid in comparison to other studies (Cousins et al. 2015; Harmon et al. 1986).

Biomass Estimations and Accuracy

The method in which Hubbard Brook Experimental Forest calculates biomass is accurate, relative to the biomass estimates in this study. Others studies have found that when including decay dynamics of standing dead trees into total above ground biomass estimates, substantial losses occur (Domke et al. 2011; Woodall 2012). Although, substantial losses in biomass did not occur, my results did illuminate that HBEF is achieving an accurate biomass estimation through an underestimation of density and an overestimation of volume. The method HBEF uses to estimate standing dead biomass is through the reduction of live tree biomass with dead to live tree ratios. As mentioned above, dead to live tree ratios found in this study are consistent with ratios HBEF uses for HB vigor class 5, but are higher than ratios used for HB Vigor class 4. Therefore, HBEF is underestimating density overall and particularly in vigor class 4. Furthermore, to achieve the accurate biomass estimate, HBEF overestimates for tree volume. These discrepancies provide evidence that understanding the processes of decomposition and degradation is complicated and further investigation is required to understand the implications of underestimating density and overestimating volume on entire forest standing dead biomass.

Comparison of standing dead tree classification systems

Although the FIA and HB classification systems are useful tools to account for carbon in dead trees, limitations exist for both. This study found evidence to support that in terms of accounting for carbon, the FIA 5-category system is redundant. Only true differences in density loss existed between FIA decay class 1-5 and FIA decay class 2-5. Therefore, in terms of accounting for carbon a two classification system may be more useful. However, in terms of monitoring for habitat the FIA decay class system is highly effective (DeMeo et al. 2013). Moreover, to bridge the connection between habitat monitoring and carbon accounting the 5-category system is effective. As demonstrated in the plasticity of achieving accurate biomass estimates for the wrong reasons, the HB classification system appears to be very useful in accounting for standing dead carbon. Currently in their monitoring methodology, HBEF classifies standing dead trees into two vigor categories 4 and 5. However, in the case of mass tree mortality (Allen et al. 2010), the inaccurate methodology for estimating biomass may result in gross overestimation of biomass and consequentially, forest carbon dynamics. Furthermore, the two-category system is very effective in accounting for carbon, but must be refined to prepare for potential future mortality dynamics in forests. Determining which classification system is more effective is highly dependent upon the objectives of the monitoring. If the objective is to monitor habitat and carbon, the FIA protocol is highly effective. However, if monitoring carbon is the primary objective the HBEF protocol is more useful.

Limitations

The largest obstacle to any study investigating standing dead trees is how to safely study them. Due to limited time and access to a professional feller, this study utilized an opportunistic sampling method. I sampled trees considered standing dead in the 2015 and transitioned to the downed dead pool by the 2017. This technique avoided the dangers of felling standing dead trees, however introduced some bias into the study. This sampling technique may have impacted the results of this study for upper/lower position impacts on density loss. As such, I cannot conclude that the patterns hypothesized for size and upper/lower position do not exist.

Secondly, the decomposition process is highly variable and nearly impossible to determine causation by any factor. Patterns of decay are extremely difficult to quantify. With this in mind, consistent sampling and data collection methods should minimize this limitation on achieving reliable results.

Conclusion

This study will contribute to the literature of decomposition patterns for tree species *Acer sacchrum, Betula alleghaniensis, Fagus grandifolia*, and *Fraxinus Americana*, as well as decomposition patterns of trees in a low elevation, Northeastern broadleaf-deciduous forest. Additionally, this study provides Hubbard Brook Experimental Forest incentive to re-evaluate their techniques for estimating standing dead biomass. Due to the site-specific conditions of decomposition processes, other forest ecosystems should have comprehensive investigations of the patterns of decay involving species, size class, bark and stem, and position. Additionally, a more in depth study on decomposing agents residing in the tree species of this study would be very helpful in understanding the gradients of decay in standing dead trees.

This study successfully quantified decay in standing dead trees in a Northeast broadleaf deciduous forest. Additionally, this study was successful in using refined densities to understand how biomass estimations at Hubbard Brook Experimental Forest are indirectly inaccurate. However, there is a diversity in decay that is nearly impossible to quantify. This study was unable to find evidence to support species and position driven differences in decay. And yet, its important that we study decay. Decomposition processes are the heartbeat of a forest, inextricably linking life and death in an ecosystem. This study is important because it quantifies how decay dynamics are linked to carbon balances, a true indicator of ecosystem health. If we want the ability to assess how healthy our forests are, we need to understand decay processes.

Acknowledgments

I would first like to thank John Battles, Patina Mendez, John Sanders, Kurt Spreyer, and my peers in ES 175 for their tremendous support and guidance during this whole process. I would also like to thank everyone at Hubbard Brook Experimental Forest for their kindness and enthusiasm over the summer of 2017. Lastly, I would like to thank my best friend Carli Jipsen and my partner David Lee for making me feel loved and infinitely supported.

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