DOWNED WOODY DEBRIS, FOREST DEVELOPMENT, AND TREE BIOMASS IN THE WHITE MOUNTAINS OF NEW HAMPSHIRE

by

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ABSTRACT

J.M. Nash. Downed Woody Debris, Forest Development, and Tree Biomass in the White Mountains of New Hampshire. 58 pages, 2 tables, 9 figures, 2022. CSE style guide used.

The downed woody debris in a stand is driven by inputs from overstory trees and outputs via decomposition throughout the stand's development. The development of an individual stand, however, takes place over long periods of time and thus is difficult to study directly. We re-sampled a chronosequence of sixteen northern hardwood stands in the White Mountains of New Hampshire to describe how volume, species composition, and decay class of downed woody debris vary with stand development. As expected, the species composition of downed woody debris was different in forests at different stages of overstory succession and total downed woody debris increased with stand age and the production of larger downed wood. Re-sampling the chronosequence revealed a decrease in downed woody debris volume from ~80 to 40 m^3/ha in a 70-year-old stand and an increase from ~50 to 120 m^3/ha in a 145-year-old stand, resulting from infrequent disturbances. Fine woody debris peaked at 30-50 years during the self-thinning of early-successional species, especially pin cherry. The 145-year-old second-growth stands were unlike true old-growth stands due to a lack of live ($p = 0.09$) and downed trees ($p = 0.06$) > 40 cm. The live aboveground biomass throughout this chronosequence was highest in one of the old growth stands at about 450 Mg/ha, while the second-growth stands appeared to level off at about 350 Mg/ha after 145 years. These results suggest that tree biomass has the potential to surpass 300 Mg/ha in stands less than 200 years old. Steady state conditions for live trees may not be reached within 150 years in this forest type, while downed woody debris biomass may fluctuate around 15 Mg/ha after 150 years depending on disturbances.

Keywords: chronosequence, downed wood, carbon cycling, northern hardwood

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CHAPTER 1: LITERATURE REVIEW

The history of the Federer chronosequence

Forest development takes place over long periods of time, and it is impractical to follow the development of a single stand for hundreds of years. In a chronosequence, stands have developed under similar climatic and edaphic conditions and differ in the time since stand initiation (Walker et al. 2010). Thus, differences among stands can be assumed to reflect development over time. While the chronosequence approach can be very useful, the interpretation of results can be confounded by changes in environmental characteristics or treatment methodology over time, such as the change from tractors to more sophisticated heavy machinery such as skidders in forest harvests (Yanai et al. 2003). One way to control for this limitation is to resample the same chronosequence to confirm or reject predictions from earlier results.

The northern hardwood chronosequence that I re-sampled in 2020-21 is located in the White Mountains of New Hampshire, where there is a long history of chronosequence studies. Sampling efforts at some of the stands included in this study began with efforts to characterize soil humus layers following forest harvests in six stands in 1960 (Hart 1961). Hart (1961) found that the weight of the humus layer decreased following increasingly intense harvest. Covington (1981) used a different chronosequence of 14 stands and fit a model to describe the change in forest floor mass, and concluded that the mass of the forest floor decreased by 40-50 % to a minimum 15 years after clearcut, increase by about 28.0 Mg/ha 15-64 following the harvest, and then slowly accumulated until 200 years, at which point he hypothesized the forest floor mass should be close to unmanaged levels. Covington (1981) posited that slash may accumulate 50% of the N mobilized from the forest floor and play an important role in forest homeostasis.

Inspired by the Covington (1981) study, which seemed unbelievable due to such drastic decreases, in 1979 Tony Federer re-sampled the Hart (1961) stands (H1-H6). There were not many eligible stands of the right age in the target area. Although the objective was to determine changes in soil horizons with stand age, Federer (1982) found that the thickness of specific horizons changed over a 30-year period, though the total thickness remained the same (Federer 1982). These discrepancies in characterizing soil horizon thickness motivated Federer to advocate for the use of the then new Soil Conservation Service definitions of soil horizons–Oi, Oe, and Oa based on the fibric content of organic soils, and Op and Ap indicating organic or mineral soils that had been plowed or otherwise mechanically disturbed. These new soil horizon definitions were more descriptive than the L, F, H, and A1 designations employed earlier, and reduced the subjectivity of surficial soil horizon determinations. In 1980, Federer (1984) added seven more stands to the chronosequence to determine if the original pattern described by Covington (1981) was empirically sound. Although Federer (1984) did not observe the 50% mass loss of the forest floor reported by Covington (1984), he did observe a decrease in forest floor mass with age and demonstrated that forest soils in mature (~100-year-old) northern hardwood stands have about 80 Mg/ha of organic matter and 1.9 Mg/ha N. According to the Covington interpretation of the chronosequence, 20 years after clearcutting, the forest floor organic matter decreased to 50 Mg/ha and N to 1.1 Mg/ha. After about 50 years, the forest floor mass returned to pre-harvest levels.

Exactly 15 years after the Federer studies (Federer 1982; Federer 1984), the forest floors were re-sampled to test whether base cation losses observed at Hubbard Brook were due to acid rain or might instead be associated with nutrient uptake by the aggrading forest biomass.

Contrary to expectations, younger stands gained base cations in forest floor rather than losing them (Yanai et al. 1999). Perhaps more importantly, the youngest chronosequence stands did not in fact lose 50% of the forest floor mass 20 years after harvest as predicted by Covington (1981), but rather only 36% (Yanai et al. 2000; Yanai et al. 2003). Furthermore, soils in the oldest chronosequence stands had about twice as much organic matter as soils in the recently cut stands. This difference was attributed to the change in logging practices from horse to mechanized logging and the reduced disruption to the forest floor provided by skidders as opposed to tractor logging. The more intense mechanized logging mixed the organic and mineral soils, reducing the organic horizons.

The chronosequence stands were inventoried for live trees in 1994-95, in 2003, and in 2012. Leaf litterfall was monitored from 1993 to 1997 to characterize nutrient concentrations and mass of leaf litter for the dominant species in the chronosequence. Nutrient concentrations were more variable across stands than within stands, especially P (56% CV across stands), but forest floor mass was more variable within sampling periods (Yanai et al. 2012). The most recent use of these chronosequence stands involved the excavation of soil pits to describe belowground C and N stocks. Soil pits revealed that non-soil belowground pools, including wood and roots, accounted for 25% or more of total belowground N and C (Vadeboncoeur et al. 2012). These data were also used to show that intensive harvests with a short rotation could rapidly deplete soil nutrients, but long rotations should not (Vadeboncoeur et al. 2014). Furthermore, of the nutrients in critical supply in the northeast, weatherable P may be the first to limit production in as few as six rotations (Vadeboncoeur et al. 2014).

Downed woody debris

Tree stems, branches, and twigs that have fallen to the forest floor are collectively called downed woody debris (DWD). Downed woody debris is important ecologically as a microhabitat for saproxylic insects (Grove 2002), small mammals (Sullivan et al. 2012), fungi (Norden et al. 2004), and as a source of moisture and a germination site for mosses and plants, especially in later stages of decomposition (Andersson and Hytteborn 1991; McGee and Birmingham 1997; McGee 2001). DWD is also an important store of carbon (C), and old-growth forests that have accumulated large DWD stocks sequester C on a scale meaningful to global C budgets (Harmon et al. 1986).

Overstory succession, life history traits of individual tree species, and stochastic disturbances influence the production of DWD volume and biomass, while rates of decomposition determine the turnover rate of accumulated debris. The decomposition of DWD is highly variable as a result of biotic and abiotic factors such as temperature, moisture, and microorganism activity (Dai et al. 2021). As wood decomposes, the C stored in the wood is absorbed by microorganisms, released to the atmosphere, and leached into soil, along with nutrients and phenolic compounds also stored in the wood. Leached C, nutrients, and phenolic compounds influence the formation of soil organic layers and soil physical and chemical properties such as nutrient availability and moisture retention (Stutz and Lang 2017). Although the process of decomposition is continuous, the state of decomposition of DWD is often characterized by decay classes. Decay classes are commonly ranked 1-5, with decay class 1 consisting of DWD that is undecomposed and with fine twigs remaining, while DWD in decay class 5 has decomposed to the extent that it has lost all structural stability (U.S Forest Service

2005). The extent to which DWD is decomposed at the time of inventory depends on how long ago it fell and the rate of decomposition, which depends on environmental conditions (Harmon et al. 1986).

Disturbances may be classified as autogenic or allogenic depending on whether the disturbance originated from conditions produced by the stand - as is the case with self-thinning, or outside of the stand - as is the case with a windstorm. Many disturbances, however, may be both autogenic and allogenic given predisposing conditions within the stand that influence the response to an outside disturbance (Oliver and Larson 1996).

Autogenic disturbances and DWD

As trees die, the overstory species of the stand are represented in the downed wood. Overstory succession follows a relatively predictable pattern of species dominance, influenced by the biotic and abiotic conditions of a particular site in time (Allison et al. 2003). Disturbances that result in loss of canopy cover play an integral role in the alteration of site conditions by increasing the amount of light that reaches the forest floor. Changes in vegetative diversity as a result of forest succession in northern hardwood forests are well documented (Leak and Yamasaki 2010; Allison et al. 2003, but DWD volume and biomass in second-growth forests are variable (Fahey et al. 2005; Siccama et al. 2007; Keeton et al. 2011).

Environmental conditions created by clearcuts are conducive to pioneer and shade-intolerant species, including many that die during stem exclusion as a result of increased competition for light (Leak and Wilson 1958; Hilmers et al. 2018). Woody debris production peaks during the stem-exclusion phase of succession, which causes individual tree mortality, in contrast to woody debris produced from disturbances such as ice storms (Fahey et al. 2020) or native or invasive insect outbreaks, which inflict large-scale tree mortality (McGee 2000; Perry et al. 2018). Particularly important during stem exclusion in northeastern forests is the mortality of pin cherry (*Prunus pensylvanica* L.). Pin cherry seeds may persist for 60 years or more in the soil seed bank (Tierney and Fahey 1998). When a disturbance allows sufficient light penetration through the forest canopy, especially in the case of entire canopy removal, pin cherry seedlings can quickly recruit and dominate the stand (Oliver and Larson 1996). Pin cherry then self-thins due to competition for limited light and diminishing nutrients and space, resulting in significant contributions to woody debris, especially of smaller size classes in stands about 20-30 years since clear cutting (Hughes and Fahey 1994; Tierney and Fahey 1998). Overstory dominance shifts from shade-intolerant species to mid-tolerant species such as sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) about 30 to 50 or more years following establishment.

The widely cited model by Bormann and Likens (1979) predicted peak aboveground biomass accumulation at about 170 years, followed by a decrease in total biomass – called the transition phase - as mortality shifts from the smaller suppressed individuals to the large, dominant, but senescent individuals. This decline in total biomass is allegedly due to a delay in time for the subcanopy to develop biomass following the death of large, dominant trees, followed by with slight variations around a steady state where inputs (mortality) and outputs (decomposition) are balanced. Bormann and Likens (1979) discuss the difficulty in finding stands that fit their model due to the influence of stochastic disturbances that influence stand development. Data from mature northern hardwood forests have suggested that aboveground biomass may approach an asymptote only 100 years after stand initiation, with peak biomass much lower than predicted by Bormann and Likens (1979), as was found at Hubbard Brook Experimental Forest (Fahey et al. 2005; Siccama et al. 2007), or may continue to accumulate late into stand development (300-400 years), as was found in a study combining data sets from stands across the Northeast (Keeton et al. 2011).

Downed woody debris in old-growth forests has been described as a steady state where C and nutrients stored in wood on the forest floor are replaced by additions from individual tree mortality, at a rate that balances the translocation of C and nutrients from wood decomposition. Woody debris of diameter equal to that of the largest overstory trees and of high states of decomposition are indicative of old-growth ecosystems (Gore and Patterson 1985; Vanderwel et al. 2008). Studies from old-growth systems have estimated that inputs and outputs of woody debris may be stabilized in northern hardwood ecosystems when mass of woody debris is 30-40 Mg/ha, when significant contributions of diameter classes 40-60 cm are found, or with volumes of DWD greater than 100 m^3/ha (Gore and Patterson 1985; Hura and Crow 2004; McGee et al. 2007).

Allogenic disturbances and DWD

In the White Mountains of New Hampshire, allogenic disturbance regimes have been categorized by pests and disease, windthrow, ice damage, and management for ecological goods or services (Bormann and Likens 1979). Woody inputs from downed trees vary in diameter, volume, and state of decomposition due to the severity of the disturbance and the presence of predisposing conditions that would result in decomposition prior to tree mortality, such as fungal infection (Harmon et al. 1986). Natural disturbances may inflict large scale tree mortality, as opposed to the small gaps created during succession from individual tree mortality. The 1938 hurricane, for example, caused extensive blowdown in New Hampshire resulting in an increase of DWD, and further resulted in a more uniform basal area distribution in live trees compared to pre-hurricane conditions, affecting future woody debris inputs (D'Amato et al. 2017). Natural allogenic disturbances including chronic windthrow, ice storms, snow damage, as well as insects and pests may result in initiation of an understory sooner than predicted by the Bormann and Likens (1979) model, creating asymptotic patterns of stand development rather than the predicted transition phase (Rhoads et al. 2002; Forrester et al. 2003).

Invasive insects and disease have significantly altered forest composition in the Northeast, though these disturbances are largely an interaction between predisposing stand conditions that influence susceptibility (autogenic phenomena) and the proximity of the stand to forests already affected (allogenic phenomena) (Berbeco et al. 2012; Perry et al. 2018). Beech bark disease (BBD) and emerald ash borer (EAB), for example, have increased mortality and led to larger volumes of DWD of American beech and ash (*Fraxinus spp*.) in northeastern forests (McGee 2000; Perry et al. 2018), though individual stands vary in susceptibility. Infestation of and susceptibility to invasive pests and diseases may also reflect the effects of a changing climate. American beech trees increase in susceptibility to damage from BBD with increases in size and bark N contents (Latty et al. 2003). Nitrogen deposition may therefore result in increased BBD severity and potentially increased mortality, contributing to a pulse of DWD. Understanding downed wood accumulation in northern hardwood forests will assist in making informed management and research decisions in a changing climate.

In the northeastern United States, mean and maximum precipitation is expected to increase until the end of the 21st century along with projected temperature increases (Wuebbles et al. 2014). Woody debris in northern hardwood forests may therefore be affected by mortality due to intense rainfall and flooding, as well as ice storms (Kraft et al. 2002).

DWD as a microhabitat

Coarse woody debris in later stages of decay can serve as an important substrate for the germination and establishment of small-seeded species such as yellow birch (*Betula alleghaniensis* Britt.), eastern hemlock (*Tsuga canadensis* L.), and red spruce (*Picea rubens* Sarg.), as the small seeds become lodged in cracks of the wood which provides a moist, nutrient rich microhabitat for germination (McGee and Birmingham 1997). Later stages of decay facilitate root penetration and supply nutrients for germinants, conditions that may peak 30 - 60 years following death of the tree depending on size, species, and environmental conditions (Zielonka 2006). Nutrient composition, size, and stage of decay largely determine the suitability of the substrate for various microorganisms, features that vary based on anatomical properties of the wood produced by different species (Arthur et al. 1992; Spears et al. 2003; Palviainen et al. 2010). Downed wood is frequently utilized as a substrate by small mammals, saproxylic insects, and fungi (Grove et al. 2002; Ucitel et al. 2003; Sullivan et al. 2012; Runnel and Lõhmus 2017). Small downed woody debris such as twigs and branches in temperate ecosystems are more closely correlated with ascomycetes and basidiomycetes fungi than larger portions of downed wood (Nordén et al. 2004). Woody debris is also among the most vital habitats for the proliferation of macrofungi (Brazee et al. 2014; Copot and Tănase 2019).

Decay classes and density

Downed woody debris is often classified into discrete decay classes in an attempt to capture the spectrum of decomposition. Decay classes (typically I-V) are based on the presence of remaining bark, fine twigs, and log shape and resistance to pressure (Pyle and Brown 1998). While resistance to decomposition varies among species (Scheu and Schauermann 1994), more comprehensive harvests, such as clearcuts, increase the decay rate of woody debris regardless of species (Hagan and Grove 1999; Finér et al. 2016). Clearcut harvests raise forest-floor temperatures via increased light penetration, resulting in greater mass loss from decomposition where sufficient moisture and N for microbial processes are present (van der Wal et al. 2007; Finér et al. 2016).

The decay rate of DWD has been empirically studied by placing wood stakes in the field for extended periods of time after which the stakes are retrieved, dried and weighed to determine mass loss (Fissore et al. 2016). Decomposition rates of DWD are not constant even for a specific species and size due to environmental influences such as moisture, temperature, and microbial community composition (Harmon et al. 2000; Van der Wal et al. 2015). Furthermore, components of logs including the bark, sapwood, and heartwood decompose at different rates due to the differing concentrations of cellulose, lignin, and phenolic compounds in these woody portions (Schowalter 1992). Species, piece length, and climatic regime have been used to model the time required for a piece of DWD to transition from one decay class to another (Russell et al. 2013). The density of a piece of DWD is directly and negatively related to its decay class. Hardwood species may decline 50% in density, while the density of softwood species may decline only 17% from live trees to decay class I (Arthur et al. 1992). Density measurements, though difficult to obtain directly, are useful to convert easily obtainable volume estimates to mass (Harmon et al. 2008).

Carbon dynamics

Biomass from DWD contributes significantly to the total terrestrial efflux of CO_2 from forests (Fissore et al. 2016); wood is generally assumed to be 50% C by dry weight (Hoover et al. 2012). In northern hardwood stands across the northeast, DWD spends the longest time in decay classes III-IV, due to the lag in decomposition at later stages of decay and the fact that the decay classes do not represent equal timeframes (Urbano and Keaton 2017). Carbon dioxide fluxes to the atmosphere as a result of DWD decomposition are highly variable due to the species, size, and position of individual pieces of wood on the landscape (Harmon et al. 2020). Forest type has a significant impact on C storage of DWD due to differences in decay rates among species. In the Northeast, hardwood forests on average store less C than softwood forests. The difference in C storage is a result of significantly larger C pools in DWD of softwood-dominated old-growth forests; 52 Mg/ha on average compared to a mean of 18 Mg/ha in hardwood-dominated old-growth forests (Hoover et al. 2012). Carbon sequestration can be enhanced in managed forests and may be similar to unmanaged stands if structural complexity and species diversity are promoted (Puhlick et al. 2020).

Increased average air and soil temperatures due to climate change result in more rapid decomposition, and therefore CO_2 efflux, especially of smaller DWD (Berbeco et al. 2012). Increased decomposition due to rising air and soil temperatures may result in larger release of CO_2 from forests (Berbeco et al. 2012). Understanding how succession will influence woody debris accumulation will therefore help more accurately describe C stocks in forested ecosystems and the effects of management strategies on CO_2 efflux.

Sampling downed woody debris

Downed woody debris is heterogeneously distributed in stands due to the nature of the disturbances that produce it. As a result, sampling methods must be robust enough to capture this spatial variability. For larger pieces of DWD, or coarse woody debris (CWD), the most common sampling procedure is the line intersect sampling (LIS) method (Van Wagner 1968). Line intersect sampling can be used as an effective method to estimate CWD volume by summing the diameter cross sections produced by individual pieces of wood that intersect the sampling transect. Often several transects are used, in varying arrangements, and averaged to produce a whole stand estimate of CWD volume (Woodall and Monleon 2008). Increasing the length of sampling transects will increase the precision of volume estimates, and models have been developed to determine the length of transect required for LIS to obtain a desired level or precision (Fraver et al. 2018). Smaller DWD, or fine woody debris (FWD), is often included in LIS efforts, down to a minimum of about 3 cm diameter. DWD less than 3 cm diameter, commonly referred to as twigs, is generally sampled using fixed area plots, in which twigs are clipped at the edge of the plot, removed, and weighed to determine a mass per unit area value. This can be repeated across several plots in a stand and averaged to estimate the mass of twigs per unit area (Woodall and Monleon 2008).

Conclusion

Downed woody debris provides habitat for wildlife and microorganisms, aids in the regeneration of trees, influences soil development, and contributes to global C budgets as both a source and a sink. While DWD is often included in forest sampling procedures (McCarthy and Bailey 1994; McGee et al. 1999; Vanderwel et al. 2008), this dynamic pool has rarely been studied at sizes < 7.5 cm, and especially < 3 cm. Repeated measures of a chronosequence to describe the volume, biomass, and composition of species and decay classes that may be found at varying stages of northern hardwood succession is lacking.

CHAPTER 2: DOWNED WOODY DEBRIS, FOREST DEVELOPMENT, AND TREE BIOMASS IN THE WHITE MOUNTAINS

Introduction

Downed woody debris (DWD) is an integral component of forest ecosystem processes including carbon (C) and nutrient cycling (Lasota et al. 2018; Harmon et al. 2020). Downed twigs are less studied but provide an important contribution to global C cycling (Woodall and Likens 2008), as well as habitat for wood-inhabiting fungi (Nordén et al. 2004). The size of woody debris is relevant for fire ecology as it determines fuel loads and severity of fires (Shang et al. 2004; Peterson et al. 2015). Physical and chemical properties of soil are altered by decomposing woody debris and the subsequent additions of organic matter, which improve water retention and promote microbial activity (Stutz et al. 2017; Piaszcyk et al. 2019).

Forest development takes place over long periods of time and as a result is difficult to study directly. One approach is to substitute space for time, studying stands of different ages that have developed under similar climatic and edaphic conditions and interpret them as a chronosequence. This approach is risky because the methods used to conduct forest management, and the conditions under which stand-replacing natural disturbances occur, are not static, but rather continue to change with technological advancements, environmental regulations, market influences, and climatic drivers. Effects due to changes in treatment methodology or in the response of forests to a changing climate could be incorrectly interpreted as a response due to time since treatment, but repeated sampling provides some control over this limitation (Yanai et al. 2000).

Downed woody debris accumulation is related to stand development and is a direct result of disturbances. Downed woody debris in a mature forest will consist of large logs and branches resulting from trees that have fallen to the forest floor. After a stand-replacing disturbance such as a clearcut, the remnant DWD remains along with any slash that was left behind as a result of the disturbance. After stand initiation, small stems and branches will accumulate on the forest floor, particularly during stem exclusion when individual tree mortality peaks (Franklin et al. 1987). This peak in mortality is evident in the ratio of downed to standing tree biomass, which is highest before the stand starts contributing to the DWD, and second highest during self-thinning (Harmon 2001). As forests mature, the major cause of mortality shifts from density-dependent factors leading to self-thinning, to stochastic disturbances such as windthrow and mortality induced by native or introduced pests or disease. This change is reflected in a more diverse array of species in DWD assemblages, compared to the shade-intolerant species that dominate during stem-exclusion (Allison et al. 2003; Vanderwel et al. 2008). Disturbances from invasive pests and diseases cause mortality for some species more than others. Mortality from beech bark disease (BBD), for example, has resulted in an increased presence of American beech (*Fagus grandifolia* Ehrh.) wood in DWD assemblages, from 21% of the total DWD in maturing forests to 22% in old-growth forests (McGee 2000). American beech is a shade-tolerant, climax species in northern hardwood forests. Increased mortality of large beech trees could result in a larger downed to standing tree biomass in mature stands. Throughout stand development, the pool of DWD is determined by the frequency and intensity of disturbances that create new DWD, combined with the rate of decomposition.

In northern hardwoods, aboveground tree biomass may stabilize less than 100 years following stand initiation (Fahey et al. 2005), it may peak and decline in less than 100 years (Siccama et al. 2007), or biomass may continue to accumulate for over 200 years (Keeton et al. 2011). Peak aboveground biomass in old growth sites has been observed at about 300 Mg/ha (Keeton et al. 2011). Carbon is stored in both standing and downed biomass, so higher levels of biomass accumulation result in higher levels of C storage. One of the defining features of old-growth forests is the presence of large standing and downed trees, which may take over 100 years to develop in northern hardwood forests (McGee et al. 1999). As a result of changing environmental drivers, however, mortality in forests may be increasing (McDowell et al. 2020), potentially influencing C storage due to increased C inputs to the forest floor.

Objectives and hypotheses

We re-sampled a northern hardwood chronosequence after 16 years to describe how volume, biomass, species contribution, and decay class of DWD vary with stand development, and we compared them to the standing tree species composition and biomass. We addressed whether coarse and fine woody debris may reach steady state conditions on different time scales, due to a shift during overstory succession to larger trees and shade-tolerant species. Additionally, we re-sampled this chronosequence to determine patterns of live tree biomass with stand age in second-growth forests, and compared the live biomass of 145-year old second-growth stands to true old-growth.

We expected to find a relationship with fine woody debris and stand age from establishment to 30 years as young stands accumulate DWD, followed by smaller volumes of fine woody debris in stands >30 years old as a result of reduced inputs of the smaller diameter classes as stands age. We also expect to see a greater contribution of pin cherry (*Prunus pensylvanica* L.f) to the coarse woody debris in young stands, shifting to a more diverse mix of species in mid aged stands and a higher prevalence of highly decayed debris in mature stands. In mature stands that have been subjected to mortality of American beech from BBD, we expect to see a higher contribution of beech to the DWD than other species, and a lower downed to standing tree biomass ratio compared to stands with a smaller component of large American beech.

We expected that live tree biomass would be lower in the second-growth stands compared to the true old-growth due to a longer time since stand replacing disturbance and therefore larger trees in the old-growth stands. We also expected that live tree biomass would still be increasing in the second-growth sites less than 100 years old. Based on observation from Keeton et al. (2011), we expected that our 145-year old second-growth sites may still be increasing in live tree biomass.

Methods

Site description

This study included a chronosequence of northern hardwood stands in the White Mountain National Forest (WMNF) of New Hampshire. The regional climate is cool-temperate humid continental, with a mean temperature range of -9 ℃ in January to 18 ℃ in July (Campbell et al. 2007). Average annual precipitation is ~140 cm, about 25% of which falls as snow (Campbell et al. 2007). A total of sixteen stands were included in the chronosequence, fourteen second-growth stands plus two old-growth stands. The chronosequence stands developed on moderately drained to well drained Orthods with a mor type forest floor and granitic glacial till parent material (Federer 1984; Hoover et al. 2012). Six stands are in Bartlett Experimental Forest (BEF), one stand is in Hubbard Brook Experimental Forest (HBEF), and seven stands are in the surrounding WMNF for a total of 14 second-growth stands. The two old-growth stands were The Bowl Research Natural Area (RNA) in Grafton County, NH and Mt. Pond, a proposed RNA near Jackson, Carroll County, NH (Figure 1).

The second-growth stands were all clearcut between ~1875 and 1990 (Table 1). Neither old-growth site has any evidence of past harvesting, and both support an overstory of mature beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), and sugar maple (*Acer saccharum* Marsh.) (Hoover et al. 2012). Hereafter stands will be referenced with the name and year cut, e.g., CC2-1989.

Live and standing dead tree inventory

Live trees were inventoried in the second-growth stands in 1994, 2004, 2012, and 2021. The 1994 inventory included 13 stands; the 2004 inventory added CC2-1989 for a total of 14 stands that were also sampled in 2012 and 2021. In 2021 the Bowl and Mt. Pond were added to the chronosequence.

In the second-growth stands, tree inventories were conducted along five transects that were previously used for a study of litterfall mass (Yanai et al. 2012). Nine of the stands were 50 m x 50 m and the transects were 50 m long. In the two old-growth stands, the measurement area was 0.5 ha, and transects were 70.7 m long. In these 11 stands we identified and measured all live and standing trees ≥ 10 cm dbh within 5 m of either side of the transect. In two of the stands (H1-1939 and CC2-1989) the size of the stand limited the transects to 30 m and we identified and measured all live and standing trees ≥ 10 cm dbh within 2.5 m of either side of the transect. _

DWD inventory

For the purpose of this study, downed woody debris (DWD) is separated into twigs, fine woody debris (FWD), and coarse woody debris (CWD). We define twigs as DWD < 3.0 cm diameter, not including leaf litter or detached bark. Fine woody debris is DWD ≥ 3.0 cm but < 7.6 cm, and CWD is DWD ≥ 7.6 cm diameter and at least 1 m in length. FWD and CWD inventories occurred at the second-growth stands in 2004, followed by twig sampling in 2006. Twigs, FWD, and CWD were re-sampled in 2020 using the same methodologies employed in

2004 and 2006. Stand H1-1939 was sampled in 2004 and 2006 but was not re-sampled in 2020 due to a human disturbance that produced DWD irrelevant to this study. Fine and coarse woody debris were inventoried at the old-growth stands in 2021. Twigs were not sampled in the two old-growth stands because the sampling methods are destructive.

FWD and CWD survey and sampling

Fine and coarse woody debris were surveyed with the line intersect sampling method (LIS) used by the U.S Forest Service for Forest Inventory and Analysis (FIA) (Van Wagner 1968; U.S Forest Service 2019). In each stand, we established three permanent clusters, each composed of three 25-m transects separated by 120° diverging from a randomly placed center point, monumented with a 1 m tall fiberglass post (see Appendix). The clusters were randomly oriented in the stands, with the constraint that they not overlap.

Exact clusters and azimuths were re-surveyed in 2020 whenever possible. If a center monument could not be relocated, its location was approximated based on hand-drawn maps created in 2004. Four clusters, rather than the usual three, were used in the two old-growth stands because they were expected to be more heterogeneous.

We surveyed FWD and CWD from the center point outward to the end of each transect. For the initial 5 m of each transect, we did not take any measurements to avoid oversampling. We recorded FWD from 5 to 35 m and CWD ≥7.6 cm from 5 to 50 m. Total transect lengths were 45 m for FWD and 180 cm for CWD in every stand where standard clusters were used (Table 2).

We included FWD or CWD in sampling if it was the target size at the point of intersection with the transect, at least 1 m long, and at least partially above the soil surface. We also included debris if it was above the soil surface but leaning at an angle <45° from the ground

(U.S Forest Service 2005; Woodall and Monleon 2008). To be counted, debris had to intersect the transect through the central axis of the piece (Waddell 2002). If a piece of debris was fractured and would pull apart easily at the intersection with the transect, we counted it as two pieces, if not, we counted it as one (U.S Forest Service 2005). We only included debris that retained enough structure to delineate the sample from the forest soil. We did not include heavily decomposed debris that had lost all original shape and form such that it could not be picked up without crumbling into pieces <3.0 cm.

We identified the species when possible and decay class (1 - least decayed, 5 - most decayed) of all debris intersected on the transects (U.S Forest Service 2005). If debris was unidentifiable to species due to advanced stages of decomposition, we identified debris to genus or at least a classification of gymnosperm or angiosperm. We recorded the length of each piece, the diameter at intersection, and the diameter of the cavity if the piece was hollow. We took all diameter measurements perpendicular to the length of the wood sample. We calculated the volume of DWD based on the line intersect sampling method, which uses only diameter at intersection and transect length to estimate volume, and averaged across transects to obtain an estimate for the stand (Van Wagner 1968).

$$V = \pi^2 \sum d^2 / 8L$$

Where V = volume of wood per unit area

d = piece diameter

L = length of sample line

Wood density measurements

Coarse woody debris density was measured in 2004 by collecting samples from the first piece of CWD of each species and decay class combination encountered along each transect.

Samples were collected by cutting a disc ~ 5 to 10 cm thick with a bow saw or chainsaw. Each CWD sample was vacuum-sealed and frozen for measurement of volume by water displacement. A calibration process, in which we measured the volume of sealed and unsealed objects, revealed that regardless of the object's size or shape, the vacuum bag added ~30 mL of volume to the measurement. The samples were removed from the vacuum bags, dried at 60°C and weighed. The volume and dry mass were used to calculate wood density. Densities were averaged across the stands for each species and decay class.

Uncertainty associated with estimating wood density is high compared to that associated with estimating volumes (Campbell et al. 2019). For this reason we used the measured densities whenever possible. For species and decay class combinations that were not found during 2004 inventories, densities were obtained from the database compiled by Harmon et al. (2008).

Twig sampling

We sampled twigs from 4 m^2 subplots. We rejected subplots if they occurred on ephemeral or perennial streams. We randomly placed each plot based on a stratified design utilizing permanently marked transects installed for forest floor and litter analysis (Yanai et al. 2000; Yanai et al. 2012). The twig sample plots were not identical for 2006 and 2020.

In each subplot established for twig sampling, we collected every part of twigs and branches 16-30 mm in diameter. We cut twigs with pruning shears where the diameter was > 30 mm, or where the debris crossed the subplot boundary. We collected twigs < 16 mm in nested 0.5 m^2 subplots in the same manner. We also collected dead branches suspended up to 2.5 m above the plot, but not attached to trees. We did not include dead branches attached to living or dead trees, unless the tree was dead and leaning at an angle < 45° from the forest floor. We also did not include twigs that were covered by leaf litter.

Twigs were separated into size classes ≤ 7.5 mm, 7.5 mm - 16 mm, and 16-30 mm. We placed all samples in labeled plastic bags in the field, before transferring to paper bags for air drying. We then oven dried twig samples at 60°C to constant mass.

Statistical analysis

To test whether the species or decay class of downed wood differed between the stand groups based on age (residual, early-successional, mid-successional, old-growth), we used a non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis distances. The main matrix data used for the ordination include 16 columns for the volume of each species found in the DWD pool in a stand, with 29 rows representing stand, age, group, and year. The effect of predictor variables age, stand group, and sampling year were tested with a permutational multivariate analysis of variance (PERMANOVA) test. To test whether the volume of downed wood changed with stand age we used analysis of variance (ANOVA) with stand age and sampling year as predictor variables. Site was a random effect in the model.

Two Anderson-Darling tests were used to test whether the distribution of live and downed stems in the oldest second-growth stands differed from the stem distributions in the true old-growth stands. Two linear regressions were used to establish the relationship between total volume of downed wood and stand age at the two sampling periods.

Statistical analyses were performed in R with the packages dplyr, ggplot, nlme, tidyr, vegan, lmertest, and nortest (R Core Team 2020).

Results

Downed wood

The volume of CWD increased with stand age across the chronosequence stands. The relationship of total DWD volume to stand age was stronger during the second sampling period, when the stands were older ($r^2 = 0.14$, $p = 0.19$ for linear regression of 2004 data, and $r^2 = 0.50$, $p = 0.01$ for linear regression of 2020 data) (Figure 2).

Two volume observations stood out: 74.2 m^3/ha in site M4-1949, age 56, and 118.3 m^3/ha in site H3-1875, age 149. These outliers were even more extreme when converted to biomass as a result of the higher density of relatively undecayed wood (Figure 3). The total volume and biomass of coarse and fine woody debris in the oldest second-growth stands were similar to the true old-growth stands (Figure 3) ($p = 0.58$ for ANOVA of volume and $p = 0.58$ for ANOVA of biomass).

Twig mass peaked around 40 years during stem exclusion, declined thereafter, then remained relatively stable (Figure 4). The oldest second-growth stands had twig mass similar to the youngest stands. The young stands that were dominated by pin cherry (M6-1978 and HB101-1970) had higher peaks in the total twig biomass than stands dominated by beech and birch.

Diameters of downed wood and live trees

The old-growth stands had only slightly larger coarse woody debris than the oldest second-growth stands (Figure 5). No CWD larger than 40 cm was found at H2-1875 (149 years old), and 12 pieces/ha > 40 cm were found at H3-1875 (149 years old). At the Bowl (uncut), 6 pieces/ha of CWD > 40 cm were found and at Mt. Pond (uncut), 4 pieces/ha were found. The distribution of CWD large-end diameters consisted of larger stems in the old-growth compared to 145 year-old second-growth sites ($p = 0.06$ for Anderson Darling test of CWD large-end diameter distributions). The distribution of CWD diameters was more variable, and not as clearly influenced by stand age as the live tree diameters (Figure 5).

The Bowl had 28 and Mt. Pond 40 live trees/ha > 50 cm, while H2-1875 and H3-1875 had 16 and 32 trees/ha, respectively of this size. The distribution of live tree diameters consisted of slightly larger stems in the old-growth compared to 145 year-old second-growth sites (p = 0.09 for Anderson Darling test of live tree diameter distributions).

Species and decay class composition

Stand age did not explain all of the variation in species dominance of live trees. Stands H2 and H3 were both harvested in ~1875 but H2 is dominantly sugar maple, while H3 is dominantly red maple (*Acer rubrum* L.) (see Appendix). Pin cherry was a greater component of the basal area in H6-1983 and HB101-1970 in the first three inventories compared to H5-1967 and CC2-1989 at similar ages.

The volume of CWD observed in the chronosequence stands could be described in four groups, which we call residual, early-successional, mixed, and old-growth, based on the contribution of species at different ages (ordination stress = 0.15) (Figure 6). The volume of CWD was significantly different across age (p = 0.008 for PERMANOVA) and group (p = 0.04 for PERMANOVA) but not across sampling years (p = 0.15 for PERMANOVA).

Total CWD volume was lowest in the residual stands and increased with stand age (Figure 3). The composition of CWD shifted from a dominance of large conifers that were highly decayed in residual stands (as in CC2-1989, 31 years old), to a dominance of not well decayed, early-successional species, especially pin cherry, from ages ~35 - 50 years. After 50 years, woody debris included a diverse mix of species and decay classes. The true old-growth stands had a greater contribution of yellow birch and highly decayed debris than the stands aged 60 - 145 years (Figure 7).

The total volume of CWD increased from the inventories in 2004 to 2020 in the oldest second-growth stands (Figure 3), while the biomass of live trees appeared to be reaching a maximum at around 350 Mg/ha (Figure 8). Compared to our oldest second-growth stands, the

Bowl is similar, while Mt. Pond had significantly higher standing alive and dead biomass. Stand M3-1910 was an outlier with standing dead biomass peaking at 100 Mg/ha in 2004 (Figure 8).

The ratio of downed-dead to standing-live tree biomass was greatest at 0.8 in the residual stand (CC2-1989) due to residual debris from the previous overstory and small standing trees. The next highest ratios were found in young stands during self-thinning, with ratios > 0.10. A ratio > 0.10 was also found after a blowdown in H3-1875 (Figure 9).

Discussion

Downed wood

Our estimates of downed wood volume and biomass (Figure 3) were similar to other studies in northern hardwood forests (Tritton 1980; McCarthy and Bailey 1994; McGee et al. 1999). The outlier volumes of downed wood were 74.2 m^3/ha in M4-1949 at age 56 and 118.3 m^3/ha at H3-1875 at age 149, resulting from large windthrow events as indicated by field notes taken during downed wood inventories.

The ratios of downed to live biomass peaked in the residual stand with low aboveground biomass and was second highest in the young stands during self-thinning (Figure 9). These ratios were relatively stable at about 0.05 across the stand ages before and after self-thinning, with episodic events creating larger ratios greater than 0.10 that decreased in the 16-year re-sampling period back to about 0.05 (Figure 9). The ratios of downed to live biomass that we observed across the chronosequence are similar to values reported by others in the northeast (Harmon 2001; Woodall et al. 2021).

The largest twig masses observed in this study occurred during stem exclusion at a stand age of ~ 40-50 years. (Figure 4.) Stands M6-1979 and HB101-1970, aged 40 and 50 years old respectively in 2006, had higher twig masses than other stands of similar ages, likely due to the higher basal area occupied by pin cherry at these stands (Figure 4). Pin cherry is a short-lived species that succumbs to mortality from self-thinning as the canopy fills and light availability declines (Nyland et al. 2007).

The contribution of certain species and decay classes to the total volume of downed wood in these stands was distinct at four stages of overstory succession: from establishment to the start of stem-exclusion at about 35 years, from about 35-55 years when there is an influx of early-successional species, and from after about 55 years until the stand reaches old-growth status, which according to our results could take longer than 150 years.

Repeated measures of a chronosequence

While the interpretation of chronosequence results can be confounded by change in treatments or environmental characteristics over time, repeated measures provide some control for this limitation (Yanai et al. 2000). We repeatedly measured live trees in this chronosequence in 1994, 2004, 2012, and 2021, FWD and CWD in 2004 and 2020, and twigs in 2006 and 2020. The repeated measures revealed outliers in the data produced from stochastic events such as windthrow or mortality of mature trees that produced large amounts of DWD. The outliers in DWD volume and biomass at M4 in 2004 and H3 in 2020 were both a result windthrow of large trees that produced high volumes of DWD.

Stem distributions

Large coarse woody debris is often used as an indicator of old-growth status, and a common cutoff in northern hardwood forests is 40-50 cm diameter (Hura and Crow 2004). The true old-growth stands had more trees > 40 cm than the oldest chronosequence stands. This difference is likely a result of a long history without disturbance at the true old-growth stands, thus very old trees which were able to grow larger than 40 cm. Based on these results, 150 years is not sufficient for a northern hardwood forest regenerating after clearcutting to reach the distribution of large stems resembling true old-growth forests.

Standing biomass

The higher standing dead biomass at the true old-growth stands is indicative of the larger trees that were present at these stands compared to the second-growth stands. The standing dead biomass at M3-1910 peaked in 2004 at 100 Mg/ha and declined to 91 Mg/ha in 2012 and 55 Mg/ha in 2021. All three of these values at M3-1910 were outliers among the standing dead biomass observations at these stands. The biomass at this site is dominated by beech trees > 30 cm, which likely died of beech bark disease. Forty-three percent of the standing dead basal area at M3-1910 in 2021 was accounted for by beech (2.5 m^2/ha of the total 5.8 m^2/ha). Standing dead red maple trees >30 cm also contributed to the high biomass at this site.

The aboveground biomass at the second-growth sites in this chronosequence was higher than reported by other studies. Aboveground biomass was predicted to peak at about 350 Mg/ha after 200 years, followed by a transition phase according to the model by Bormann and Likens (1979). Re-sampling Watershed 6 at Hubbard Brook Experimental Forest, the source of the data for the Bormann and Likens (1979) model, revealed that aboveground biomass peaked around 220 Mg/ha after about 100 years and shows possible declines (Fahey et al. 2005). Aboveground biomass in other portions of the forest, however, is increasing toward 260 Mg/ha after 100 years (Siccama et al. 2007). Aboveground biomass may also continue to increase after for 300 years or more, with observations of about 300 Mg/ha in stands 300-400 years old (Keeton et al. 2011). Our results suggest that aboveground biomass in northern hardwood forests has the potential to increase rapidly in the first 100 years of stand development and reach 300 Mg/ha much earlier than previously observed, after only 150 years.

CHAPTER 3: CONCLUSIONS AND REFLECTIONS

Overview

The first chapter of this thesis presents previous findings from this chronosequence, as well as a review of the scientific literature regarding DWD. Specifically, the interplay between forest succession and resulting changes in the pool of downed wood in a stand were discussed in detail. Many disturbances produce DWD, but the nature of the disturbance and susceptibility of the stand play an important role in determining the impact of the disturbance and the resulting pulse of DWD. I also present in Chapter 1 an overview of the literature surrounding the decay classes used to characterize DWD, and the influence of decomposition on terrestrial C cycles.

Chapter 2 of this thesis presents the resampling of a northern hardwood chronosequence to describe the volume, biomass, and composition of species and decay classes of DWD pools in secondary and old-growth northern hardwood forests. The results of Chapter 2 relate the influence of overstory succession and stand age to the pool of DWD in a stand. Chapter 2 also compares the DWD and aboveground biomass of 150-year-old secondary forests to old-growth forests.

Limitations of this study

The results reported in Chapter 2 include live tree inventories from 1994, 2003, 2012, and 2021, and downed wood inventories in 2004, 2006, and 2020. Resampling the same chronosequences stands gave some protection from the pitfall of falsely interpreting changes in the treatment over time as changes since time of treatment (Yanai et al. 2003). There are, however, inherent limitations to the interpretation of results from this chronosequence study. The second-growth forests used in this chronosequence were at a maximum 150 years old at the time of sampling in 2020-2021, on the verge of what we thought would be considered old-growth. For this reason, true old-growth stands at the Bowl and Mt. Pond were added to sampling in 2021, and one of the objectives of this study was to compare the DWD and aboveground biomass in the oldest secondary forests to that of old-growth northern hardwoods. However, because of time constraints, the sampling efforts in these stands were not as comprehensive as they could have been given the spatial variation present in old-growth stands. Furthermore, because the old-growth stands were not added to the sampling efforts until 2021 these stands were sampled only once for live and standing dead trees and DWD, compared to the four tree inventories and two DWD inventories in the other stands.

Novel contributions of this study

To my knowledge, this is the most comprehensive study of a re-sampling of all the size classes of downed wood across a variety of stand ages in northern hardwood forests. Chapter 2 includes observations of twigs (< 3 cm), FWD (>3 cm, < 7.5 cm), and CWD (>7.5 cm) volumes and biomass. We did not observe CWD as large as the largest living trees at our oldest second-growth stands, and the frequency of live tree and CWD diameters > 40 cm was similar for one of the old-growth stands and oldest second-growth stands, but not the other two. These results suggest that northern hardwood forests have the capacity to accumulate higher levels of aboveground biomass in stands less than 200 years old than previously observed or predicted (Fahey et al. 2005; Siccama et al. 2007; Keeton et al. 2011). These results agree with Keeton et al. (2011) and suggest that biomass accumulation has the capacity to increase after 150 years in northern hardwood forests.

Opportunities for future study

Downed wood provides an important contribution to terrestrial nutrient cycles and nutrient stores in forests, but nutrient concentrations are not reported in this thesis. Samples from the downed wood inventories in 2004 and 2020 were analyzed for nutrient concentrations using inductively coupled plasma–optical emission spectrometry (ICP-OES). All of the nutrient data regarding CWD samples obtained in 2004 and 2020 are complete, but twig samples obtained in 2020 have not yet been analyzed. An opportunity exists for a future study to report the nutrient concentrations and nutrient storage of both size classes of DWD in these stands. The biomass estimates reported in Chapter 2 of this thesis should be used to scale nutrient concentrations to contents at a stand level. As nutrient concentrations differ among tree species, changes in overstory dominance during succession may be evident in the nutrient content of DWD in a stand at a particular age. Pin cherry, for instance, succumbs to mortality from self-thinning about 30-50 years following stand initiation, and a large pulse of pin cherry wood can be found in the DWD pool at this time. This large pulse of pin cherry wood may leave a distinct fingerprint in the nutrient content of the DWD pool. The nutrient contents that a future study could provide would be useful for nutrient budgets in northern hardwood forests and could further an understanding of the nutrient storage capability of DWD.

Conclusion

Repeated measures allow us to assess the reliability of this chronosequence. We are confident that these stands are not headed for the peak biomass predicted by earlier models and observations. Our 150-year-old sites do not look like the old-growth, but we do not know how these 150-year-old stands will progress due to a lack of observations in stands older than 150 years. It will be difficult to improve predictions of biomass projections because there are few old-growth forests to use as a reference in the northern hardwood forest type. These results have implications for C budgets as forests may accumulate higher levels of aboveground biomass than previously observed after less than 200 years following stand initiation.

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TABLES

Table 1. Stand descriptions. White Mountain National Forest, New Hampshire**.**

Stand	Lat	Long	Location	Site History	Treatment year	Aspect	Slope (%)	Elevation (m)
CC2	44.1	-71.3	BEF	Clearcut	1989	SSW	21	330
H6	44.1	-71.3	BEF	Clearcut	1983-1984	Flat to NW	6	330
M6	44.0	-71.4	Kancamagus Hwy	Clearcut	1979-80	Flat	2	540
M5	44.2	-71.2	Ellis River	Clearcut, followed by timber stand improvement thinning	1976-77	Flat	3	630
101	43.9	-71.7	HBEF	Clearcut	1970	Flat	5	520
H5	44.1	-71.3	BEF	Clearcut strips, scarified	1967	NNE	18	360
T20	44.1	-71.4	Sawyer's River	Heavily cut, with some cull trees girdled	1958	NNE	18	540
M4	44.2	-71.2	Iron Mountain Rd.	Clearcut	1949-50	NNE	12	460
T30	44.2	-71.2	Iron Mountain Rd.	Intensity of cut unknown	1948	SSW	26	550
H1	44.1	-71.3	BEF	Clearcut after 1938 hurricane, removing all stems >2" diam	1939	NNE	9	320
H4	44.1	-71.3	BEF	Clearcut. Thinning in 1959 - 45% of basal area removed	1933-35	SSW	28	350
M3	44.2	-71.3	Ellis River	Presumed clearcut	1910	WNW	19	580
H2	44.1	-71.3	BEF	Clearcut, used as pasture. Thinned in 1936 - 20-30% removed	~1875	ESE	14	320
H3	44.1	-71.3	BEF	Clearcut, used as pasture	~1875	NNE	13	320
The Bowl	43.9	-71.4	Sandwich	Uncut	-	ESE	10	610
Mt. Pond	44.2	-71.1	Chatham	Uncut	-	Flat to SE	7	518

Table 2. Total fine (FWD) and coarse (CWD) woody debris transect lengths in each site**.**

Stand	Total FWD Transect Lengths (m)	Total CWD Transect Lengths (m)
CC2 - 1989	30	120
H6 - 1983-84	45	180
M6 - 1979-80	35	180
M5 - 1976-77	45	180
HB101 - 1970	45	180
H5 - 1967	45	180
T20 - 1958	40	160
M4 - 1949-50	45	180
T30 - 1948	45	180
H4 - 1933-35	45	175
M3 - 1910	45	180
H2 - 1875	45	180
H3 - 1875	45	180
The Bowl - Uncut	60	240
Mt. Pond - Uncut	60	240

FIGURES

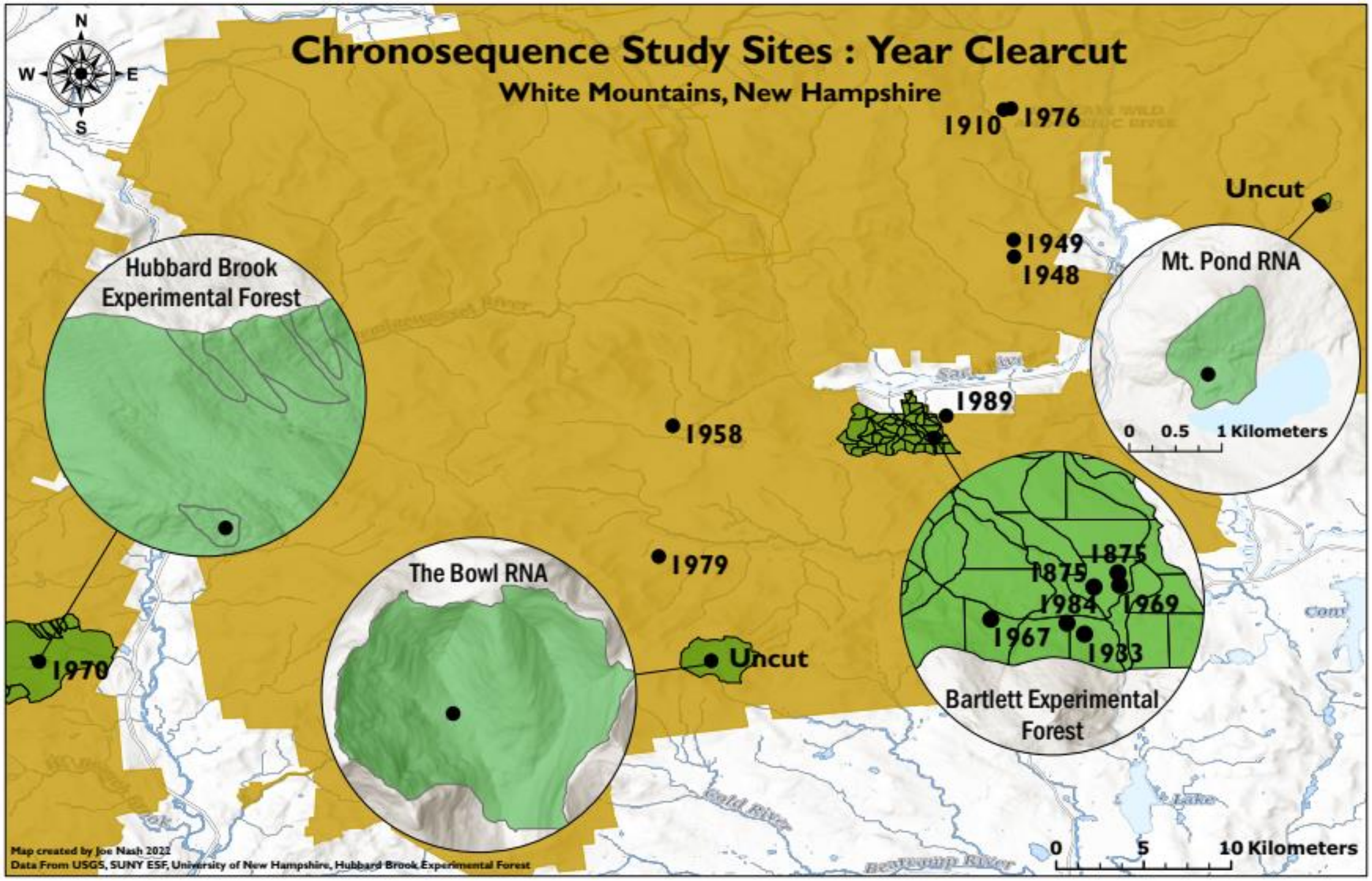


Figure 1. Sites included in this chronosequence study. The yellow boundary is the White Mountain National Forest, located in central New Hampshire. All inset maps are to the same scale.

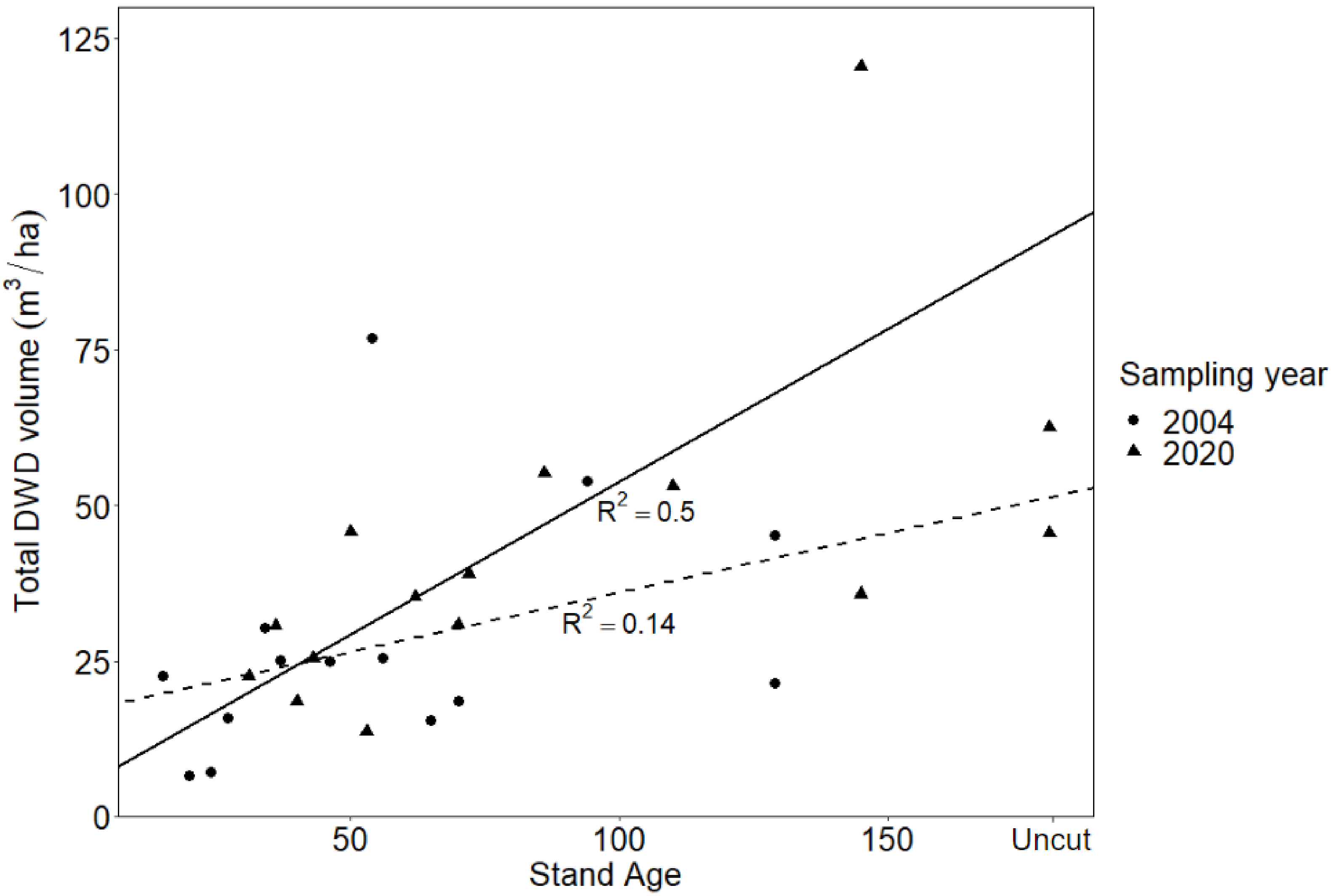


Figure 2. Total downed woody debris (DWD) volume for each of the stands sampled in 2004 and 2020. The dashed line is the regression for 2004 data ($p = 0.20$) and the solid line is the regression for 2020 data ($p = 0.01$).

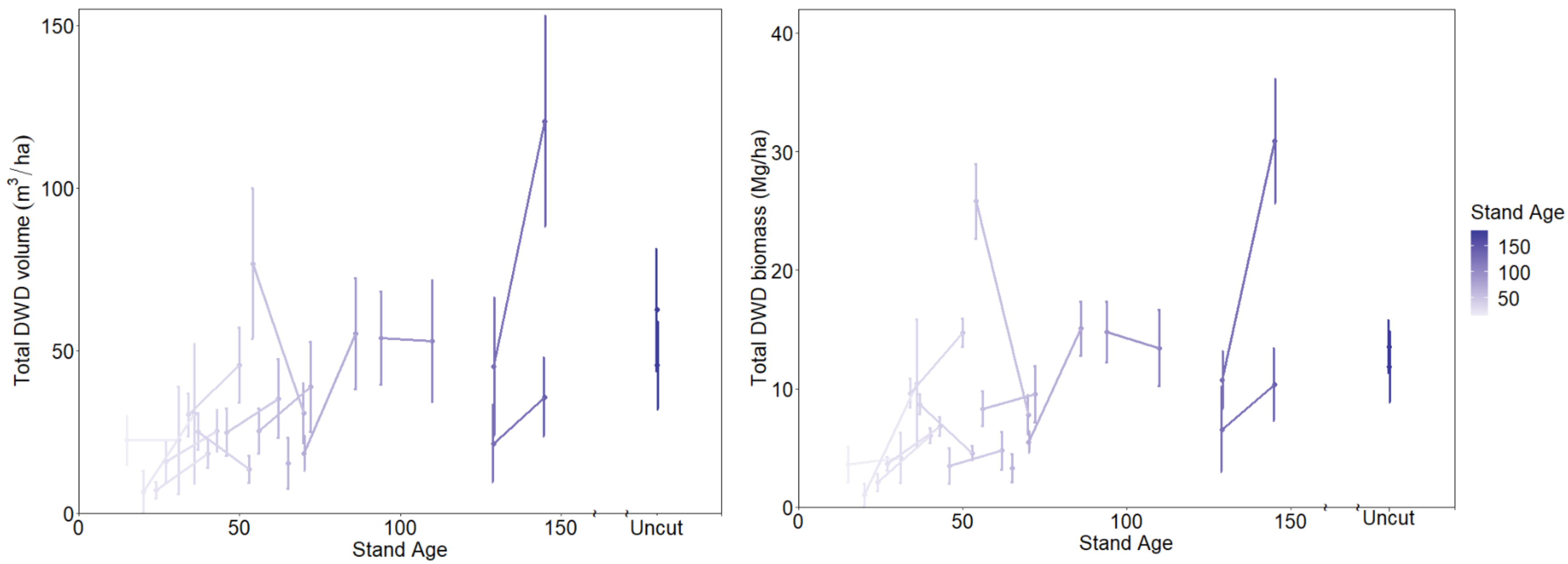


Figure 3. Total volume (left) and biomass (right) of total downed woody debris (DWD) at the 16 stands included in this study, sampled in 2004 and 2020. Points represent estimates of stand volume or biomass and error bars are ± 1 standard error.

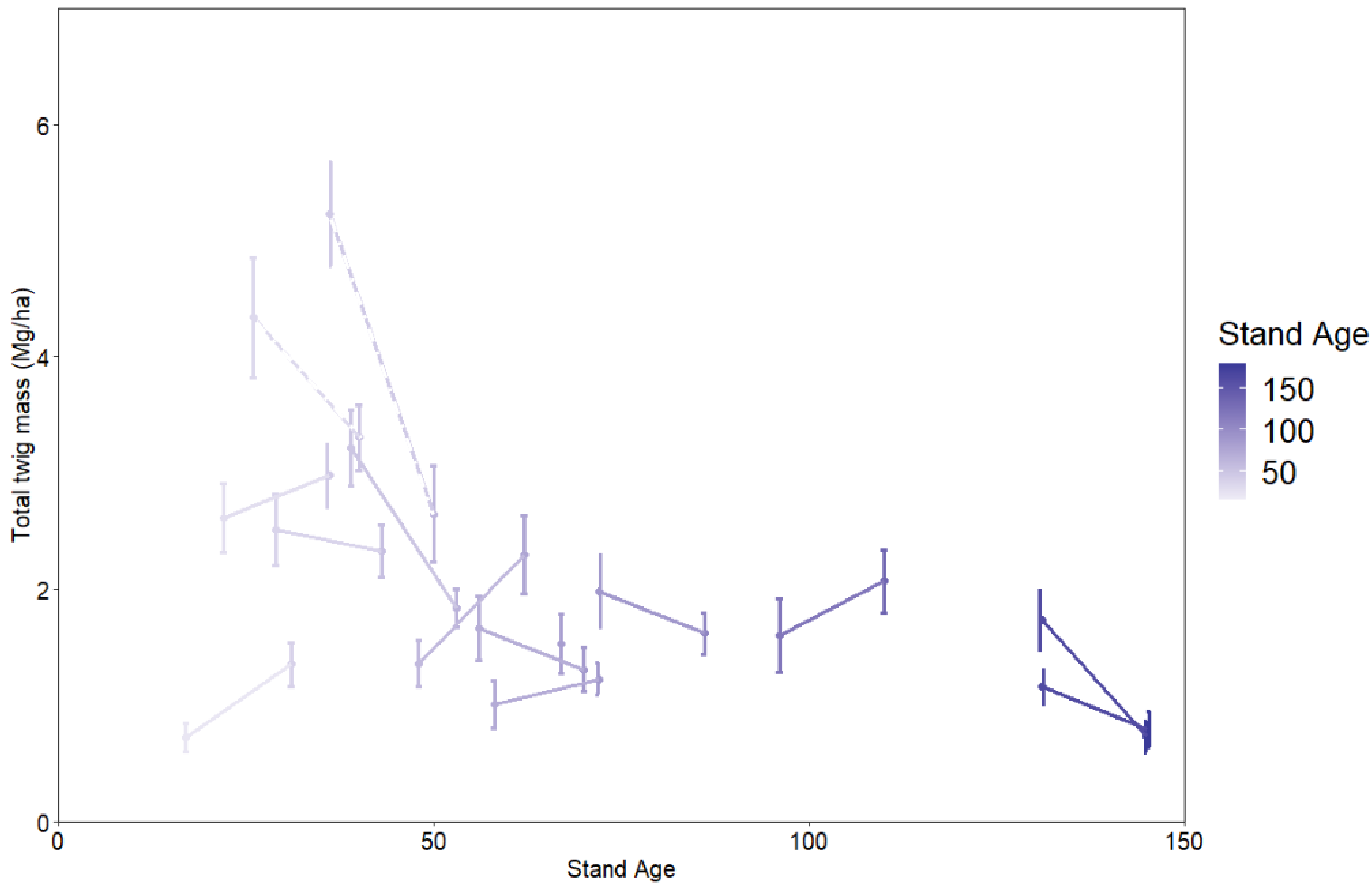


Figure 4. Total twig (downed woody debris < 3.0 cm) biomass at the 16 stands included in this study, sampled in 2006 and 2020. Stands with >20% basal area occupied by pin cherry (*Prunus penslyvanica* L.f) are shown in dashed lines. Points represent estimates of stand biomass and error bars are ± 1 standard error.

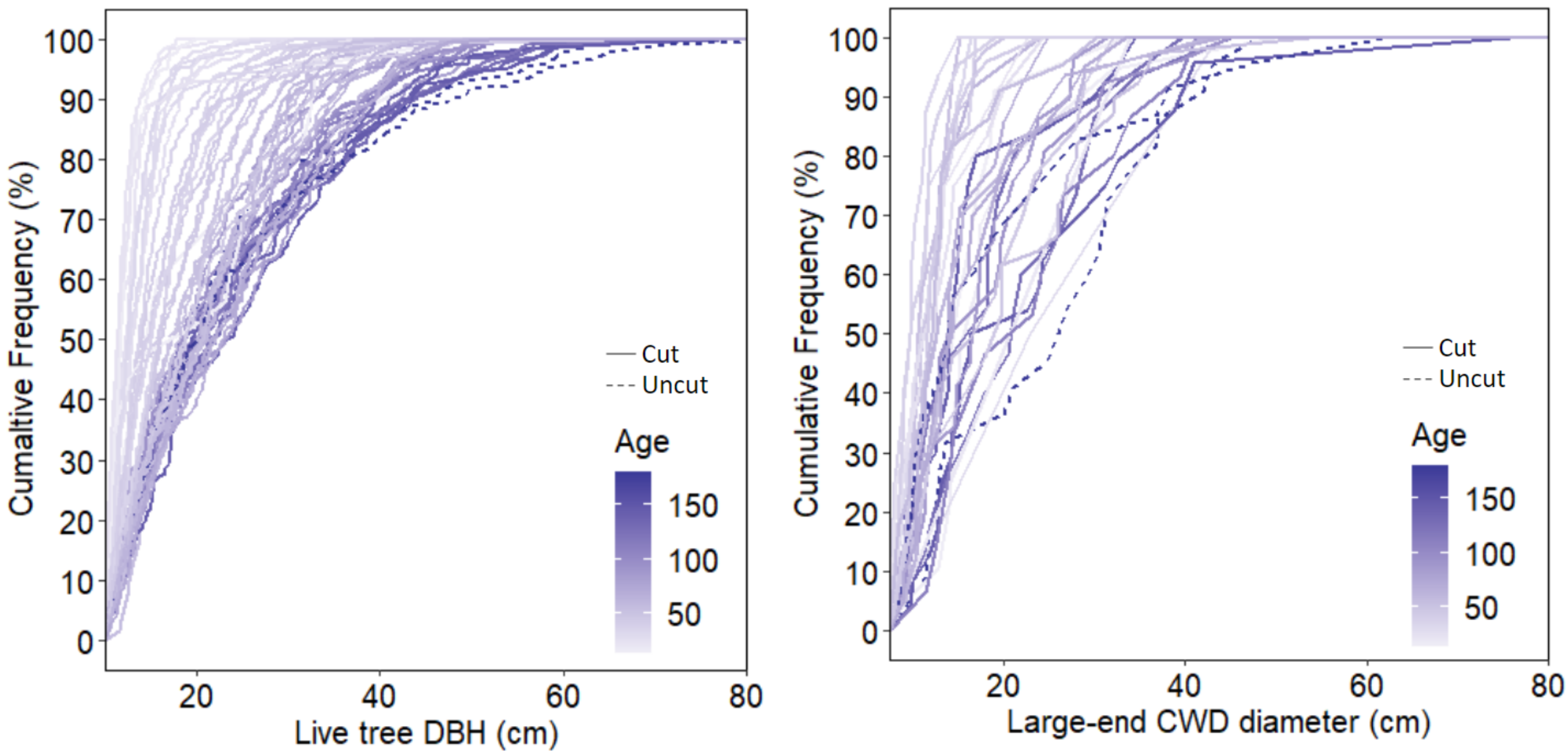


Figure 5. Cumulative frequency of live tree diameter at breast height (dbh) (left), and large-end coarse woody debris (CWD) diameters (right) for the 16 stands included in this study at each sampling period; 1994, 2004, 2012, 2021 for live trees, 2004 and 2020 for coarse woody debris.

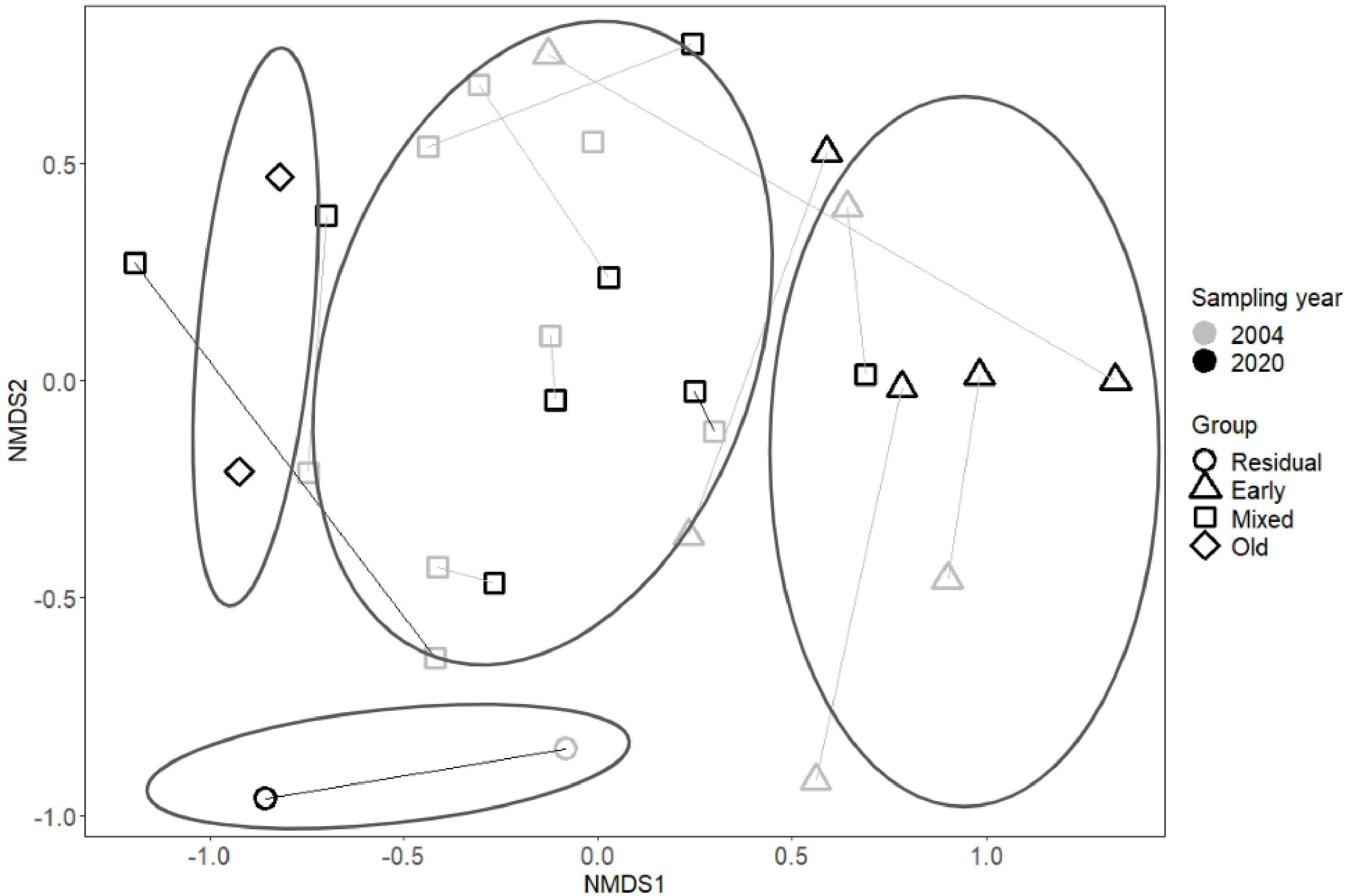


Figure 6. Non-metric multi-dimensional scaling (NMDS) using Bray-Curtis distances of coarse woody debris (CWD) volumes in each of the 16 stands in this study sampled in 2004 (grey) and 2020 (black). Lines connect stands, ellipses are shown around groups of similar stands. Stress = 0.15.

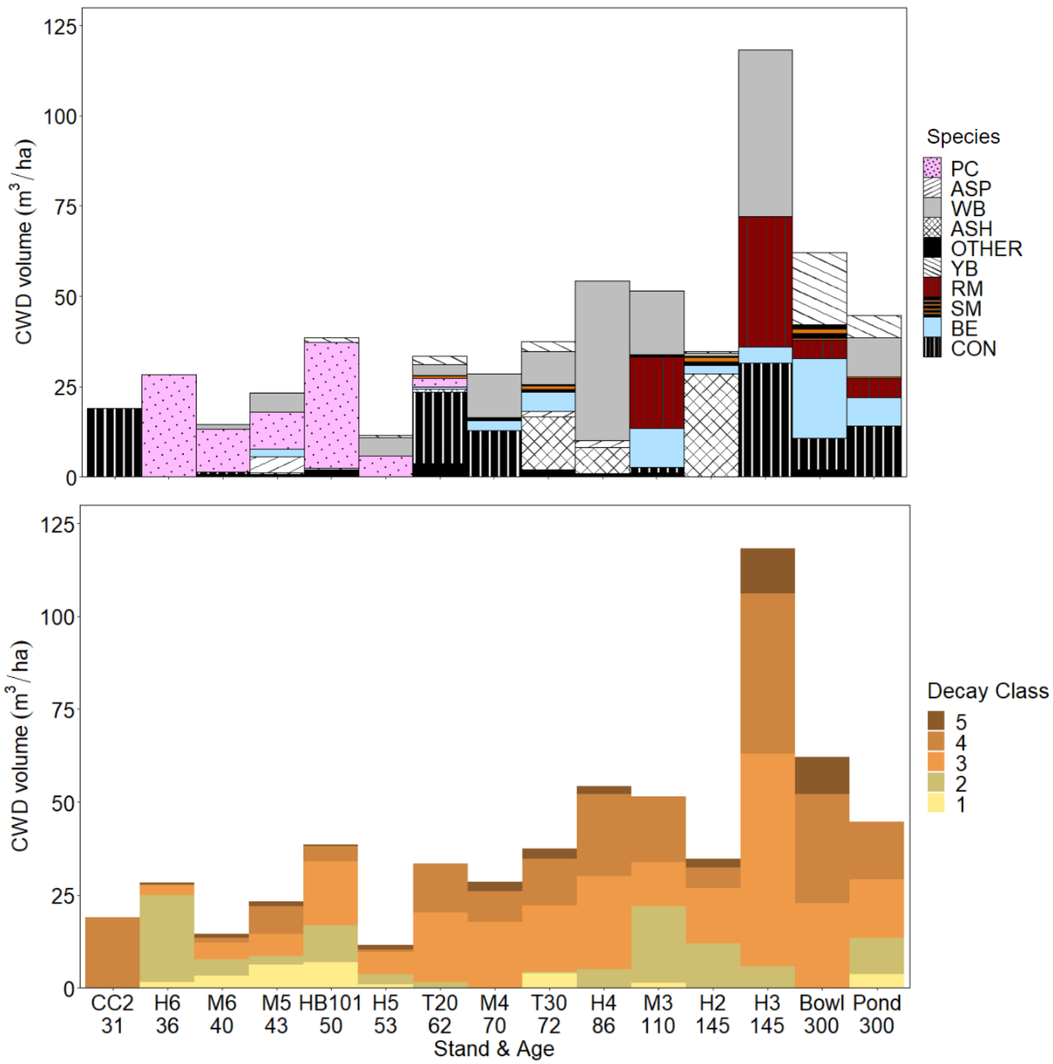


Figure 7. Species (top) and decay classes (bottom) of coarse woody debris (CWD) volume in the 16 stands included in this study in 2020. PC = pin cherry, ASP = aspen, WB = white birch, ASH = ash, OTHER = mountain maple, striped maple, ironwood, YB = yellow birch, RM = red maple, SM = sugar maple, BE = American beech, CON = conifers.

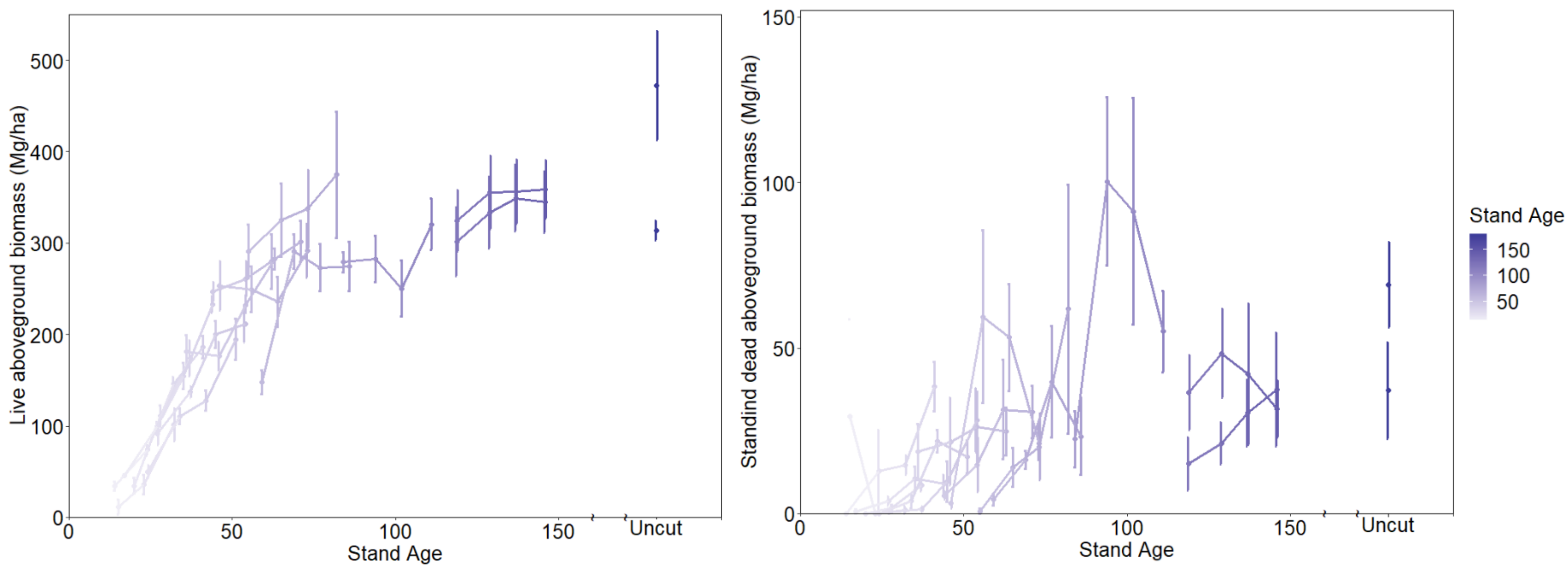


Figure 8. Live (left) and dead (right) overstory (>10 cm dbh) tree aboveground biomass at the 16 stands included in this study, sampled in 1994, 2004, 2012, and 2021. Points represent estimates of stand biomass and error bars are ± 1 standard error.

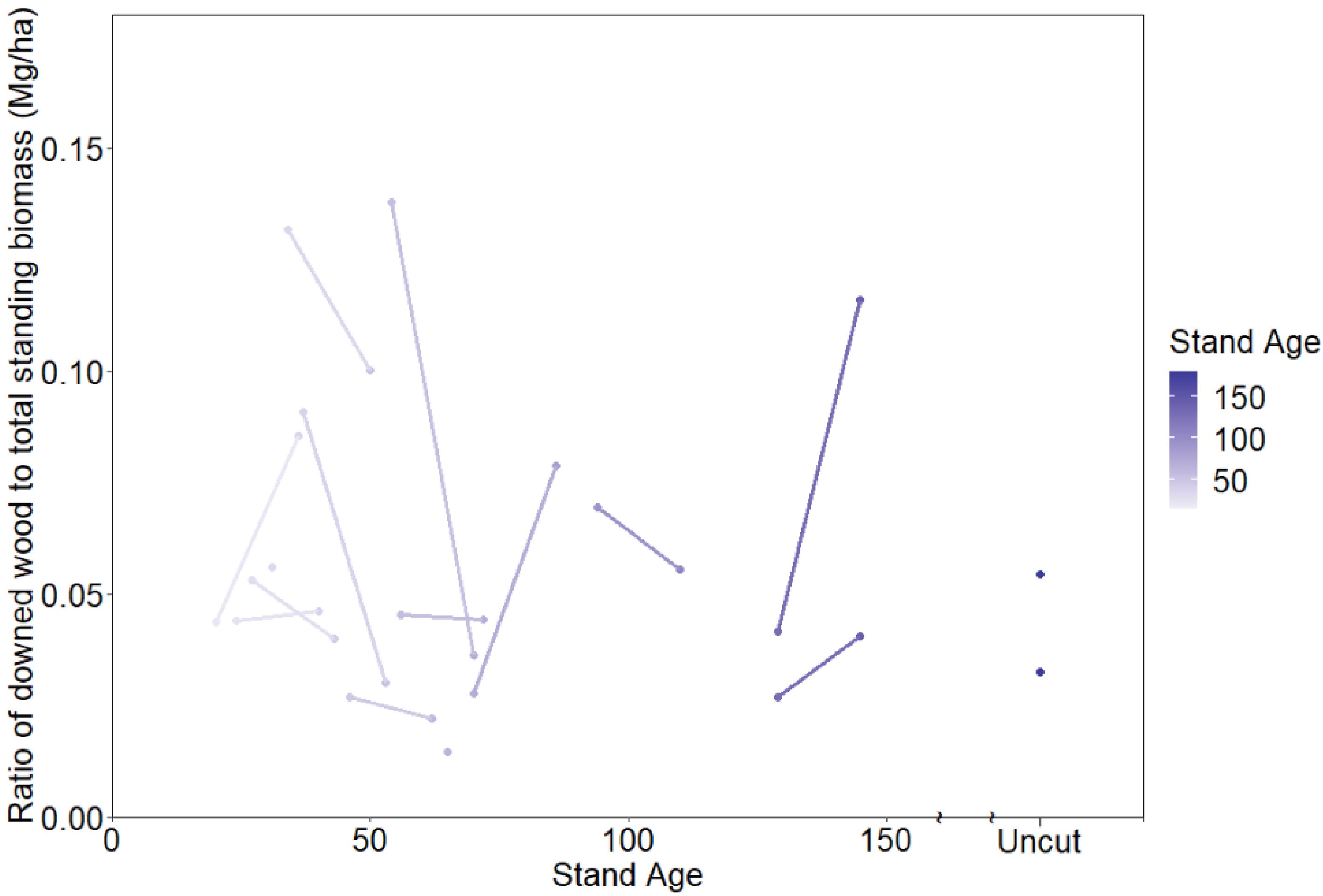


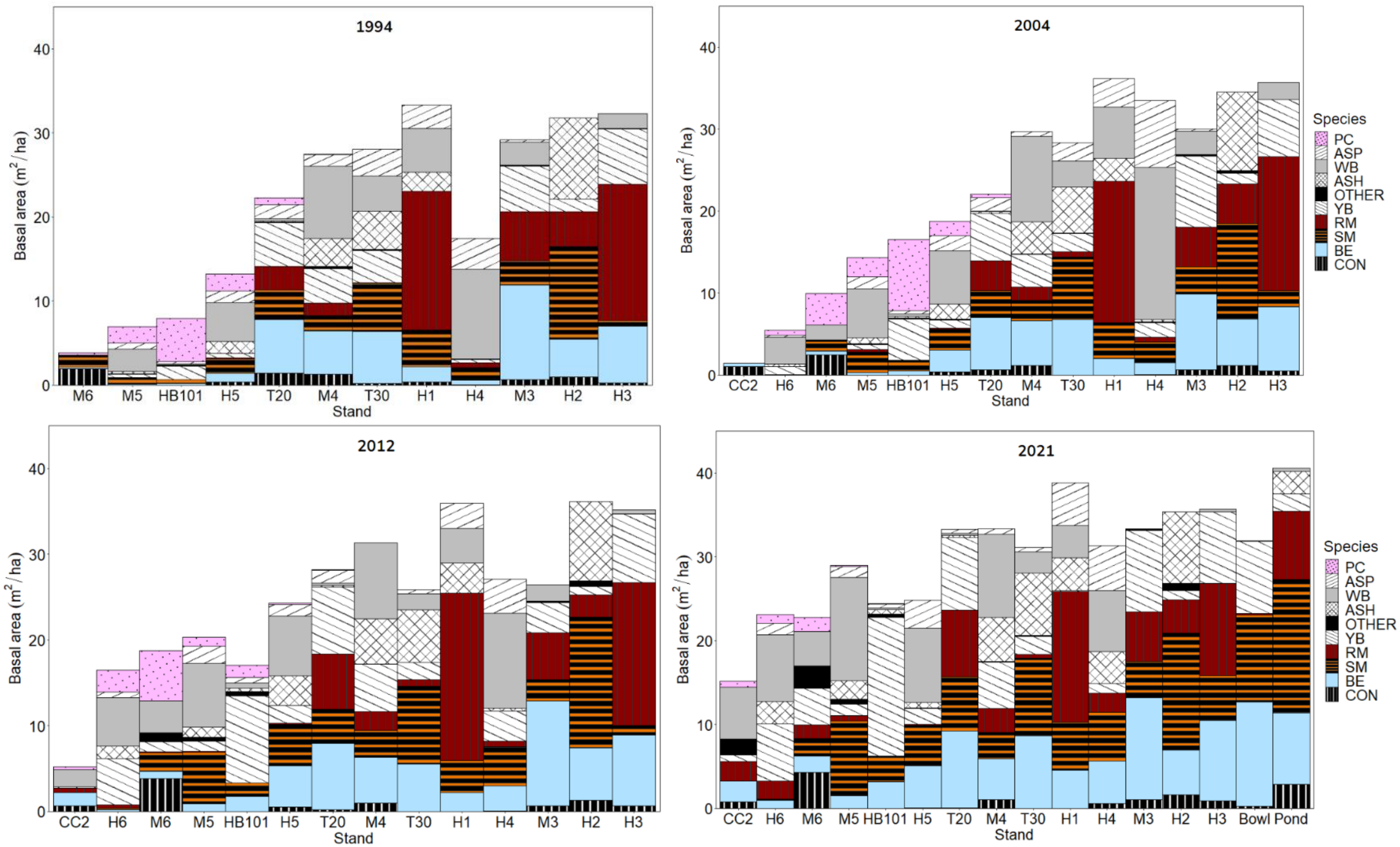
Figure 9. The ratio of downed wood to standing tree biomass at each site sampled in 2004 and 2020.

APPENDICES

Appendix A

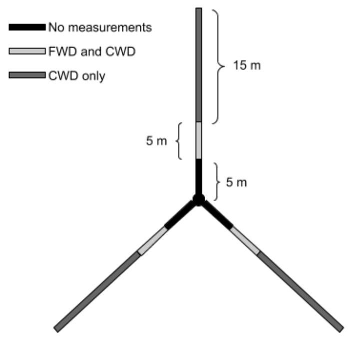
Basal area of each species > 10 cm in the live tree inventories (1994, 2004, 2012, and 2021) of the 16 stands included in this study.

PC = pin cherry, ASP = aspen, WB = white birch, ASH = ash, OTHER = mountain maple, striped maple, ironwood, YB = yellow birch, RM = red maple, SM = sugar maple, BE = American beech, CON = conifers.



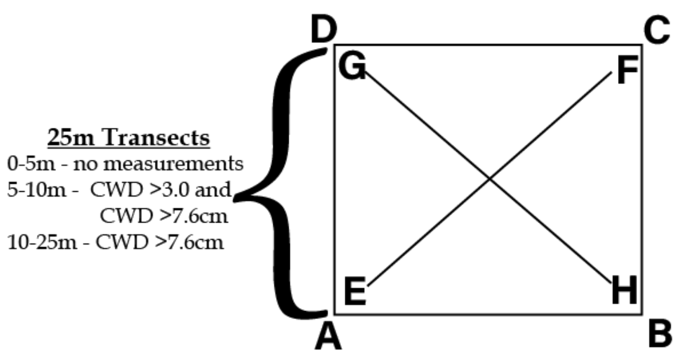
Appendix B

Fine and coarse woody debris standard cluster sampling design, three 25 m transects diverging from a center point.



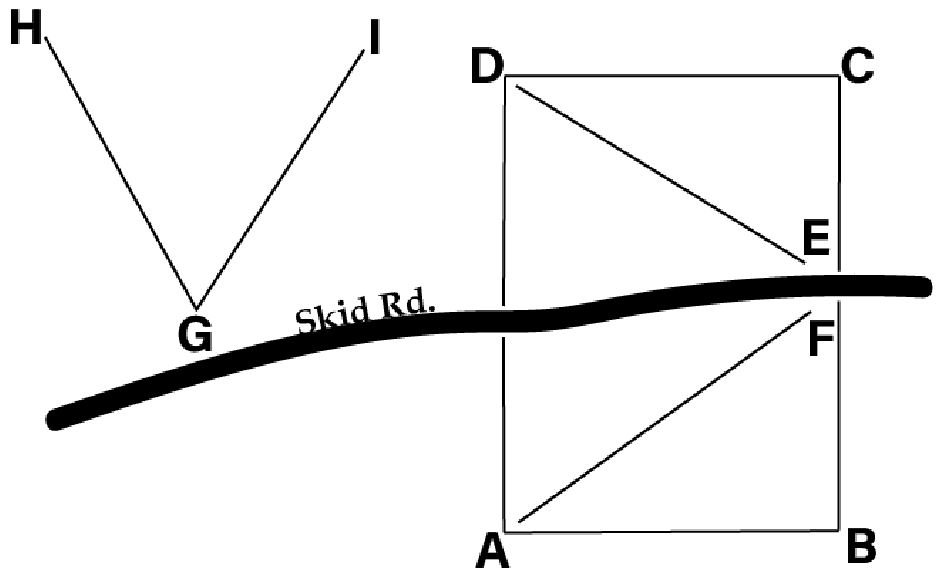
Appendix C

Fine and coarse woody debris alternate transect sampling design used in site CC2-1989 due to limited size.



Appendix D

Fine and coarse woody debris alternate transect sampling design used in site T20-1958 to avoid skid rd.



CURRICULUM VITAE

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Education

M.S. Sustainable Resource Management. State University of New York College of Environmental Science and Forestry, Graduating May 2022

B.S in Forestry. cum laude. Michigan Technological University, May 2020

Work Experience

Graduate Research Assistant - MELNHE and QUERCA 01/2021 - 06/2021, 01/2022 - 06/2022

SUNY College of Environmental Science and Forestry. 20 hrs/week

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- Uncertainty in carbon accounting
- Quantifying uncertainty in deforestation/degradation/afforestation for countries that have submitted reports to the Forest Carbon Partnership Facility (FCPF).
- Compiling and organizing data for submission to the Ecological Data Initiative (EDI)

Graduate Teaching Assistant - Introduction to Forest Soils 08/2021 - 12/2021, 08/2020 - 12/2020

SUNY College of Environmental Science and Forestry. 20 hrs/week

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- Leading lab weekly lab session
- Grading homework and lab reports
- Office hours and assisting students

Research Crew Co-Leader 06/2020 - 08/2020, 06/2020 - 08/2021

White Mountains, NH. 40 hrs/week

MELNHE Research Group: Dr. Ruth Yanai - 315.470.6955 rdyanai@esf.edu

Co-leading a field crew of five undergrad/recently graduated students in order to guide and implement research projects including:

- Fertilization and litter collection as part of a long-term (>10yr) factorial NxP northern hardwood fertilization in the white mountains of NH.
- Woody debris inventory and analysis for my graduate thesis
- Forest plot stem mapping

Undergraduate Research Assistant 06/2018 - 06/2020

Houghton, MI. ~40 hrs/week

Wood Stakes Research Project: Dr. Martin Jurgensen - 906.487.2206 mfjurgen@mtu.edu

Michigan Technological University School of Forest Resource and Environmental Science

- Summarizing and compiling data effectively

- Systematic data collection of decayed wood stakes
- Careful analysis of specimens
- Proficiency of proper lab safety techniques

Undergraduate Research Assistant 05/2019 - 05/2020
Houghton, MI. ~20 hrs/week
Wood Decomposition Research Project: Chris Miller - 906.487.1058 camiller@mtu.edu
Michigan Technological University School of Forest Resources and Environmental Science

- Critical review of relevant literature
- Careful research plan formulation
- Accurate and neat data collection
- Thorough knowledge and familiarity of soil composition and texture
- Optimization of individual time management and reliable supervision
- Proficiency of proper lab safety techniques
- Optimization of limited resources

Forest Technician - Timber Sale Preparation 05/2019 - 06/2019
Houghton, MI. ~30 hrs/week
Nara Property Timber Sale Preparation: Jim Schmierer - 906.487.2963 jmschmie@mtu.edu
Michigan Technological University School of Forest Resources and Environmental Science

- Dependable boundary designation, line running
- Accurate plot establishment, prism sampling
- Consistent forest Inventory data collection
- Reliable tree grading, timber marking
- Precise regeneration counts and analyses
- Dependable navigation with maps and GPS Effective balance of stakeholder involvement
- Optimization of individual time management

Published Research

Nash, J.M, F.M Diggs, R.D Yanai. 2022. Length and colonization rates of roots associated with arbuscular or ectomycorrhizal fungi decline differentially with depth in two northern hardwood forests. *Mycorrhiza.* https://doi.org/10.1007/s00572-022-01071-8

Membership in Professional Associations

Ecological Society of America (ESA)	03/2021 - Present
Society of American Foresters (SAF)	03/2021 - Present
American Association for the Advancement of Science (AAAS)	02/2021 - Present
Forest Stewards Guild	06/2019 - Present

Accomplishments/Accolades

2021-2022 MS C. Eugene Farnsworth Fellow 08/2021 - 05/2022
2021-2022 Bob Marshall Scholarship 08/2021 - 05/2022
Edna Bailey Sussman Fund Paid Graduate Research Internship 06/2021 - 08/2021
"2020 Outstanding Senior in Forestry" - Michigan Technology University 05/2020
Michigan Technology University Dean's List 09/2018 - 05/2020

Professional Meetings

Hubbard Brook Annual Cooperators Meeting 06/2020, 07/2021
Reported current research, discussed fellow researcher's ongoing studies.

Hubbard Brook Monthly Diversity Equity and Inclusion Meetings Monthly starting 08/2020
Open discussion and planning to promote inclusion and involvement by underrepresented individuals or groups (particularly indigenous and non-whites) in the scientific community.

Calumet Area Trails Planning Group Meeting 10/2019
Public open house to discuss trail planning and recommendations.

Volunteer Experience

Michigan Department of Natural Resources 01/2020
Assisted with sampling and banding of bats, detection of white-nose syndrome. Underground mine safety.

Keweenaw Land Trust 09/2019 - 05/2020
Removal of invasive species, replanting native vegetation. Population delineation, GPS navigation.

Superior Search and Rescue 09/2019 - 05/2020
Wilderness safety and navigation. Effective teamwork and communication. Mindful awareness of surroundings.

S.N.A.P Animal Shelter 06/2013 - 07/2013, 06/2014 - 07/2014

Port Huron, MI Soup Kitchen 10/2012, 10/2013, 10/2014
