Forest Ecology and Management 493 (2021) 119266

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Relative influence of stand and site factors on aboveground live-tree carbon sequestration and mortality in managed and unmanaged forests

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ARTICLE INFO

Keywords:
Research networks
Experimental forests
Climate factors
Silviculture
Aboveground carbon sequestration
Carbon loss

ABSTRACT

We compiled data from several independent, long-term silvicultural studies on USDA Forest Service experimental forests across a latitudinal gradient in the northeastern and north-central U.S.A. to evaluate factors influencing aboveground live-tree carbon sequestration and mortality. Data represent five sites with more than 70,000 repeated tree records spanning eight decades, five ecoregions, and a range of stand conditions. We used these data to test the relative influence of factors such as climate, treatment history (uneven-aged or no management), species composition, and stand structural conditions on aboveground live-tree carbon sequestration and mortality in repeatedly measured trees. Relative to no management, we found that uneven-aged management tended to have a positive effect on carbon sequestration at low stocking levels and in areas of favorable climate (expressed as a combination of growing season precipitation and annual growing degree days > 5 °C). In addition, losses of carbon from the aboveground live-tree pool due to tree mortality were lower in managed than unmanaged stands. These findings suggest that there may be conditions at which rate of sequestration in living trees is higher in stands managed with uneven-aged silviculture than in unmanaged stands, and that this benefit is greatest where climate is favorable.

1. Introduction

Increased carbon dioxide (CO_2) in the atmosphere has been linked to climate change and continues to be of global concern. Policy makers are urged to support processes or activities that limit sources of CO_2 emissions or remove (sequester) CO_2 from the atmosphere (IPCC, 2013). Carbon (C) sequestration processes and activities, including forest management, are growing areas of forestry research (Huang et al., 2020). As the terrestrial ecosystem's largest carbon pool, forests have great potential to reduce CO_2 through carbon sequestration. Trees both sequester C through uptake of atmospheric CO_2 for photosynthesis and release CO_2 (C loss) to the atmosphere through respiration and mortality (decay). The rates of C exchange in forests are influenced by temperature and local climate (Black et al., 2000) and by tree age as young, aggrading forests tend to have high C sequestration and low C loss (including tree mortality) compared to old-growth forests (Harmon et al., 2009). Forest management activities are often aimed at supporting vigorous tree growth and minimizing tree mortality and, consequently, increasing net C uptake (Smith et al., 1997; Society of American Foresters, 2008). Thus, both C sequestration and tree mortality influence the potential of managed forests to reduce atmospheric CO_2 through the growth processes of living trees.

In addition to age and climate, the balance of C sequestration in live trees and loss from that pool through tree mortality is influenced by a variety of factors, such as site quality and species composition. For example, aspen (*Populus* spp.) stands in Minnesota, U.S.A. with a higher site index (quality) were associated with greater C sequestration than lower-quality sites (Reinikainen et al., 2014). The same study found that composition mattered; mixedwoods of aspen and conifers had higher C sequestration than pure aspen stands (Reinikainen et al., 2014). Tree composition also had a strong effect on C sequestration in Mediterranean mountain forests (Alvarez et al., 2016). Often forest compositions that include late-successional species maintain higher C sequestration rates longer than compositions dominated by pioneer species (Jandl et al., 2007a). Moreover, stand density influences stand-level C

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Received 29 January 2021; Received in revised form 9 April 2021; Accepted 11 April 2021 0378-1127/Published by Elsevier B.V.

https://doi.org/10.1016/j.foreco.2021.119266

sequestration, with high density often associated with greater C stores or sequestration but not both (D'Amato et al., 2011; Harmon et al., 2009).

Forest management activities also have potential to be highly influential on C sequestration with expectations for live and dead tree pools consistent with patterns observed for stand-level growth and mortality in past work examining growth-growing stock relationships. With few exceptions (i.e., salvage), harvesting removes trees to produce wood products before they succumb to natural mortality (C loss) such that post-harvest stocking is often lower than in the pre-harvest stand (e.g., D'Amato et al., 2011). In the case of thinning, which is often applied in dense, immature stands, the management objective is to redistribute aboveground growth, or aboveground C sequestration, from many, small trees to few, large trees for the purpose of growing more valuable trees faster than in unmanaged forests (Curtis et al., 1997; Zeide, 2001). The residual trees in managed stands such as these tend to be more vigorous than in dense, unmanaged stands, increasing tree-level sequestration and reducing losses of C from the live-tree pool through mortality (Jandl et al., 2007b). At the forest scale, managed forests typically contain younger stands, which can have higher C sequestration rates than unmanaged forests of older stands (Jandl et al., 2007b). Managed forests with lower stand densities also tend to have more available nutrients, less inter-tree competition, and lower total C stocks than unmanaged forests (Noormets et al., 2015). Overall, the improved growing conditions (e.g. lower density) resulting from silvicultural treatments may facilitate the effect of favorable climate by minimizing other factors limiting growth, further enhancing growth and C sequestration in managed stands (e.g., Di´e et al., 2015).

Less clear is how management strategy affects C exchange. Even- aged management focuses on removing all mature trees in one or few harvests to regenerate a new cohort. Though young stands sequester C rapidly, replacing the C stores that were on site before harvest can take a substantial length of time (Harmon et al., 2009). In contrast, uneven- aged management aims to maintain multiple cohorts within the same stand; harvests remove only a portion of the residual stand at intervals such that on-site C stores remain relatively stable. Over a 60-year period, selection cutting, an uneven-aged method, resulted in higher C storage than clearcutting, an even-aged method, in a northern conifer forest in Maine, U.S.A. (Puhlick et al., 2016). Uneven-aged methods had favorable C sequestration outcomes relative to other management strategies, according to a simulation study of aboveground tree biomass and harvested wood products in the northeastern U.S.A. (Nunery and Keeton, 2010). Uneven-aged methods also usually remove less wood volume in one or a few entries than even-aged methods and some variants have been proposed as a mitigation approach for onsite retention of C (Soceity of American Society of American Foresters, 2008). However, this idea has not been fully tested across a large spatial scale and/or multiple forest types.

The combination and interaction of factors that affect C exchange are also unclear. For instance, a study of harvest, climate, and CO_2 concentrations found rotation age to be an important explanatory variable, in that longer rotations increased C sequestration (Ueyama et al., 2011). In a different study, among structural diversity, composition, density, soil, and light variables, the most important factors explaining net C changes were tree density, composition, and soil characteristics (Cai et al., 2020). However, density was the overall best predictor of residual- tree C sequestration (Cai et al., 2020). Density and climate appear important to C sequestration and mortality patterns but their relative influence, along with other site and stand factors across multiple scales and different management histories, has not been studied. Evaluating multiple factors can highlight the most influential factors to C exchange and areas to adjust forest management activities.

1.1. Scale and synthesis in ecological research

Addressing knowledge gaps in the ecology and management of forests has mostly been based on site-specific studies. Recently, the emergence of research questions at regional and continental scales has generated scientific interest in large-scale, long-term dynamics of forest ecosystems and variability therein (Baeten et al., 2013; Burton, 2006; Hobbie et al., 2003). The synthesis of silvicultural experiments, in particular, provides unique opportunities to understand mechanisms behind ecological processes associated with various human and natural disturbances (Knapp et al., 2012). The U.S. Department of Agriculture (USDA) Forest Service experimental forests and ranges (EFRs) have a wide range of manipulative and observational silvicultural and ecological studies across North America that span multiple decades to over a century (Adams et al., 2010; Hayes et al., 2014). Some EFR studies have been synthesized with methodologies and analyses that were not intended by the initial study design, e.g., an observational continental- scale study of ice phenology (Baker et al., 2000), multi-site studies of managed stand structure and composition (D'Amato et al., 2011), and drought and competition effects on tree growth (Gleason et al., 2017). This scientific approach is potentially important for unraveling the complex effects of climate, management, and other factors on forest C cycles.

The goal of the work reported here is to use harmonized forest inventory data from multiple silvicultural experiments in the northeastern and north-central U.S.A. to determine whether uneven-aged silviculture (as a low-intensity management strategy) has a detectable effect on C exchange compared to no management, and whether outcomes can be generalized with similar effects on live-tree C sequestration and mortality across forest types regardless of the variety of factors, such as site or climate, that might be influential. Our focus is on C sequestration and loss from the aboveground portions of live trees, i.e., exclusive of exchange in other ecosystem pools such as coarse woody material and the forest floor (a sizable pool in forested ecosystems also affected by disturbance; Puhlick et al., 2016) or harvested wood products. Specific research objectives were to (1) use robust exploratory methods (i.e. machine learning) to identify influential stand, site, and climate factors on live-tree C sequestration and mortality; (2) evaluate effects of identified influential factors with formal statistical hypothesis testing after accounting for the hierarchical nature of the data (i.e. using linear mixed models); and (3) assess predicted trends across the full range of conditions analyzed. Of the various factors considered (e.g. climate, density, diversity, soil, silviculture, and composition), we expected climate and density to have a greater relative influence on C sequestration and tree mortality than other factors and that would vary based on past silviculture across sites.

2. Materials and methods

2.1. Study area

We limited our scope of inference to the northeastern quadrant of the U.S.A. This area encompasses a complex mosaic of temperate forest types, ages, compositions, densities, and climatic and biophysical settings (Shifley et al., 2012). It provides a temporally rich research resource under the unified jurisdiction of the USDA Forest Service, Northern Research Station (NRS), which includes 22 EFRs. We limited our study sites to those with silvicultural experiments, although other types of experiments exist on EFRs (e.g., paired watershed studies). Silvicultural experiments on EFRs include very detailed tree-level measurements on repeatedly sampled permanent plots with data records spanning decades – facilitating flexible, multi-scale tree to stand analyses.

2.2. Site selection

We queried NRS EFRs for silviculture studies with long-term (minimum 20-year) responses and paired stands of unmanaged areas (i.e. unharvested control treatment) and managed areas treated with uneven- aged silviculture (i.e., selection cutting). Selection cutting is applied to improve residual stand composition, growth, quality, and structure by removing mature trees, tending immature growing stock, and establishing new cohorts at regular intervals. Harvests of individual or small groups of trees are conducted at intervals and generally maintain residual stocking at a higher level and with a narrower range than some even- or two-aged silvicultural methods (Frank and Bjorkbom, 1973; e.

g., Niese and Strong, 1992). By limiting our sample to those sites where the selection system had been applied on approximately 10-year cutting cycles, we were able to investigate a common and comparable silvicultural treatment with similar disturbance intervals across multiple locations.

Five EFRs had suitable study designs and data (Fig. 1), representing a range of forest types, geology, physiography, and physical site characteristics typical across the northeastern and north-central U.S.A. (Table 1). The five specific locations used in this analysis were:

1. The Argonne Experimental Forest (AEF) study area is located on the Chequamegon-Nicolet National Forest in northeastern Wisconsin where loamy soils (Alfic Oxyaquic Fragiorthods and Alfic Oxyaquic Haplorthods) formed in glacial till or mudflow deposits and the climate is humid continental. The northern hardwood stands are second-growth that originated from region-wide exploitive harvests circa 1905. Sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), American basswood (*Tilia americana* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) with minor components of black cherry (*Prunus serotina* Ehrh.), quaking aspen (*Populus tremuloides* Michx.), northern red oak (*Quercus rubra* L.), and ironwood (*Ostrya virginiana* (Mill.) K. Koch) dominate the study area. Long-term silvicultural studies at the AEF are the basis for regional northern hardwood management guides (e.g., Tubbs, 1977).

2. The Dukes Experimental Forest (DEF) study area is located in the Upper Peninsula of Michigan where soils are moderately to somewhat poorly drained sandy loams (Argic Fragiaquods) that formed in glacial till and the climate is humid continental. While settlement in the region (late 1800 s to early 1900 s) resulted in largely second-growth forests, the DEF study area was not cleared during that time and was an old, late- successional forest when the study began in the 1920 s. The species composition is similar to AEF. Results from the long-term silvicultural studies were used to develop one of the earliest marking guides for northern hardwoods (Arbogast, 1957).

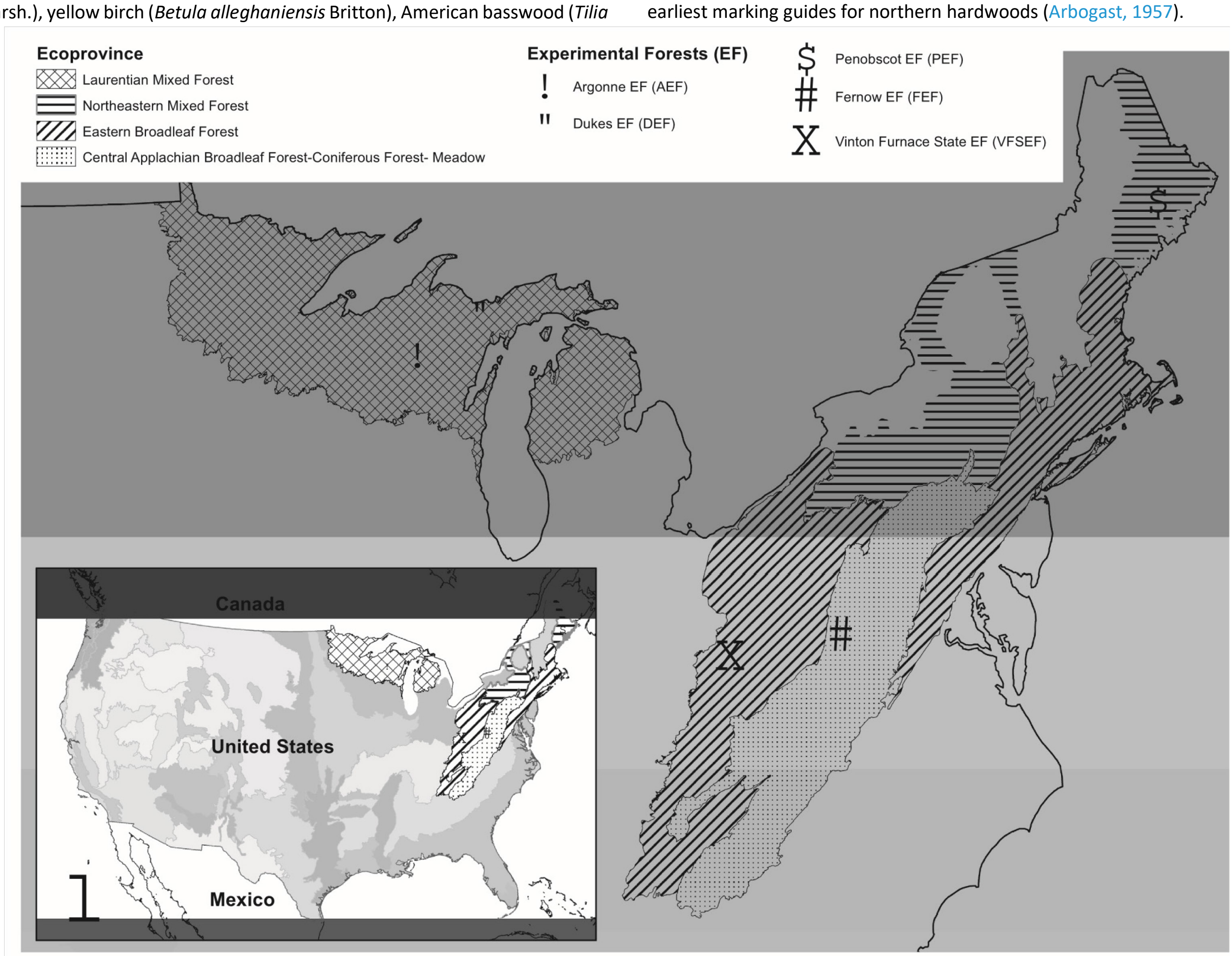

Fig. 1. Locations of five sites and associated ecoprovinces used for creation of the database used for this study.

Table 1

Site	Forest Types	Ecoregion[1] (section)	Parent Material	Primary Landform	Precipit- ation[2] (cm)	Growing Degree Days[2] (°C)	Latitude, Longitude	Reference
AEF	Northern Hardwood	Southern Superior Uplands	Glacial	Drumlins and Moraines	79 ± 6	2,349 ± 127	45.750, −89.000	Strong et al. (1995)
DEF	Northern Hardwood	Northern Great Lakes	Glacial	Moraines	86 ± 5	2,322 ± 30	46.350, −87.166	Eyre and Zillgitt (1953); Gronewold et al. (2010)
FEF	Appalachian Hardwood	Allegheny Mountains	Residuum	Mountains and Ridges	140 ± 4	2,589 ± 60	39.054, −79.680	Schuler et al. (2017)
PEF	Mixed Northern Conifer	Central Maine Coastal and Interior	Glacial	Drumlins and Plains	105 ± 8	2,533 ± 51	44.866, −68.633	Brissette et al. (2012)

VFSEF	Central Hardwoods	Southern Unglaciated Allegheny Plateau	Residuum	Hills	106 ± 10	2,891 ± 134	44.866, −68.633	Brown et al. (2004)

Description of study sites. Site abbreviations are listed in Fig. 1. Growing degree days were calculated using 5˚C as a generalized base temperature. References refer to datasets that are available online or described with more detail in another publication.

[1] As defined in Bailey (1983).

[2] Climate data (mean ± SE) for individual factors were extracted from the PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 4 Feb 2004.

3. The Fernow Experimental Forest (FEF) study area is located in the central Appalachian Mountains in West Virginia where soils are well- drained, medium-textured loams and silt loams (Typic Dystrudepts) formed in residuum from sandstone and siltstone and the climate is humid continental. The central hardwood forests are second-growth originating from region-wide exploitive harvests between the late 1800 s and early 1900 s. Northern red oak, sugar maple, chestnut oak (*Quercus prinus* L.), and red maple (*Acer rubrum* L.) constitute the dominant species. The long-term silvicultural studies there were the basis of regional central hardwood management guides (e.g., Trimble Jr. and Smith, 1976).

4. The Penobscot Experimental Forest (PEF) study area is located in east-central Maine where soils are characterized by thin, shallow, often wet soils that range from well-drained sandy loams (Typic Haplorthods) on glacial till ridges to very poorly drained silt loams (Typic Epiaquepts) on glaciomarine sediments and the climate is humid continental. The PEF was repeatedly partially cut for lumber and pulpwood between the late 1700 s and early 1900 s. Dominant species include red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock, northern white-cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.), red maple, paper birch (*Betula papyrifera* Marsh.), and aspen (*Populus* spp.). Long-term silvicultural studies at the PEF were the basis of regional spruce – fir forest management guides (e.g,. Frank and Bjorkbom, 1973).

5. The Vinton Furnace State Experimental Forest (VFSEF) is located in southern Ohio where soils are well-drained silt loams (Typic Dystrudepts) formed in residuum derived from sandstone and conglomerate and the climate is humid continental. The study area was heavily harvested for timber and fuelwood in the 1860 s. Main tree species include chestnut oak (*Quercus prinus* L.), scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), white oak (*Quercus alba* L.), red maple, hickories (*Carya* spp.), Ohio buckeye (*Aesculus glabra* Willd.), and yellow poplar (*Liriodendron tulipifera* L.). Results of these long-term studies informed regional management recommendations for central hardwoods (e.g, Roach and Gingrich, 1968).

Available primary and secondary data were harmonized, synthesized, and compiled with the finest level of detail at tree-level data so that common patterns across sites could be identified. Ancillary data (soils, growing degree days, etc.) were integrated at the stand and site levels. The unmanaged and uneven-aged managed (single-tree selection) treatments from the five sites resulted in 1,812 repeated plot measurements (71,320 repeated live tree-level records) in our analyses (Table 2). The measurement inventory intervals varied greatly between sites and were often much shorter than the 10-year cutting cycle. The percentage of forest composition in hardwood species ranged from 0 to 100% of plot-level basal area; stand density ranged from 99 to 1,050 trees ha^{-1}. Measurement period-specific climatic factors varied, with mean annual temperature ranging from 3.3 to 12.1 °C and mean annual

Table 2
Plot and data record information (for trees ≥ 11.7 cm diameter at breast height) for studies included in the database. Site abbreviations are listed in Fig. 1. Treatment type abbreviations are unmanaged (UN) and uneven-aged (UEA) treatments.

Site	Number of Plots	Years of Data Record (Number of years)	Number of Tree Records by Treatment: UN	Number of Tree Records by Treatment: UEA	Mean Inventory Interval (Years)
AEF	60	1951–2006 (55)	6,938	11,160	2.1
DEF	123	1932–1973 (41)	969	9,388	5.4
FEF	16	1979–2009 (30)	4,919	1,938	5.6
PEF	55	1977–2014 (37)	4,338	10,502	5.4
VFSEF	7	1976–2010 (34)	12,055	9,113	1.2

precipitation ranging from 67.8 to 146.8 cm (Table 1). Additional details about data compilation and data types can be found in Appendix A.

2.3. Statistical analysis

With the compiled dataset, we calculated periodic annual aboveground woody carbon sequestration rates (C_{SEQ}, Mg C ha^{-1} y^{-1}), or accretion on trees ≥ 11.7 cm in diameter at breast height (DBH) surviving the beginning and end of each measurement period (ingrowth was included once it exceeded the DBH threshold) (Kershaw et al., 2017), and periodic annual carbon loss from the live-tree pool through mortality (C_{LOSS}, Mg C ha^{-1} y^{-1}) as the response variables. Harvested trees were not considered mortality and therefore not included in the C_{LOSS}. Aboveground total woody carbon stock (C_{STOCK}, Mg C ha^{-1}) in the live-tree pool was calculated by quantifying aboveground total biomass estimated at the tree scale using species-specific estimators from Jenkins et al. (2003) and then converting individual tree biomass into carbon mass using carbon content estimators from Lamlom and Savidge (2003), Thomas and Martin (2012), and Martin et al. (2015). A conversion factor of 0.5 was used for observations with missing species- and genus-specific carbon content estimators.

Due to the complexity and amount of data, and number of potential predictor variables, we used variable selection random forest models (explained further below) by treatment (unmanaged or managed stands), as well as site and the function VSURF (Genuer et al., 2015) of the programming software R version 3.5.1 (R Core Team, 2018), to determine the number and importance of various influences on C_{SEQ} and C_{LOSS}. VSURF was used to screen and select potentially important covariates given the high number of variables considered and relatively high correlations among them. Once variables were selected, linear mixed-effects modeling was then utilized to test variable significance and potential interactions after accounting for the hierarchical and repeated nature of the underlying data.

Random forest is a non-parametric technique that combines many binary decision trees (Breiman et al., 1984) built using several bootstrap samples coming from a learning sample and choosing randomly at each node a subset of explanatory variables (Breiman, 2001; Genuer et al., 2015). The technique is useful for data with non-linear responses, multiple types of predictors, and complex predictor interactions, which can be used to effectively discern the influence of factors (Cutler et al., 2007). We used random forest scores of importance to quantify explanatory variable significance in explaining the responses, C_{SEQ} and C_{LOSS} (Cutler et al., 2007; Genuer et al., 2015). Based on the random forest technique, VSURF calculates random forest importance scores and out-of-bag error (prediction error in terms of mean square residuals) for all explanatory variables and eliminates variables that are unimportant for predicting the response based on a data-driven threshold for variable importance (Teets et al., 2018). Explanatory variable-specific importance scores were derived as averages over 50 forests with 2,000 trees, five variables per node, and an approximate 35% out-of-bag sample (the percentage of data excluded from bootstrap samples and used to estimate classification error as trees are added to the forest) (Genuer et al.,

Class	Acronym	Mean	SD	Min	Max	Description
Silviculture	TRT	0.68	0.47	0	1	Treatment factor, 0 = unmanaged, 1 = managed
	TSH	3.45	3.13	0	9.5	Years since last harvest, control = 0
Density	C_{STOCK} TPH	83.13	32.36	10.10	179.42	Total aboveground woody carbon stock, Mg C ha^{-1} Live
		328.91	167.08	98.84	1,050.20	trees ha^{-1}
	QMD	31.49	6.16	15.68 5.44	47.50	Quadratic mean diameter, cm
	BA	23.35	8.28	112.38	60	
	SDI RD	406.57	143.17	0.09	1,072.34	
		0.48	0.16		1.02	

[1] Stand density index was estimated with the summation methods (Weiskittel et al., 2011).

Exploratory analysis of over 40 explanatory variables of six different

Table 3
Comprehensive listing of explanatory variables used in this study. Variables were collected at the plot level except climate (site-level) and soil factors (replication- level). Variable "Class" is the broad theme of a group of related variables.

						Standing live basal area, m^{1} ha^{-1} Additive stand density index, trees ha^{-1} [1] Relative density [2]
Diversity	DBH$_{RANGE}$	38.88	13.17	7.11	92.46	Range in DBH, cm
	DBH$_{SD}$	11.43	3.65	2.27	22.13	Standard deviation of DBH, cm
	GINI$_{DBH}$	0.21	0.06	0.03	0.36	DBH based Gini coefficient
	SKEW	0.42	0.63	− 1.39	2.85	Skewness of DBH distribution
	KURT	2.60	1.12	1.07	12.1	Kurtosis of DBH distribution
	SPPDIV	3.91	2.79	1	19	Species richness
	H$_{SPP}$	0.80	0.58	0	2.22	Shannon diversity index
Composition	PBAHW	86.90	29.35	0	100	Percentage of basal area in hardwood species
	PBASHADE	71.23	31.95	0	100	Percentage of basal area in shade-tolerant species
	SHADE	4.22	0.55	2.54	4.84	Average plot-level shade tolerance weighted by basal area
	SHADE$_{SD}$	0.52	0.34	0	1.40	Standard deviation of plot-level shade-tolerance
	GINI$_{SHADE}$	0.06	0.05	0	0.24	Plot-level shade tolerance-based Gini coefficient
	H$_{SHADE}$	0.71	0.56	0	2.22	Plot-level shade tolerance-based Shannon diversity index
Climate	MAT	5.44	2.04	3.32	12.05	Mean annual temperature, °C
	MAP	88.57	16.29	67.83	146.82	Mean annual precipitation, mm
	GST	15.76	1.42	13.98	20.43	Mean growing season temperature, °C
	GSP	47.90	6.66	35.30	70.87	Growing season precipitation, mm
	MTCM	− 9.66	3.38	− 14.09	2.88	Mean temperature of the coldest month, °C
	MINTCM	− 18.28	3.98	− 24.26	− 2.43	Minimum temperature of the coldest month, °C
	MTWM	18.94	1.48	16.42	23.50	Mean temperature of the warmest month, °C
	MAXTWM	27.01	1.58	24.17	32.29	Maximum temperature of the warmest month, °C
	MINGST	2.77	2.18	− 0.47	10.87	Minimum growing season temperature, °C
	MINGSP	38.76	8.96	22.01	66.08	Minimum growing season precipitation, mm
	DD5	2,423.62	190.29	2,076.49	3,165.60	Annual degree days > 5 °C, °C
	GSPDD5	116.17	19.73	87.61	195.24	GSP*DD5/1000, mm °C
Soil	WHC	2.31	1.10	1	5	Water holding capacity class: 1 = 0–8 cm, 2 = 8–15 cm, 3 = 15–21 cm, 4 = 21–30 cm, 5 = 30–37 cm
	DTWT	2.55	1.79	1	5	Depth to water table class, 1 = 0–51 cm, 2 = 51–102 cm, 3 = 102–153 cm, 4 = 153–203 cm, 5=>203 cm
	DTRL	4.61	1.07	1	5	Depth to restrictive layer class: 1 = 0–51 cm, 2 = 51–102 cm, 3 = 102–153 cm, 4 = 153–203 cm, 5=>203 cm
	DRAIN	4.22	0.91	1	5	Drainage class: 1 = very poorly drained, 2 = poorly drained, 3 = moderately well drained, 4 = well drained, 5 = somewhat excessively drained
	SLOPE	2.52	0.90	1	6	Slope class: 1 = 0–1%, 2 = 1–6%, 3 = 6–15%, 4 = 15–25%, 5 = 25–40%, 6 = 25–60%
	PM	–	–	–	–	Parent material class: G = glacial, R = residuum base
	CRSFRAGM	17.81	10.74	0	55	Midpoint of coarse fragments in soil by volume, %
	LF	–	–	–	–	Landform: depression, drumlin, hill, kame, moraine, mountain slope, plain, ridge

2015).

variable classes related to silvicultural treatment, stand density and

[1] Relative density is the ratio of SDI to maximum SDI with maximum SDI estimated using methodology for mixed species stands (Woodall et al., 2005) and a specific gravity at 12% moisture content.

composition, diversity (Shannon index) in species and tree DBH, climate, and soils data were used to populate our models (Table 3). Climate data (e.g. growing season precipitation (GSP), annual growing degree days > 5 °C (DD5) and the combination of both (GSPDD5 = GSP*DD5/1000)) were extracted from the PRISM Climate Group (Oregon State University, http://prism.oregonstate.edu) based on the dates of the specific measurement intervals. Thus, the climate varied over time, representing weather of the specific time period, which was expected to be more directly related to observed patterns than climate normals. For interpretation, the random forest models were derived by treatment as well as by site. Treatment-level random forest models (managed and unmanaged stands) were then used to identify the most influential variables for each treatment. Variables deemed most influential and thus significant were those indicated in the prediction step of the VSURF analysis (Genuer et al., 2015). In addition, average importance score by explanatory variable class (Table 3) and EFR site were evaluated to detect trends across sites not evident in the treatment-level random forest models.

We evaluated the findings from our final C_{SEQ} random forest models using a linear mixed model approach to specifically evaluate the direct effect of treatment (managed and unmanaged stands) and its potential interaction with additional factors using the function lme of the package nlme (Pinheiro et al., 2018) in R. The fixed effects were those identified as the significant variables in the treatment-level random forest models and the random effects were replication within EFR site within year. Explanatory variables were transformed if necessary to comply with model assumptions. Multicollinearity among potential predictor variables was tested using the variance inflation factor (VIF), which was quantified using the 'corvif' function in R (Zuur et al., 2009). Inclusion of additional variable interactions was evaluated based on plausibility, statistical significance, and effect on model fit (prediction accuracy evaluated based on Akaike's information criterion (AIC) and mean absolute bias (MAB, absolute value of observed minus predicted)). Variance structures to account for variance heterogeneity (R function 'varComb' (Zuur et al., 2009)) were incorporated in the final model and model residuals were checked for fit and concurrence with model assumptions.

Because of the large number of zeros among the observed values (N = 1,277), C_{LOSS} was further examined using a two-step or hurdle mixed effects modeling approach to verify findings of the corresponding random forest models. The two-step modeling approach evaluated the zero portion of the C_{LOSS} data in a first step and subsequently analyzed the non-zero part in a second step. Using transformed binomial data (0/1 for no/yes), the first modeling step predicted the probability of C_{LOSS} occurrence (probability of tree mortality) on a certain plot on an absence/presence level (Zuur et al., 2009). Using presence data only by excluding zeros, the second modeling step predicted the amount of C_{LOSS} on an individual plot. Using the nlme function of the nlme package in R, C_{LOSS} occurrence in the first step was analyzed by means of a logistic function of the form $y = (1/(1 + \exp(-(X\beta))))^{(1/YIP)}$ where y is probability of C_{LOSS} occurrence, Xβ is the model-specific explanatory variable design matrix with the associated estimated fixed and random parameters, and YIP is years in period to allow for the prediction of annualized values by accounting for the varying inventory intervals (Table 2). Because generalized liner mixed models with a Gamma error structure did not converge, non-zero absolute C_{LOSS} observations of the second modelling step were log-transformed and analyzed with the lme function of the nlme package similar to C_{SEQ} (Zuur and Ieno, 2016). Selection of fixed and random effects followed the procedures described for the C_{SEQ} linear mixed-effects models. Overall, predicted C_{LOSS} was finally calculated by multiplying the outcome of modeling step 1 with the outcome of modeling step 2.

3. Results

3.1. Carbon sequestration Observed C_{SEQ} was highly variable, both within and among sites, with an overall average of 1.90 ± 0.79 Mg C $ha^{-1} yr^{-1}$ (mean ± SD) while varying between 0 and 4.95 Mg C $ha^{-1} yr^{-1}$. Climatic predictors were dominant among factors identified as significant explanatory variables in both treatment-level (unmanaged and managed) C_{SEQ} random forest models (Table 4). Variable classes of composition, density, and diversity were also important and represented in each treatment-level model with at least one significant predictor, while variables of variable class soil and silviculture were only found in the model of managed stands. Similar results were derived for the random forest model that included plots of both unmanaged and managed stands (Table 4).

Evaluation of average importance scores by explanatory variable class and EFR confirmed findings from the treatment-level random forest models (Fig. 2). Climate, composition, and/or density variables were among the most influential predictors, but significance of each variable class substantially varied across EFRs. We also found additional differences across EFRs revealing trends not evident in treatment-level analyses (Fig. 2). The silviculture variable time since last harvest, for example, was among the major drivers of C_{SEQ} for DEF and PEF plots, while importance of diversity variables in FEF plots was mainly driven by the Shannon species diversity index (data not shown).

The pool of significant explanatory variables within the treatment- level random forest models (Table 4) was further reduced for inclusion in mixed models by considering only factors with above-average importance scores across all variables by random forest model (Table 4). Moreover, because of the strong correlation among

Table 4

Variable	Class	Importance score	Variable	Class	Importance score	Variable	Class	Importance score
MAP	Climate	**0.1523**	RD	Density	**0.1184**	RD	Density	**0.1087**
GSPDD5	Climate	**0.0973**	MINTGS	Climate	**0.1031**	MAP	Climate	**0.0997**
PBAHW	Composition	**0.0807**	GST	Climate	**0.0776**	GSPDD5	Climate	**0.0955**
DBH_{RANGE}	Diversity	**0.0700**	MTWM	Climate	**0.0464**	GST	Climate	**0.0929**
GST	Climate	**0.0658**	GSPDD5	Climate	**0.0462**	MINTGS	Climate	**0.0927**
QMD	Density	**0.0648**	TPH	Density	**0.035**	C_{STOCK}	Density	**0.0563**
MINTGS	Climate	**0.0509**	MTCM	Climate	**0.0303**	MTCM	Climate	**0.0555**
MTWM	Climate	**0.0507**	SDI	Density	**0.0303**	PBAHW	Composition	**0.0531**
C_{STOCK}	Density	0.0350	SHADE	Composition	**0.0268**	SHADE	Composition	**0.0426**
$SHADE_{SD}$	Composition	0.0338	MINGSP	Climate	0.0242	DD5	Climate	**0.0397**
			BA	Density	0.0236	LF	Soil	**0.0376**
			$SHADE_{SD}$	Composition	0.0204	TPH	Density	0.0318
			WHC	Soil	0.0194	DBH_{RANGE}	Diversity	0.0313
			MAXTWM	Climate	0.0178	H_{SHADE}	Composition	0.0231
			PBASHADE	Composition	0.0177	H_{SPP}	Diversity	0.0218
			DBH_{SD}	Diversity	0.0165			
			DBH_{RANGE}	Diversity	0.0156			

H_{SPP}	Diversity	0.0147
SKEW	Diversity	0.0135
TST	Silviculture	0.0129
LF	Soil	0.0090
SLOPE	Soil	0.0087
KURT	Diversity	0.0080

Unmanaged		Managed		All	

Importance scores and variable class of significant explanatory variables derived from treatment-level C_{SEQ} random forest models for unmanaged, managed, and all unmanaged and managed stands combined ("All") and as indicated in the prediction step of the underlying VSURF (Genuer et al., 2015) analyses. Bold importance scores signal above-average scores across all variables by random forest model. See Table 3 for variable descriptions.

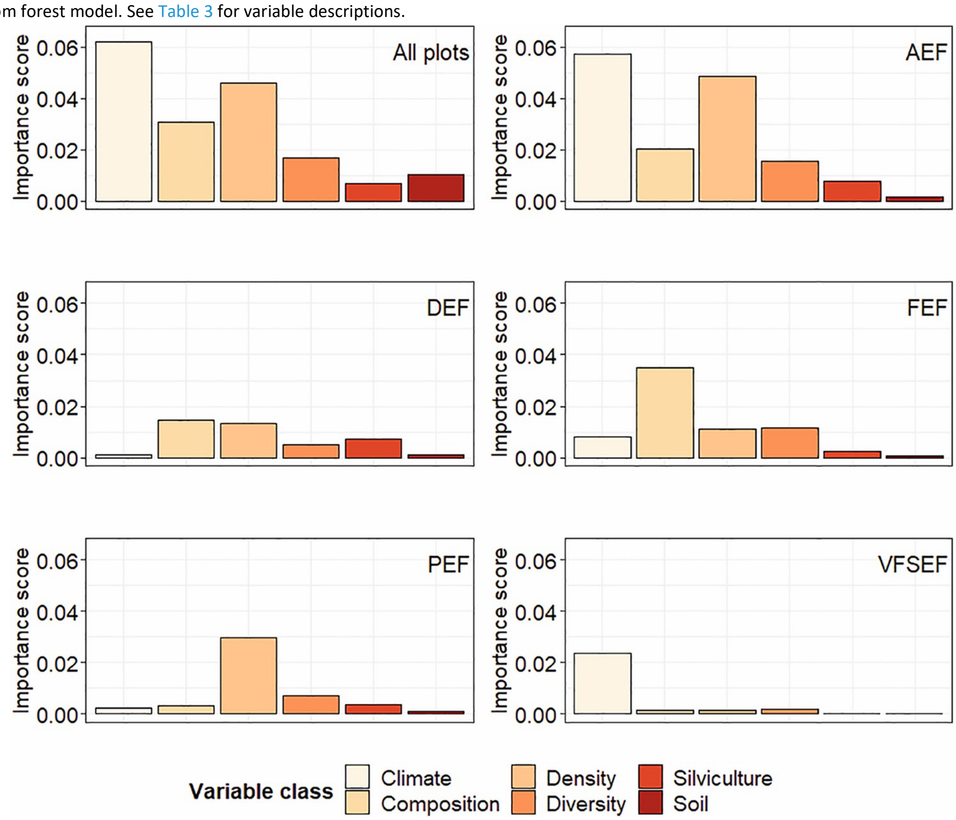

Fig. 2. Average importance scores of explanatory variables by variable class and Experimental Forest and Range (EFR) derived from random forest models predicting periodic annual aboveground woody carbon sequestration (C_{SEQ}, Mg C ha^{-1} y^{-1}). Site abbreviations are listed in Fig. 1.

explanatory variables of the same variable class (Table 3) in the treatment-level random forest models (Table 4), linear mixed models only included total live-tree carbon stock (averaging 83.13 Mg C ha^{-1} and varying between 10.10 and 179.42 Mg C ha^{-1}; variable class density), treatment (silviculture), time since last harvest (0.5 to 9.5 years; silviculture), GSPDD5 (climate), percentage of basal area in hardwood species (composition), range in DBH (diversity), and mean shade tolerance (composition). Instead of incorporating the less easily interpretable, multi-level variable landform, we created a new predictor, landform2 (soil), indicating depressions and plains. VIFs of these eight base explanatory variables were all below 5 with treatment and biomass exhibiting the largest VIF values of 4.2 and 3.3, respectively.

Our formal statistical assessment (linear mixed model) of the findings from the random forest models supported the notion that variables

Table 5
Parameter estimates from the linear mixed model predicting periodic annual aboveground woody carbon sequestration (C_{SEQ}, Mg C ha^{-1} y^{-1}) by treatment (managed and unmanaged stands) and explanatory variables of significant influence. See Table 3 for explanation of explanatory variables.

Variable	Estimate	SE	t-value	p-value
Intercept	− 9.6585	1.6421	− 5.8817	<0.0001
ln(C_{STOCK})	0.9975	0.0886	11.2532	<0.0001
TRT	− 2.9804	1.5229	− 1.9571	0.0505
TSH	− 0.1893	0.0435	− 4.3513	<0.0001
ln(TSH + 0.1)	0.4117	0.1352	3.0452	0.0024
ln(GSPDD5)	1.0587	0.3084	3.4328	0.0009
sqrt(PBAHW)	0.0732	0.0074	9.8655	<0.0001
ln(DBH_{RANGE})	0.2991	0.0484	6.1837	<0.0001
ln(SHADE) LF2[a]	0.8216	0.1389	5.9166	<0.0001
	− 0.3037	0.0828	− 3.6663	0.0003
ln(C_{STOCK}):TRT	− 0.4281	0.0907	− 4.7182	<0.0001
ln(GSPDD5):TRT	0.9843	0.2944	3.3439	0.0008

[a] LF2 is a reclassification of landform indicating depressions and plains.

in addition to climate were influential on C_{SEQ} (Table 5). While DBH_{RANGE} (diversity), percentage of basal area in hardwood species (composition), and mean shade tolerance (composition) had a positive effect, landform2 (soil) resulted in decreasing C_{SEQ}. In contrast, the effect of time since harvest exhibited unimodal behavior, peaking in effect on C_{SEQ} approximately 2–3 years after treatment. C_{SEQ} of managed and unmanaged stands were different from each other and that difference depended on live tree carbon stock and

GSPDD5 (Table 5). Least-square means and standard error of C_{SEQ} were overall slightly higher for unmanaged (2.46 ± 0.35 Mg C ha^{-1} y^{-1}) than managed forests (2.27 ± 0.09 Mg C ha^{-1} y^{-1}). The positive effect of management on C_{SEQ} at carbon stock levels < 60 Mg C ha^{-1} turned negative with further increasing carbon stock (Fig. 3). In contrast, we found a positive effect of GSPDD5 on C_{SEQ} of managed stands at levels > 140 mm °C (Fig. 3).

3.2. Carbon loss

Observed C_{LOSS} in the form of tree mortality was highly variable, both within and among sites, with an overall average of 0.40 ± 1.33 Mg C ha^{-1} yr^{-1} (mean ± SD), varying between 0 and 17.18 Mg C ha^{-1} yr^{-1}. C_{LOSS} averaged 0.94 ± 2.09 and 0.14 ± 0.57 Mg C ha^{-1} yr^{-1} in unmanaged and managed stands, respectively. Predictors of the variable class density were dominant among the factors identified as significant explanatory variables in both treatment-level (unmanaged and managed) C_{LOSS} random forest models (Table 6). Variable classes climate and composition were also important, but only represented in the unmanaged model with one significant predictor. Similar results were derived for the random forest model that included plots of both unmanaged and managed stands (Table 6).

Evaluation of average importance scores by explanatory variable class and EFR confirmed findings from the treatment-level random forest models (data not shown). Density variables were the most influential predictors of C_{LOSS} across EFR sites. With the exception of PEF plots,

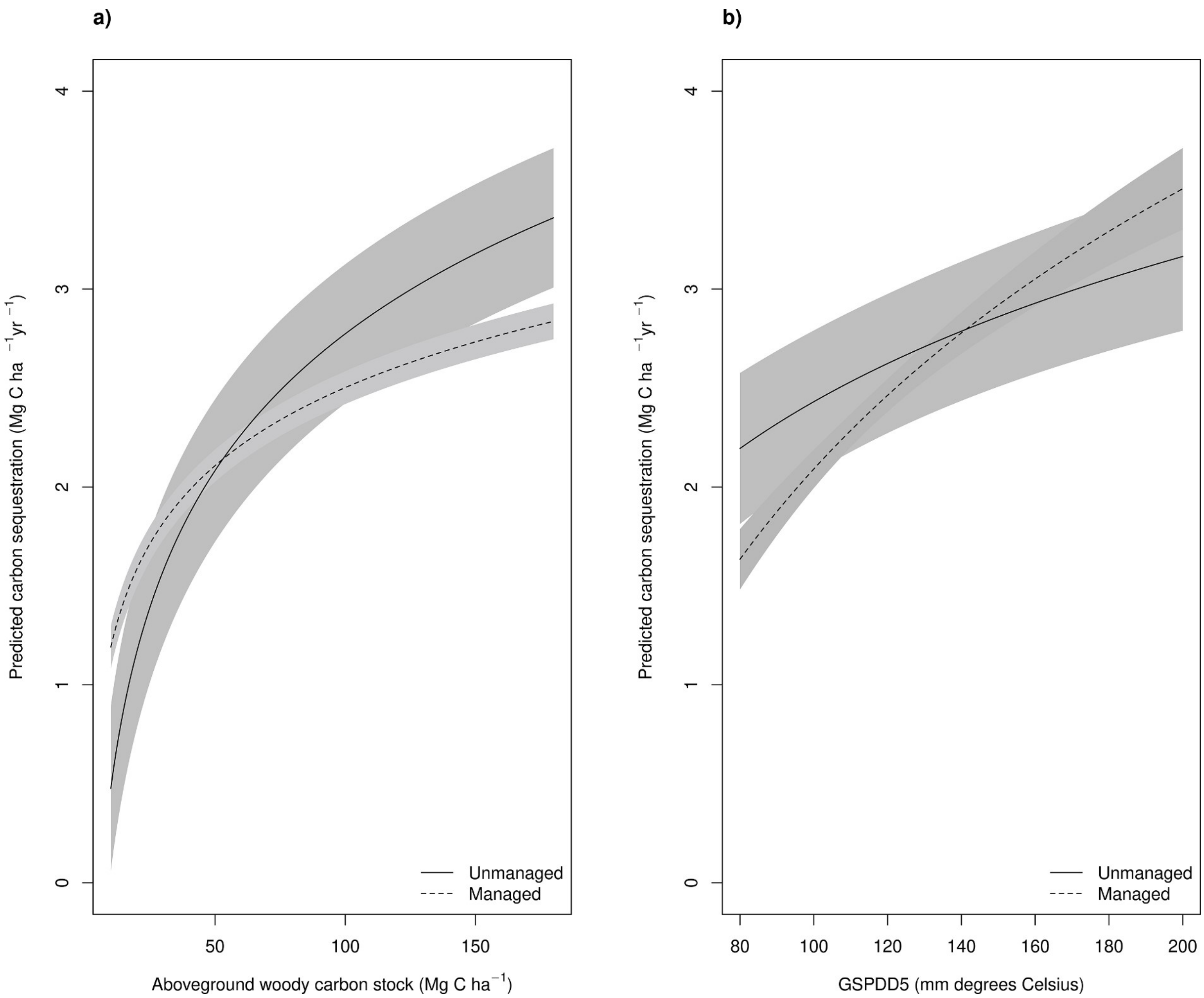

Fig. 3. Predicted change in periodic annual aboveground woody carbon sequestration (C_{SEQ}, Mg C ha^{-1} y^{-1}) of trees surviving the measurement period and ≥ 11.7 cm DBH excluding ingrowth over a) aboveground carbon stock and by treatment, i.e. unmanaged and uneven-aged management with a 10-year cutting cycle (managed) as well as b) GSPDD5 (growing season precipitation (GSP, mm) * growing degree days > 5 °C (DD5, °C)) and by treatment. Data were derived from the linear-mixed effects model predicting C_{SEQ} with explanatory variables not depicted in a graph set to their population means. Bands represent ± 1 standard error.

Table 6

Importance scores and variable class of significant explanatory variables derived from treatment-level C_{LOSS} random forest models for unmanaged, managed, and all stands and as indicated in the prediction step of the underlying VSURF (Genuer et al., 2015) analyses. See Table 3 for variable descriptions.

Unmanaged			Managed			All		
Variable	Class	Importance score	Variable	Class	Importance score	Variable	Class	Importance score
BA	Density	1.8378	TPH	Density	0.2624	BA	Density	0.7194
SDI	Density	1.6461	QMD	Density	0.1833	SDI	Density	0.6056
MINGST	Climate	1.2625	RD	Density	0.1344	C_{STOCK}	Density	0.5955
PBASHADE	Composition	0.9844	C_{STOCK}	Density	0.1313	RD	Density	0.5133
C_{STOCK}	Density	0.8913				TPH	Density	0.4634
						PBASHADE	Composition	0.3477

species shade tolerance associated predictors (variable class composition) were also found to be important irrespective of EFR site. We found additional differences across EFRs revealing trends not evident in treatment-level analyses. The silviculture variables were among the major drivers of C_{LOSS} for AEF and PEF plots, while importance of diversity variables in AEF, DEF, and FEF plots was mainly driven by the Shannon species diversity index (data not shown).

Consequently, explanatory variables considered in the two-step hurdle mixed-effects modeling approach to predict C_{LOSS} included total live carbon stock (variable class density), treatment (silviculture), time since last harvest (silviculture), minimum growing season temperature (MINGST; climate), and percentage of basal area in shade- tolerant species (composition). VIFs of these five base explanatory variables were below 5 with treatment and time since last harvesting exhibiting the largest VIF values of 3.8 and 2.5, respectively.

Our formal test (two-step mixed model) in part supported the findings from the random forest models on variables influential on C_{LOSS} (Table 7). While time since harvest increased C_{LOSS}, the effect of live carbon stock was significantly altered by treatment. Increasing live carbon stock resulted in higher C_{LOSS} in unmanaged stands (Fig. 4). In contrast, effects of the variables MINGST (climate) and percentage of basal area in shade-tolerant species (composition) on C_{LOSS} were found to be not significant and/or implausible.

Table 7
Parameter estimates from the two-step hurdle mixed effect model predicting periodic annual carbon loss through tree death (C_{LOSS}, Mg C ha^{-1} y^{-1}) by treatment (managed and unmanaged stands) and explanatory variables of significant influence. The first modeling step predicted the probability of C_{LOSS} occurrence, and the second modeling step predicted the amount of C_{LOSS}. See Table 3 for explanation of explanatory variables.

Variable	Estimate	SE	t-value	p-value
Probability of C_{LOSS} occurring				
Intercept	− 2.3586	0.5025	− 4.6934	<0.0001
TRT	− 2.8888	0.2968	− 9.7320	<0.0001
Intercept	− 2.3586	0.5025	− 4.6934	<0.0001
TRT	− 2.8888	0.2968	− 9.7320	<0.0001
MINGST	0.4066	0.0904	4.4973	<0.0001
Amount of C_{LOSS}				
Intercept	− 2.4099	1.0522	− 2.2903	0.0226
ln(C_{STOCK})	0.5144	0.2248	2.2881	0.0227
TRT	1.5386	1.2818	1.2003	0.2308
TSH_2	0.0190	0.0057	3.3223	0.0010
ln(C_{STOCK}):TRT	− 0.6651	0.2885	− 2.3057	0.0217

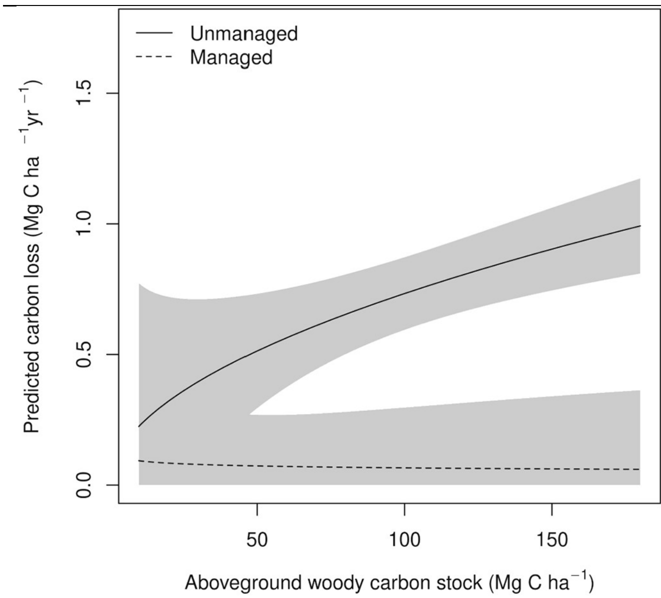

Fig. 4. Predicted change in periodic annual aboveground carbon loss through tree death (C_{LOSS}, Mg C ha^{-1} y^{-1}) for individuals ≥ 11.7 cm DBH over aboveground woody carbon stock and by treatment, i.e. unmanaged and uneven-aged management with a 10-year cutting cycle (managed). Bands represent ± 1 standard error.

4. Discussion

In this study, we evaluated the influence of uneven-aged management (single-tree selection applied for 60 to 80 years on a 10-year cutting cycle) on aboveground live-tree C sequestration and tree mortality over large spatial and temporal scales across various forest types using multiple independent and long-term silviculture studies. Relative to no management, uneven-aged management tended to have a slight positive effect on C sequestration at low stocking levels and in areas of favorable climate. C loss from the live-tree pool through mortality was high and increased with increasing stocking in unmanaged; in managed stands, mortality was consistently low and independent of stocking. Thus, our hypothesis about the relative influence of stand-level (e.g., stocking) and climate variables on C sequestration and tree mortality was partially supported at the large spatial scale and for the silviculture treatment we examined.

We did not find a difference in C sequestration between managed and unmanaged stands at moderate densities or moderate climates.
Nevertheless, our results suggest mitigation potential (in the form of increased rates of C sequestration relative to unmanaged stands) for uneven-aged management as applied on our study sites under certain conditions, i.e., at relatively low stocking levels (<60 Mg C ha^{-1}) and in favorable climatic conditions (GSPDD5 > 140). Tree mortality amounts were low in managed stands regardless of stocking or investigated climate variables. Overall, these findings suggest that some product extraction and mitigation objectives might both be met through application of selection cutting, although the relative positive effect of uneven-aged management on C sequestration was contingent on limited climate and stocking conditions across the sites we examined..

In Japanese forests, climate explained the interannual variation of C sequestration and, generally, favorable climate benefited aboveground C sequestration (Noormets et al., 2015; Ueyama et al., 2011). Globally, mid-latitudes of moderate climate, such as our study area, are areas where forests tend to have high C pools (Liu et al., 2014). Forest structure, i.e. density, was also the best predictor of C sequestration in Chinese forests (Cai et al., 2020). Lowering tree density through timber harvest can reduce inter-tree competition for limiting resources and increase growth of crop trees (Villegas et al., 2009). In a study of a range of cutting methods in pine and maple-dominated forests, stands with < 60 Mg C ha^{-1} or low to moderate densities tended to have high C sequestration and represented common stocking levels of managed stands (D'Amato et al., 2011). Manipulating density has been foundational to silvicultural treatments (Kubiske et al., 2019), and traditional application of single-tree selection cutting requires designation of both a target residual stocking and distribution of trees across size (DBH) classes (Nyland, 1998). The implementation of uneven-aged management for mitigation can be guided by climate-specific density management (site occupancy) strategies that result in positive C sequestration.

We also found that uneven-aged management simplified the influential factors on C loss from the live-tree pool through mortality. In managed stands, stocking was the only influential factor on mortality, whereas, in unmanaged stands, a range of class factors (density, composition, and climate) affected C loss (Table 6). In general, mortality was simply less prevalent in managed than unmanaged stands, because uneven-aged management purposely aims to harvest trees likely to die before the next cutting cycle. C loss through live-tree mortality has been reported to be a major driver of net C change in Chinese forests (Cai et al., 2020).

C sequestration was highest a few years after harvest, suggesting that short cutting cycles might prove advantageous for C management using uneven-aged silviculture of the type investigated here. This trend may be explained by a short-term increase in plant-essential resources immediately after harvest (Aakala et al., 2013; Keyser and Zarnoch, 2012; Kuehne et al., 2016), including selection systems (Jerabkova et al., 2011). Few studies of cutting cycle effects on C sequestration in uneven-aged stands exist. Numerous studies of even-aged management indicate that shorter rotation ages lead to less C sequestration (e.g., Harmon et al., 2009). However, uneven-aged studies have been less conclusive on cutting cycle length; this is partially explained by complex stand and prescription conditions of uneven-aged stands, such as residual stocking, stand structure, age class distribution, and species composition traits (e.g., shade tolerance) (Parajuli and Chang, 2012). Puhlick et al. (2020) compared C sequestration over 65 years in selection stands with 5-, 10-, and 20-year cutting cycles on the PEF, but failed to detect a significant difference in live-tree C sequestration rates among cutting cycle lengths. Investigations of this factor in additional forest types are warranted.

While our results suggest that uneven-aged management affected the factors influencing C exchange through live-tree sequestration and mortality, it did not override the effects of climate. The results of other studies suggest silviculture can have greater influence than climate on C sequestration in certain circumstances. For instance, in a study of harvesting, climate, and CO_2, the harvesting disturbance was important to modeling observed C sequestration, and resulted in increasing sequestration levels above the influence of climate alone (Ueyama et al., 2011). Our study highlights the interconnectedness of climate and silviculture for mid-latitude, temperate forests, especially for the uneven-aged approach or low-severity partial harvests of single-tree selection. Future analyses could reveal relationships between harvest level, species' traits, competitive environments, seasonal patterns of temperature and precipitation, and management activities (Aussenac, 2000; e.g., Cescatti and Piutti, 1998; Curzon et al., 2017; Niinemets and Valladares, 2006), thus providing additional insight into management opportunities and challenges under anticipated climate change.

Lastly, our study brought the variation of sites together to identify general trends in live-tree C sequestration and mortality. In most cases, silviculture treatments are evaluated at stand scales to develop specific management actions to attain short- and long-term goals. Our site level results reveal great variation in factor influence. Yet, when combined across very different sites, climate and density were relatively more influential than other factors on live-tree aboveground C sequestration and mortality. This is a unique contribution to understanding the broad applicability of uneven-aged management potential for not only sustained wood production (i.e., the purpose for which it has traditionally been applied), but also potential climate change mitigation. However, nuances of outcomes at specific sites merit further consideration before developing silvicultural prescriptions based on this work. For instance, when FEF is evaluated alone, composition is relatively important to C sequestration and would require further investigation in relation to density and climate effects.

4.1. Potential of historical experimental forest data

Over the years, researchers at the five EFRs used for the present analysis focused on developing local management guidelines as a result of observed treatment (silvicultural) effects. Independently, these sites provided specific management information for a number of major commercial forest types. As a result, the study areas have been foundational to forest management guidelines across the northeastern U.S. (Table 1) (Hayes et al., 2014). Despite their focus on specific forest types, synthesizing data from these sites across a range of species compositions and growing conditions allowed us to examine regional trends in management, regardless of forest type. Thus, this work demonstrates the potential for synthesis of existing, long-term silvicultural studies to address new and emerging research questions outside the scope of the original hypotheses. Given the difficulty and expense of collecting and maintaining long-term data from manipulative studies, the value and need for repurposing existing studies as part of a portfolio of forest science investments is imperative.

Our research approach quantified complicated relationships between climate, stand attributes, and forest C sequestration in living trees, which are important to understanding mitigation approaches to climate change. Due to the unique nature of this dataset, no independent test or validation/verification dataset was available. Consequently, the models developed in this analysis should not be used for extrapolations outside similar forest types without further validation. The continued measurement of these long-term studies and inclusion of additional sites would be the only robust means for effectively assessing the findings of this current analysis.

Finally, our investigation quantified C sequestration and loss (via tree mortality) from the aboveground portions of live trees and did not include other ecosystem pools or harvested wood products. Soil (forest floor) C, for example, is a sizable pool in forested ecosystems affected by disturbance (harvesting) and deadwood decay among other processes (Puhlick et al., 2016). In addition, tree mortality represents not only loss from the live-tree pool but gain by the deadwood pool, from which C is lost over time at varying rates depending on a number of factors (e.g., contact with the forest floor, climate, etc.) (Bradford et al., 2012; Kuehne et al., 2008; Mackensen et al., 2003). In managed stands, capture of C in harvested wood products may contribute positively to C storage depending on use (e.g., fuel wood versus lumber); past research suggests that selection cutting results in large (sawtimber) trees with the potential to produce wood products with relatively long residence times (Puhlick et al., 2020). Though further work is needed to develop a complete understanding of these pools in the study stands, the work presented here is an important first step in investigating the effects of management and other factors on C dynamics across a wide gradient of sites, species, and climates.

5. Conclusions

Forests represent the largest aboveground terrestrial C pool and exchange large amounts of CO_2 with the atmosphere. Thus, understanding the mitigation potential of forests and their management is an important area of climate change research. Although this work does not represent a full life cycle analysis, our findings do provide some robust evidence to consider uneven-aged management in the form of the selection system to enhance in-forest rates of sequestration in live-tree biomass. Interestingly, the managed stands in this study increased the mean difference between C sequestration and loss via mortality in the aboveground live- tree pool, a difference that was about 1.5 times that observed in unmanaged stands. This large gap between C sequestration and mortality in the aboveground live-tree pool indicates more carbon is being sequestered than lost in stands managed with selection methods of the type included in this study than in comparable unmanaged stands in mid-latitude, temperate forests of the northeastern U.S. region. Further research on this topic is needed to address potential limitations of this analysis such as increased replication across forest types, more detailed C assessment of removals and residence times in forest products, and refined accounting of key local or microsite driving factors.

Our primary results suggest that, with thoughtful application in forest types where it is appropriate, uneven-aged management such as single-tree selection used here can be used to mitigate climate change while supporting commercial forestry and ecological services. The cutting cycle provides opportunity for regular timber product extraction and also C sequestration in the residual stand. Future research should examine specific practices and guides for uneven-aged management to optimize C sequestration and storage. Further, we synthesized unique datasets from independent manipulative experiments to address large- scale research questions. While this work utilizes FS data and EFR locations, we believe this approach has application to other long-term ecological research sites, networks, and other areas of study including hydrology, soil sciences, and climatology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank John Brissette (retired), Doug Kastendick, Texas Nall, Michael Rains (retired), Todd Ristau, Tom Schmidt (retired), Mark Twery (retired), Freddie Wood, Dan Yaussy (retired), and Heather Jensen of the USDA Forest Service, Northern Research Station; Bethany Munoz Delgado of the USDA Farm Production and Conservation Busi˜ ness Center (formerly of the Northern Research Station); Jeremy Wilson of the Harris Center (formerly of the University of Maine), and Laurie Porth and Dave Rugg of the USDA Forest Service, Research Data Services. An earlier version of this manuscript was reviewed by Dave Rugg, Matthew Russell of the University of Minnesota, Lindsey Rustad, Susan Stout (retired) of the Northern Research Station, and two anonymous reviewers. We recognize and appreciate the generations of men and women who had the foresight to initiate and maintain the long-term studies used for this collaborative effort.

Funding

This work was supported by the USDA Forest Service, Northern Research Station; the Northeastern States Research Cooperative; the University of Maine; the NSF RII Track-2 FEC (#1920908); and NSF Center for Advanced Forestry Systems (#1915078).

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