

Analyzing the impacts of forest disturbance on individual tree diameter increment across the US Lake States

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Abstract Disturbances play a critical role in forest ecosystem dynamics. Disturbances cause changes in forest structure which in turn influence the species composition of the site and alter landscape patterns over time. The impacts of disturbance are seen over a broad spectrum of spatial scales and varying intensities, ranging from biotic agents such as insect and leaf disease outbreaks to abiotic agents such as a windstorm (a stand-replacing disturbance). This study utilized Forest Inventory and Analysis (FIA) data collected between 1999 and 2014 in the US Lake States (Michigan, Minnesota, and Wisconsin) to examine the impacts that disturbances have on the growth of residual trees using species-specific diameter increment equations. Results showed that animal and weather damage were the most common disturbance agents and fires were the least common in the region. Results also indicated that while the diameter increment equations performed well on average (overprediction of 0.08 ± 1.98 cm/10 years in non-disturbed stands), when the data were analyzed by species and disturbance agent, the model equation was

rarely validated using equivalence tests (underprediction of 0.30 ± 2.24 cm/10 years in non-disturbed stands). This study highlights the importance of monitoring forest disturbances for their impacts on forest growth and yield.

Keywords Tree growth · Growth and yield · Validation · Forest Inventory and Analysis

Introduction

Disturbances, both human-induced and natural, play a crucial role in shaping the dynamics of forest systems by influencing composition, structure, and functional processes (Dale et al. 2001). Disturbances are also responsible for shifting and altering landscape patterns, creating an ever-changing mosaic over time (Baker 1995). Disturbances can be large and high intensity causing significant ecological changes to forested ecosystems, or can be low intensity and affect small areas. While disturbances damage forest ecosystems as a whole, individual trees that survive through a disturbance outbreak may be better suited to thrive post-disturbance due to additional available growing space and site resources such as water and nutrient availability.

Forest growth and yield models are commonly used by natural resource managers to predict forest growth over time in response to a variety of treatments. This approach allows managers to determine which harvesting methods and silvicultural practices will most likely produce the desired future conditions of a site and meet

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landowner objectives. These models are numerous and come in many forms, from whole-stand models which model stand-level growth using variables like stand density, tree height, and site productivity, to individual tree models which model individual tree growth as a function of tree size, site index, and competitive status (e.g., Payandeh and Papadopol 1994; Crookston and Dixon 2005; Dixon and Keyser 2008). Further, individual tree models can be broken into two categories, where distance-dependent models are driven by density and spatial arrangement and distance-independent models are not affected by spatial patterns (Munro 1974).

Forest yield of various size and product classes is predicted by estimating tree distribution on sample plots and extrapolating over areas (García 2006). Most forest growth and yield models are sets of growth equations derived from empirical data recorded over time, using small, uniformly structured fixed-area research plots (Bruce 1977). In the USA, the Forest Vegetation Simulator (FVS) is the primary growth and yield model used on federal lands and is distance-independent in its design (Crookston and Dixon 2005). Recent research efforts to validate the Lake States variant of FVS (FVS-LS) using growth equations that are now outdated fared poorly, failing to validate diameter increment equations for a single species in the US Lake States (Minnesota, Wisconsin, and Michigan; Pokharel and Froese 2008). Other research suggested that fitting model equations to local data improves the accuracy of predictions and results in a lower estimation error (Lacerte et al. 2006). New diameter increment equations in the Lake States were recently developed to include a variety of stand- and tree-level predictors to improve model performance (Deo and Froese 2013) and are implemented in FVS-LS (Dixon and Keyser 2008).

Researchers have begun utilizing different data sources and alternative model parameters in an attempt to improve growth and yield model accuracy by accounting for biotic and abiotic factors (Woods and Coates 2013). The type and severity of forest disturbances cause differences in forest carbon stocks as indicated by growth and yield model output (Raymond et al. 2015). However, many forest growth and yield models do not include environmental factors such as temperature, precipitation, and soil properties as predictors of tree growth (Johnsen et al. 2001; Henning and Burk 2004). It is also common for individual trees, plots, or entire sample units to be dropped from growth and yield experiments if forest disturbances have influenced site

characteristics (Pretzsch 2005). Although some growth models have been extended to incorporate specific forest disturbance agents in western US forest types (e.g., Crookston et al. 1990; Marsden et al. 1993), most forest growth and yield models do not account for chronic forest disturbance or stochastic events that cause major alterations to stand density (Fox et al. 2001). Improving growth and yield models to better account for disturbances and stochastic events is now crucial for managers to successfully manage forests where forest disturbances are present. In doing so, forest managers can prescribe appropriate intermediate stand treatments such as thinning to improve tree vigor to mitigate insect and disease damage (Waring and O'Hara 2005) and understand the role of disturbances in forest biomass and carbon storage (Seidl et al. 2014; Raymond et al. 2015; Russell et al. 2018).

The overall goal of this study is to quantify the diameter increment of residual trees in the presence and absence of a variety of forest disturbance agents. Specific objectives were to (1) quantify the extent of common forest disturbance agents across the US Lake States and (2) analyze the performance of species-specific diameter increment equations in the US Lake States in the presence and absence of disturbance.

Materials and methods

Forest Inventory and Analysis data

The data used for this project were collected by the US Department of Agriculture-Forest Service as part of the Forest Inventory and Analysis (FIA) program (Fig. 1). The FIA program monitors forestland conditions using an annual inventory of fixed-radius, permanent sample plots (Bechtold and Patterson 2005). In 1998, Federal legislation changed the FIA to an annual inventory of each state, with 20% of the plots within a state measured each year in the Lake States, equating to each plot being remeasured every 5 years on average. This new inventory method has the advantage of an increased ability to quickly and consistently measure the effects of events that occur over large areas, such as hurricanes, ice storms, and windstorms.

To meet the desired accuracy, a sampling intensity of one fixed-radius plot per approximately 2400 forested hectares is used, providing an evenly distributed representation of the landscape (Brand et al. 2000). There are

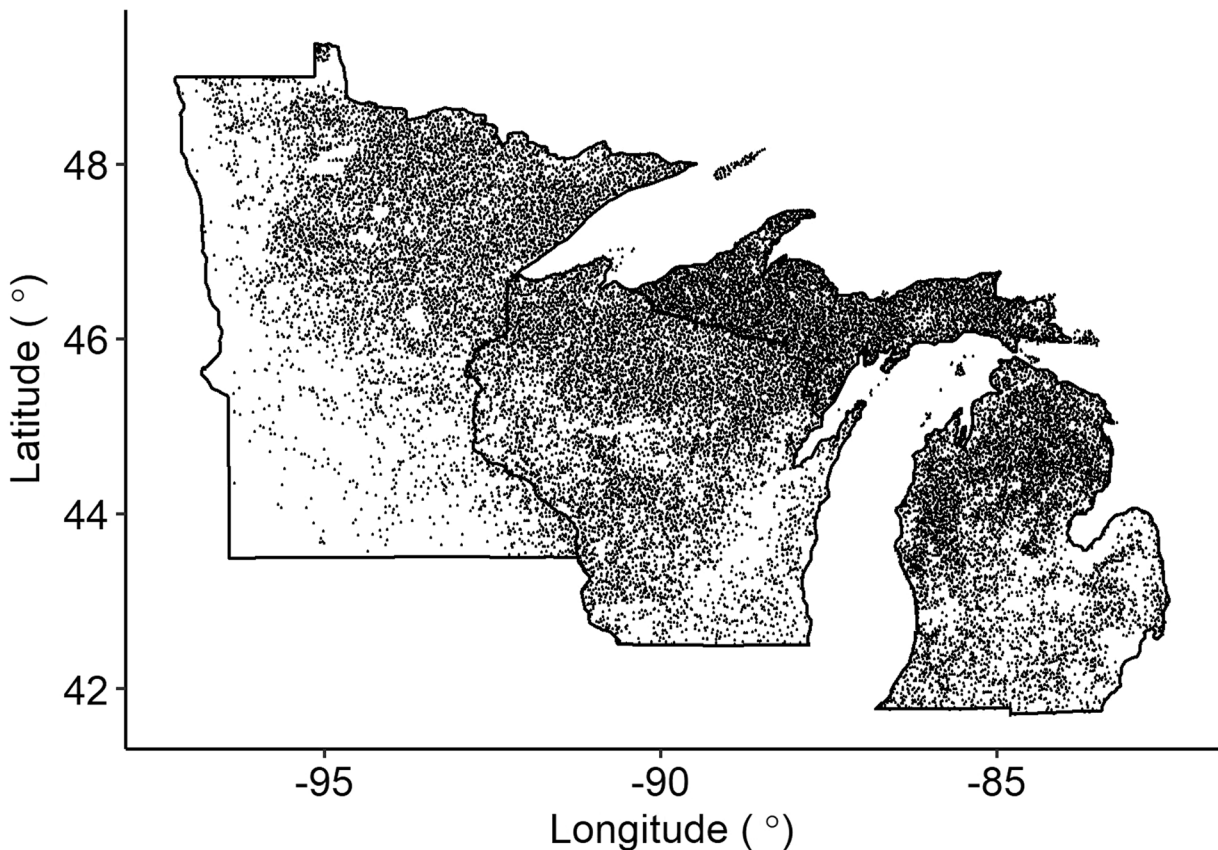


Fig. 1 Approximate locations of forest inventory plots across the US Lake States, 1999–2014

three measurement phases for these plots. The first phase employs remote sensing tools to determine if the land is forested or non-forested, the second phase consists of plot and tree measurements, and the third phase measures a suite of forest health characteristics such as downed woody materials, understory vegetation, soils, lichen, and ozone. For this project, plot, condition, and individual tree measurements collected on phase two plots were used from Minnesota, Michigan, and Wisconsin (<http://apps.fs.fed.us/fiadb-downloads/datamart.html>, download date 29 Oct 2014). To reduce edge bias, only plots with a single forested condition were used in this analysis. A single condition plot was defined as a plot that was fully encompassed by a single forest type, reserved status (i.e., management prohibited or not), ownership group (i.e., federal, state, local government, or private), and regeneration status (i.e., natural or planted stand). Analyses were based on the FIA forest type group level (US Forest Service 2014) and included aspen/birch, elm/ash/cottonwood, maple/beech/birch, oak/hickory, oak/pine, spruce fir, and white/red/jack pine. Only trees

greater than or equal to 12.7 cm in diameter at breast height (DIA) at the time of inventory were analyzed in this study. This size class was analyzed because it represents potential trees for future harvest that have a greater impact on stand stocking and reflects the minimum diameter of the large-tree growth equations in FVS-LS.

Disturbance was defined from the FIA database. If a plot record contained a disturbance code, it indicated the plot experienced a disturbance since the last plot inventory (i.e., within the last 5 years). For a plot to be considered disturbed, the disturbance must equal or exceed one acre (0.40 ha) in size and affect 25% of the trees in the condition (US Forest Service 2014). The data were analyzed to include non-disturbed plots and the six most common disturbance classes (Table 1): animal, disease, fire, insect, weather, and human disturbance. Human disturbance was defined as human-caused damage, other than timber harvesting. Harvesting and silvicultural treatments done by humans was considered a treatment and identified separately (US Forest Service 2014).

Table 1 Number and percent of Forest Inventory and Analysis plots by disturbance type in the US Lake States, 1999 through 2014

Disturbance type	Specific disturbance types	Plots	Percent
Animal	Beaver, porcupine, deer/ungulate, bear, rabbit, domestic animal/livestock	754	1.7%
Disease	Disease damage to understory vegetation and/or trees (including seedlings and saplings)	386	0.9%
Fire	Ground or crown fire	113	0.2%
Human	Any human-caused damage that is not a different disturbance or treatment	466	1.0%
Insect	Insect damage to understory vegetation and/or trees (including seedlings and saplings)	361	0.8%
None	No visible disturbance	42,591	93.9%
Weather	Ice, wind, flooding, drought	614	1.4%

Individual tree diameter increment

Diameter increment equations recently developed by Deo and Froese (2013) and implemented in FVS-LS (Dixon and Keyser 2008) for the Lake States and Central States were used in this analysis. These species-specific equations used tree size and vigor, competition, and site quality variables in a single equation with an intercept and up to ten covariates. The Deo and Froese (2013) equations were developed using permanent sample plots on tribal forestlands from the Bureau of Indian Affairs (collected from 1991 through 2006 in Minnesota and Wisconsin, only) and all forestlands from FIA (collected from 1998 through 2010 in Minnesota, Wisconsin, and Michigan). The Deo and Froese (2013) equations predict 10-year outside bark diameter increment squared (dds) at time $i + 10$. Deo and Froese (2013) use the following predictor variables to determine dds: diameter at breast height (DIA_i ; inches), stand-level quadratic mean diameter (QMD_i ; inches), stand basal area (SBA_i ; $\text{ft}^2 \text{ac}^{-1}$), basal area of larger trees (BAL_i ; $\text{ft}^2 \text{ac}^{-1}$), crown ratio (CR_i ; % live), and site index (SI_i ; average height of dominant trees at 50 years):

$$\begin{aligned} \ln(dds_{i+10}) = & \beta_0 + \beta_1 \left(\frac{1}{DIA_i} \right) + \beta_2 (DIA_i) \\ & + \beta_3 (DIA_i^2) + \beta_4 \left(\frac{DIA_i}{QMD_i} \right) \\ & + \beta_5 \left(\frac{DIA_i^2}{QMD_i} \right) + \beta_6 (SBA_i) \\ & + \beta_7 (BAL_i) + \beta_8 (CR_i) + \beta_9 (CR_i^2) \\ & + \beta_{10} (SI_i) \end{aligned} \quad (1)$$

Species-specific parameter estimates can be obtained from Deo and Froese (2013).

Most trees in the FIA dataset had at least two, but up to four inventory records. Not all plots and trees were remeasured exactly 5 years apart (although 98% of plots were). As growth and yield models typically operate on a 10-year time step in the Lake States and analyses are typically conducted at this scale across the region (e.g., Canavan and Ramm 2000; Pokharel and Froese 2008; Russell et al. 2015), growth observations were standardized to a 10-year interval for comparison with model predictions:

$$\Delta DIA_{10} = \frac{DIA_2 - DIA_1}{YEAR_2 - YEAR_1} * 10 \quad (2)$$

Disturbance records at the beginning of an observed growth cycle (time 1) were used to predict growth using Eq. 1. The data were aligned so that the disturbance measured at time 1 was compared with growth between time 1 and time 2. This ensured that observed growth calculations were obtained from measurements collected shortly after the disturbance (within 5 years) so diameter increment response to disturbance could be analyzed by excluding growth occurring in years prior to a disturbance event.

Bias was calculated for trees in disturbed and non-disturbed plots by subtracting predicted growth (Eq. 1) from observed growth. A negative bias indicated overprediction and a positive bias indicated underprediction. Mean observed and predicted increment, mean bias, root mean square error, and standard deviation of mean bias were calculated. Results were analyzed by disturbance agent and species/disturbance agent groupings. Equivalence tests were conducted comparing observed and predicted 10-year diameter increment using two one-sided tests assuming a null hypothesis of dissimilarity (Wellek 2003; Robinson and Froese 2004). Equivalence tests allow a dissimilarity based on a

specified threshold to permit varied amounts of disagreement between observed and predicted values (Pokharel and Froese 2008). In our case, we analyzed the difference in diameter increment from the observed (as measured from the FIA program) and predicted (as estimated from FVS-LS) values. The magnitude of the region of similarity was specified as 20% of the standard deviation of the difference in observed and predicted increment to allow for some disagreement while still holding the model to strict accuracy standards. We chose this region of similarity because small differences in diameter increment can lead compounding errors that influence stand-level attributes (e.g., a 10% bias in tree diameter may result in a 25% error in stand basal area ([Gertner and Dzialowy 1984]). As the specifications of regions of similarity are subjective, we also calculated the minimum percentage that would have resulted in a successful validation, termed the minimum detectable negligible difference (MDND; Parkhurst 2001). We used the “equivalence” package in R to perform these tests (Robinson 2016).

Results

Approximately 6% of all plots inventoried between 1999 and 2014 that contained trees with a diameter at breast height greater than 12.7 cm experienced one of the six most common forest disturbances ($n = 2694$). Ninety-four percent of these plots were non-disturbed ($n = 42,591$). Animal and weather were the most common disturbances observed in the region (Table 1). The elm/ash/cottonwood forest type group had the highest relative disturbance frequency with 9.5% of plots being disturbed, while the white/red/jack pine forest type group experienced the least amount of disturbance relative to all other forest type groups (3.2% of plots experienced a disturbance). Plots containing multiple disturbance records for a given inventory period were not common and made up only 0.3% of all FIA plot records.

For all species combined, trees on plots experiencing a disturbance had an average observed diameter increment of 2.69 ± 2.34 cm/10 years; (mean \pm standard deviation [$n = 7036$]). Average observed diameter increment for non-disturbed trees was 2.24 ± 2.08 cm/10 years. When compared to predictions using the Deo and Froese (2013) equations, mean bias (observed-predicted) of diameter increment for disturbed trees was 0.30 ± 2.24 cm/10 years, indicating underprediction

of diameter increment in disturbed forests. Compared to trees on non-disturbed plots, the Deo and Froese (2013) equations slightly overpredicted diameter increment (mean bias of -0.08 ± 1.98 cm/10 years). The difference in observed diameter increment between trees on disturbed and non-disturbed plots averaged 0.46 cm/10 years (Fig. 2).

We failed to reject equivalence tests with a null hypothesis of dissimilarity when comparing observed and predicted diameter increment for trees growing in disturbed plots; however, for plots that did not see a disturbance, equivalence tests with a null hypothesis of dissimilarity were rejected. Trees on plots disturbed by animals ($n = 1607$) had the largest mean bias, resulting in underprediction of diameter increment by 0.81 ± 2.64 cm/10 years. The Deo and Froese (2013) equations performed the best for trees on plots with fire disturbance ($n = 367$), underpredicting diameter increment by 0.03 ± 1.85 cm/10 years. This was slightly better than the non-disturbed plots which overpredicted diameter increment by -0.08 ± 1.98 cm/10 years. Only trees on plots disturbed by insects ($n = 751$) had lower observed growth than non-disturbed plots (Fig. 3). Results from equivalence tests indicate that for non-disturbed plots, the Deo and Froese (2013) predictions were equivalent

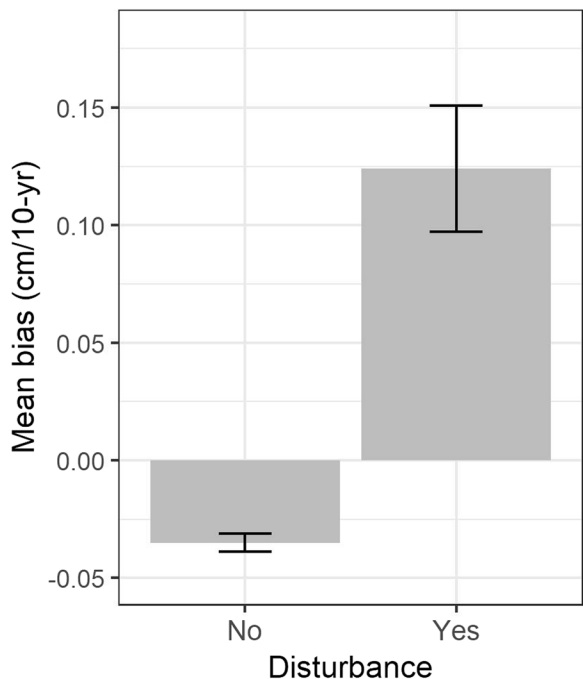


Fig. 2 Mean bias (\pm standard error) of predicted diameter increment based on whether or not the plot was disturbed

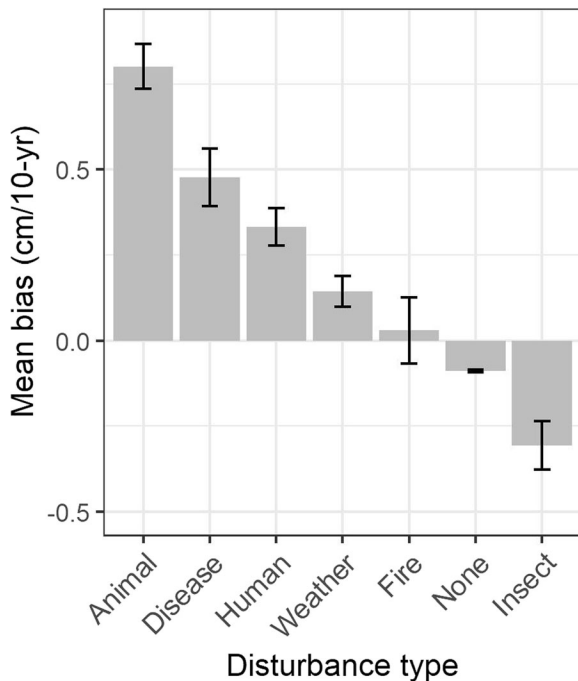


Fig. 3 Mean bias (\pm standard error) of predicted diameter increment by disturbance agent

when compared to observed growth. Equivalence tests were rejected when comparing observed and predicted diameter increment on plots that were disturbed by animals, disease, humans, and insects.

When analyzed by species, the Deo and Froese (2013) predictions displayed the largest mean bias for hardwoods commonly found in the region. American elm (*Ulmus americana* L.) had the highest mean bias for both disturbed and non-disturbed trees, averaging underpredictions of 2.39 ± 3.40 and 1.80 ± 2.97 cm/10 years, respectively. Growth prediction for quaking aspen (*Populus tremuloides* Michx.), a dominant species in the region, performed poorly on disturbed plots with a mean bias of 1.47 ± 2.39 cm/10 years. For five of the 14 hardwood species, the Deo and Froese (2013) equations performed better in the presence of disturbance (Table 2). Equations tended to overpredict diameter increment for northern hardwood species on plots with no disturbance. Balsam poplar (*Populus balsamifera* L.) and red maple (*Acer rubrum* L.) were most successfully modeled by the Deo and Froese (2013) equations on plots lacking disturbance, having a mean bias of 0.05 ± 1.91 and 0.18 ± 1.78 cm/10 years, respectively. For plots experiencing disturbance, only red maple had

observed growth equivalent to those predicted by the Deo and Froese (2013) equations.

For conifer species common to the region, the Deo and Froese (2013) equations performed best when modeling jack pine (*Pinus banksiana* Lamb.) diameter increment, overpredicting growth by -0.15 ± 1.73 cm/10 years in non-disturbed stands and -0.10 ± 1.73 cm/10 years in disturbed stands. The equations also performed well for modeling diameter increment of tamarack (*Larix laricina* [Du Roi] K. Koch) on both disturbed and non-disturbed plots. Equations performed poorly for red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.) by underpredicting diameter increment, especially for trees on plots experiencing disturbance. Northern white-cedar (*Thuja occidentalis* L.) saw large overpredictions for both disturbed and non-disturbed plots, though bias was similar for the two groups, each having a mean bias of 0.10 cm/10 years. Mean bias was higher for trees on disturbed plots for four of the seven conifer species in this study (Table 3). For conifer species in non-disturbed plots, observed diameter increment for jack pine, tamarack, and balsam fir (*Abies balsamea* [L.] Mill) resulted in equivalence to predicted increment. Tamarack was the only species in this study that tested equivalent in the presence of disturbance.

Discussion

While diameter increment equations performed well on average, it is apparent that when applied to individual species, the predictions underestimated or overestimated diameter increment to the extent that equivalence tests failed to validate the model predictions. Furthermore, aside from insects, the equations resulted in substantial underprediction in the presence of disturbance, likely due to the model not accounting for increased light and reduced competition following disturbances. This is of particular concern for managers that administer a range of forest types where disturbance is present, as miscalculated diameters will result in compounding errors when determining stand-level metrics. Other studies have found that former implementations of the FVS-LS growth equations had a tendency to significantly miscalculate basal area as a result of errors in diameter growth (Lacerte et al. 2006; Pokharel and Froese 2008; Russell et al. 2015). Our mean bias values for diameter increment of -0.08 and 0.30 cm/10 years are slightly

Table 2 Average observed 10-year diameter increment (cm), predicted increment, mean bias, and equivalence test results by the primary hardwood species and disturbance status for Forest Inventory and Analysis data collected between 1999 and 2014 in the US Lakes States

Species common name	Species scientific name	Disturbance	<i>n</i>	Mean observed (cm)	Mean predicted (cm)	Mean bias (cm)	SD bias (cm)	Result ^a	MDND (%) ^b
American basswood	<i>Tilia americana</i>	No	7929	2.06	2.34	-0.28	2.10	E	16
		Yes	217	2.92	2.36	0.56	2.71	NE	32
American elm	<i>Ulmus americana</i>	No	4462	4.47	2.65	1.81	2.97	NE	64
		Yes	220	5.06	2.66	2.40	3.40	NE	82
Balsam poplar	<i>Populus balsamifera</i>	No	3182	2.69	2.63	0.06	1.91	E	6
		Yes	104	3.61	2.63	0.99	2.07	NE	64
Big tooth aspen	<i>Populus grandidentata</i>	No	6153	3.53	2.61	0.92	2.14	NE	46
		Yes	111	3.04	2.59	0.45	2.38	NE	36
Black ash	<i>Fraxinus nigra</i>	No	13,862	1.62	2.18	-0.57	1.35	NE	44
		Yes	340	1.77	2.21	-0.44	1.61	NE	37
Black cherry	<i>Prunus serotina</i>	No	4332	2.71	2.34	0.38	2.51	E	18
		Yes	146	2.92	2.40	0.52	2.24	NE	37
Bur oak	<i>Quercus macrocarpa</i>	No	4231	1.87	2.35	-0.48	1.50	NE	35
		Yes	178	2.18	2.32	-0.14	1.58	NE	22
Green ash	<i>Fraxinus pennsylvanica</i>	No	4888	2.75	2.40	0.35	2.10	E	19
		Yes	214	2.95	2.46	0.48	2.17	NE	34
Northern red oak	<i>Quercus rubra</i>	No	5344	3.06	2.57	0.49	2.41	NE	23
		Yes	142	3.60	2.56	1.05	2.70	NE	53
Paper birch	<i>Betula papyrifera</i>	No	14,628	1.56	2.15	-0.59	2.55	NE	25
		Yes	483	1.86	2.21	-0.34	1.60	NE	30
Quaking aspen	<i>Populus tremuloides</i>	No	28,241	3.59	2.64	0.95	2.15	NE	46
		Yes	993	4.13	2.645	1.48	2.39	NE	68
Red maple	<i>Acer rubrum</i>	No	32,670	2.15	2.32	-0.17	1.78	E	11
		Yes	928	2.66	2.33	0.33	2.30	E	20
Sugar maple	<i>Acer saccharum</i>	No	32,592	1.75	2.28	-0.54	1.60	NE	35
		Yes	1102	1.97	2.24	-0.26	1.69	NE	21
Yellow birch	<i>Betula alleghaniensis</i>	No	3691	1.80	2.30	-0.50	1.66	NE	33
		Yes	77	1.70	2.32	-0.63	1.67	NE	57

^aEquivalent (E) or not equivalent (NE)

^bMinimum detectable negligible difference (MDND) required to reject dissimilarity, expressed in percent of standard deviation

lower than what has been observed for similar species in the Lake States using the TWIGS model (e.g., 0.53 to 1.07 cm/10 years for trees ≥ 12.7 cm in diameter; Canavan and Ramm 2000). During model development, species-specific observed versus predicted correlation values were often less than 0.4 (Deo and Froese 2013). This benchmarking exercise is an important early step to better identify future improvements to growth and yield models in the US Lake States.

While the model did perform well in a few specific cases, results suggest that accounting for growth

changes due to weather disturbances is necessary (Fig. 3). Past research has indicated the need to account for climate patterns while attempting to accurately model individual tree growth (Crookston et al. 2010; Trasobares et al. 2016). Other research suggests that accurately representing the temporal change of site characteristics is crucial to predicting the likelihood and severity of disturbances, as well as the response of the vegetation present on the site (Crocker et al. 2016). Similarly, while changing climate regimes may lead to increased forest productivity, these gains may be

Table 3 Average observed 10-year diameter increment, predicted increment, mean bias, and equivalence test results by the primary conifer species and disturbance status for Forest Inventory and Analysis data collected between 1999 and 2014 in the US Lakes States

Species common name	Species scientific name	Disturbance	<i>n</i>	Mean observed (cm)	Mean predicted (cm)	Mean bias (cm)	SD bias (cm)	Result ^a	MDND (%) ^b
Balsam fir	<i>Abies balsamea</i>	No	15,906	2.66	2.41	0.25	1.78	E	16
		Yes	386	3.33	2.43	0.90	2.08	NE	32
Eastern white pine	<i>Pinus strobus</i>	No	5271	3.31	2.58	0.73	2.93	NE	64
		Yes	141	3.39	2.51	0.88	2.89	NE	82
Jack pine	<i>Pinus banksiana</i>	No	7774	2.25	2.41	-0.16	1.72	E	6
		Yes	123	2.30	2.40	-0.10	1.72	NE	64
Northern white-cedar	<i>Thuja occidentalis</i>	No	34,511	1.30	2.31	-1.01	1.25	NE	46
		Yes	500	1.36	2.39	-1.03	1.35	NE	36
Red pine	<i>Pinus resinosa</i>	No	14,681	3.21	2.57	0.64	2.34	NE	44
		Yes	91	3.76	2.64	1.12	3.51	NE	37
Tamarack	<i>Larix laricina</i>	No	11,149	1.69	1.97	-0.27	1.55	E	18
		Yes	193	1.93	1.94	-0.01	1.28	E	37
White spruce	<i>Picea glauca</i>	No	4236	2.95	2.51	0.43	2.35	NE	35
		Yes	60	2.62	2.53	0.10	2.73	NE	22

^aEquivalent (E) or not equivalent (NE)

^bMinimum detectable negligible difference (MDND) required to reject dissimilarity, expressed in percent of standard deviation

negated by increased natural disturbances (Reyer et al. 2017). This provides additional challenge to managers to assess the influence of changing site productivity on forest growth.

The Deo and Froese (2013) diameter increment equations performed well in the presence of some disturbance agents (i.e., weather and fire), but when all disturbance agents were analyzed together, equivalence tests failed to validate the equation, suggesting further model refinement may be necessary to portray diameter increment of residual trees in disturbed forests. Aside from crown ratio, research suggests that additional predictor variables such as crown class (Lessard et al. 2001) and crown defoliation from insects (Russell et al. 2015; Chen et al. 2017) influence diameter increment. Accounting for biotic disturbance agents (e.g., insects and diseases) is extremely important when generating realistic predictions of stand-level growth (Woods and Coates 2013). Accounting for the overestimation of growth due to insect disturbance observed in this study may indicate that 10-year diameter increment needs to be reduced by approximately two thirds (Russell et al. 2015). The overprediction of growth in stands disturbed by insects may be due to low-endemic pests such as the eastern spruce budworm (*Choristoneura fumiferana*

Clemens) that have cyclical outbreaks in the Lake States but do not always result in tree mortality. As an example of animal disturbance, white-tailed deer primarily affect only understory trees and shrubs by browsing seedlings and saplings and preventing recruitment (Cornett et al. 2000). This study analyzed trees larger than 12.7 cm in diameter; hence, plots experiencing animal damage may have resembled non-disturbed plots because the disturbance primarily affected understory trees and shrubs (and not accounted for in large-tree diameter increment models). The underestimation of diameter increment in stands disturbed by animals could be partially explained by additional site resources that are available to overstory trees. Human disturbances would include events like land development (i.e., building houses or cabins), clearing and planting wildlife food plots, and clearing shooting lanes for hunting. It should be noted that human disturbances must have been severe enough to qualify as a disturbance but not change the land use (i.e., the plot remains forestland). The disconnection between condition-level disturbances and tree-level growth could explain why animal disturbance had a large impact on tree diameter increment. Per the FIA definition of disturbance, 25% of the trees in the condition (i.e., plot in this case) must have been

damaged or affected and the area must have been larger than one acre in size. Results presented herein indicate the important role that recording disturbance type can have on refining tree-level growth predictions.

The annual disturbance rate of 0.4% observed in this study (6% of all plot measurements disturbed over 15 years) is lower than other disturbance rates calculated for across the region. Using forest land area that created gaps, Runkle (1982) proposed an annual disturbance rate of 1% for old-growth mesic forests in the eastern USA. Similarly, Frelich and Lorimer (1991) determined natural disturbance rates of 5.7 to 6.9% per decade (0.57 to 0.69% per year) for non-logged forests across western Upper Michigan. These studies quantified disturbance rates by examining the formation of gaps (Runkle 1982) or dendroecological methods (Frelich and Lorimer 1991), and although they examined old-growth conditions that may not be representative of current Lake States forests, their findings provide perspectives toward this study. The lower annual disturbance rates observed for FIA plots are likely due to the FIA disturbance definition which does not capture small gaps as a disturbance agent. The formation of small gaps, which may be defined as those up to 100 m² (0.02 acres) in size (Runkle 1982), may not be large enough to meet the FIA disturbance criteria of affecting 25% of the trees in the condition with an area greater than one acre in size. Other approaches have used FIA data to examine specific agents of mortality to individual trees (e.g., Crocker et al. 2016); however, these methods would not be adaptable to trees that survive a forest disturbance.

There is an immediate and continuing need to benchmark and improve forest growth and yield models for a range of stand conditions. There has been little effort and few research studies evaluating a model's ability to predict tree growth response to biotic and abiotic disturbances (Russell et al. 2015). The Deo and Froese (2013) diameter increment equations were designed for use in the Lake States and Central States using data from stands that may or may not have been subject to a disturbance, yet there have been no studies attempting to quantify or validate the accuracy of the equations. It is important to note that when implementing diameter increment equations into a growth and yield simulator such as FVS, features such as self-calibration, record tripling, transition from small (< 12.7 cm) to large trees (≥ 12.7 cm), and user-specified parameters can alter trends in diameter increment (Crookston and Dixon 2005). In addition, using tree measurements gathered

from FIA plots served well to validate these distance-independent models; however, the spatial dependence of FIA plots that are relatively small in area may be a characteristic important to users of distance-dependent models. To improve model output in disturbed stands, modifications of growth and mortality could be developed for specific agents (e.g., Crookston et al. 1990; Marsden et al. 1993) and time since disturbance could be incorporated into growth models as a covariate. Following model runs, users may implement growth modifiers if the interest lies in a refined estimate of individual tree growth in stands affected by specific disturbance agents. Stand volume is primarily driven by diameter increment in growth and yield models, so improving the model's capacity to precisely and accurately predict diameter increment in the presence (or absence) of disturbance is extremely important for forest managers that seek to implement both short- and long-term silvicultural strategies (Russell et al. 2015).

Conclusions

Disturbances are generally considered to be rare events and can alter the structure, composition, and function of forested ecosystems. However, the impact of disturbances on the growth of residual trees (or those individuals which survive through a disturbance) is not well understood, primarily due to the lack of long-term measurements of individual trees in post-disturbed stands. Understanding the growth response of residual trees is needed to adequately forecast stand volume and composition into the future and to apply appropriate forest management treatments.

While most forest growth and yield models are parameterized with data from forests that have not been disturbed, a disadvantage of using these forecasting tools in disturbed stands is that they will not estimate growth with a high degree of accuracy. In summary, quantifying how commonly used growth and yield models perform in disturbed stands will better depict future forest conditions.

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