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Performance of the Forest Vegetation Simulator in Managed White Spruce Plantations Influenced by Eastern Spruce Budworm in Northern Minnesota

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Silvicultural strategies such as thinning may minimize productivity losses from a variety of forest disturbances, including forest insects. This study analyzed the 10-year postthinning response of stands and individual trees in thinned white spruce (*Picea glauca* [Moench] Voss) plantations in northern Minnesota, USA, with light to moderate defoliation from eastern spruce budworm (*Choristoneura fumiferana* Clemens). Using the Forest Vegetation Simulator, model results suggested overprediction of stand basal area growth and tree diameter increment in these stands. Growth modifiers indicated that trees growing in unthinned stands and with greater defoliation levels (i.e., 20–32%) would need the largest adjustment for diameter increment. Modifiers for height were similarly specified to compensate for the underprediction of height increment in these stands. Thinned stands continued to maintain target live crown ratios in excess of 0.40, suggesting long-term productivity. Results highlight the need for simulation models that represent appropriate responses to stands and trees affected by forest insects and diseases. Ultimately, accurate representations of growth and development in these models that account for influences of biotic disturbance agents are essential under future global change scenarios, particularly as silvicultural strategies are implemented to reduce the impacts of forest health threats and other stressors.

Keywords: silviculture, forest thinning, Forest Vegetation Simulator, *Picea glauca*, *Choristoneura fumiferana*

Disturbances influence forest composition, structure, and functional processes and ultimately result in social and economic consequences (Dale et al. 2001, Turner 2010). Recent surveys suggest that biotic and abiotic disturbances are increasingly affecting the productivity and health of natural and managed forest stands across large areas of North America and elsewhere (Turner 2010, Woodall et al. 2011, Tkacz et al. 2013, Woods and Coates 2013). To minimize the effects of these disturbances, silvicultural options that seek to maintain healthy crowns and thus mitigate growth declines and decrease mortality in vulnerable stands may be implemented. One such strategy for reducing stand vulnerability and susceptibility to forest insects is thinning (Mitchell et al. 1983, Waring and O'Hara 2005).

The eastern spruce budworm (*Choristoneura fumiferana* Clemens; SBW) is a native forest insect of particular concern across the eastern Canadian boreal forest and Laurentian mixed forest province (Seymour 1992, McKinnon et al. 2006, Hennigar and MacLean 2010). Outbreaks of SBW in these forests typically last up to 15 years and occur cyclically every 30–40 years (Royama 1984). However, in the state of Minnesota, SBW activity has been observed annually since 1954, representing an endemic population of nearly 60 years. Recent estimates suggest that SBW defoliation occurred in approximately 55,000 and 33,000 ha of Minnesota's northeastern forests in 2011 and 2012, respectively (Minnesota Department of Natural Resources [MNDNR] 2011, 2012). In total, white spruce plantations comprise >72,000 ha of forestland across the US Lake

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m^2): 1 m^2 = 10.8 ft^2; hectares (ha): 1 ha = 2.47 ac.

States (Michigan, Minnesota, and Wisconsin) (Rauscher 1984, D'Amato et al. 2011). Plantations are routinely managed on 60- to 80-year rotations with a midrotation thinning commonly applied (MNDNR 1994, Wisconsin Department of Natural Resources 2006).

Although spruce species can tolerate repeated defoliations of current-year foliage, the subsequent growth of individual trees is reduced (Piene 2003). For example, just 2 years of defoliation can result in white spruce volume growth reductions of up to 27% over 2 years (Piene 1991). Silviculture can be an integral tool to prevent, mitigate, and restore forest ecosystems threatened by forest insects (Waring and O'Hara 2005). Hence, thinning strategies have been considered to offset and potentially minimize the impact of repeated defoliations through sustaining growth and productivity (as evidenced in balsam fir [*Abies balsamea* L.]) (MacLean and Piene 1995, Bauce 1996).

Previous analyses highlight the importance of incorporating forest health threats into quantifying regional wood supplies (MacLean et al. 2001) and maintaining forest and wood product carbon storage (Kurz et al. 2008, Amiro et al. 2010, Hennigar and MacLean 2010). Modeling impacts of forest health threats at the individual tree level will aid managers in determining appropriate responses to forest insect and disease outbreaks on white spruce (Régnière and You 1991, Magnusson et al. 2005). For example, growth-and-yield simulators have been calibrated to depict changes in stand structure and composition from severe SBW defoliations in New Brunswick (Erdle and MacLean 1999). However, such model evaluations remain unknown for characterizing the low to moderate SBW defoliations that are a common chronic condition throughout many spruce-fir forest types in the US Lake States (e.g., MNDNR 2011, 2012).

Incorporation of insect defoliation scenarios is essential as forest managers evaluate the influence of forest disturbances in simulation models (Crookston et al. 2010). Modifiers to key individual growth equations have been developed that reflect the benefits to growth if thinning is considered (Hann et al. 2003) and for stand conditions with diverse management scenarios (Ray et al. 2009). Given the relatively young age of many white spruce plantations, particularly in Minnesota (MNDNR 2013), little is known on how accurately their dynamics are represented in contemporary growth-and-yield models, especially during extended periods of low- to moderate-level SBW infestations. Applications of models to stand conditions outside of those used for initial model development have often yielded poor performance. Using the Forest Vegetation Simulator (FVS), this was recently demonstrated by diameter increment of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in multiaged stands (Ex and Smith 2014) and for small-diameter trees in the southwestern United States (Petrova et al. 2014).

The overall objective of this study was to assess and refine the performance of the Lake States variant of FVS (FVS-LS) for representing stand and tree dynamics of endemic SBW populations in white spruce plantations 10 years postthinning. The specific objectives of this analysis were to project short-term (10-year) stand (e.g., basal area) and tree dynamics (e.g., diameter and height increment) to determine the ability of FVS-LS to characterize the composition and structure of thinned white spruce plantations with SBW defoliation and to refine FVS-LS model output by applying multipliers to diameter and height increment submodels dependent on thinning regime and past SBW defoliation.

Table 1. Site characteristics for white spruce plantations in northern Minnesota thinned 10 years previously.

Site name	Ownership	Stand age (yr)	Date thinned	Site index (m at 50 yr)
Aitkin County	Private	36	Fall 1999	23
Johnson Landing	Public	48	Winter 2000	15
Larson Lake	Public	42	Winter 2000	12
Power Line	Public	56	Winter 2000	16
Plantation Road	Public	40	Fall 1998	20
Smith Creek	Private	39	Fall 1999	18
Sam Welch's	Public	45	Summer 1999	20
Spruce Alley	Public	36	Summer 2002	20
Taconite Trail	Public	51	Winter 2001	18
Warba	Private	35	Winter 2002	21

Methods

Study Area

Data for this study were collected from 10 white spruce plantations established across northern Minnesota on lands owned and/or managed by MNDNR, the USDA Forest Service, and UPM-Blandin (Table 1) (D'Amato et al. 2011). These plantations were selected to represent the variation in SBW activity and stand ages by targeting stands in which thinning was recently conducted or was scheduled to occur at the initiation of this study. This study was initiated to examine the growth and mortality of white spruce in thinned and unthinned plantations affected by SBW and to determine the role that thinning can play in minimizing the impact of SBW in lieu of more costly alternatives (e.g., insecticides). Plantations ranged in size from 2.4 to 33.6 ha. Unthinned (i.e., reserves) and thinned portions, which were a minimum 1.2 ha in size and separated by at least a 15.2-m unharvested buffer, were established in these plantations. Site index varied across stands (range from 12 to 23 m at 50 years) and initial planting density ranged from 1,482 to 3,212 stems ha^{-1}. Thinning was accomplished through a combination of row and low thinning to a suggested relative density provided by a density management diagram (Saunders and Puettmann 2000). Thinning occurred at ages ranging from 25 to 46 years where, on average, 51% of stand basal area was removed (Table 2) (D'Amato et al. 2011).

Measurements

Three circular measurement plots of 0.016 ha in size (7.3-m radius) were randomly established in both thinned and unthinned portions at each site, except for one site where four plots were established. All sites were measured before thinning with the exception of four sites, where stump measurements were recorded to estimate prethinning tree size and basal area. For these sites, equations predicting tree dbh from stump diameter were developed from all trees on the remaining six sites (using a total of 826 observations). On all sites, measurements were recorded before the growing season and immediately after thinning. This analysis uses measurements from the initial and final measurement periods (years 0 and 10, respectively). The degree of SBW damage, however, was estimated at each site annually through 10 years by an assessment of current-year defoliation (Fettes 1950). Defoliation was recorded by examining the percentage of current year shoots on trees with needles missing in four categories: none (no visible disturbance), low (1–33%), moderate (34–66%), or heavy (67–100%). Hence, SBW was analyzed for each site/thinning combination by averaging the annual defoliation levels observed for the 10-year period (Table 2). To examine trends in defoliation levels, SBW impact was assigned to

Table 2. Stand characteristics for white spruce plantations in northern Minnesota 10 years since thinning in unthinned and thinned portions.

Site name	Portion	n^a	SBW DEFOL (%)	TPH (stems ha^{-1})	BA (m^2 ha^{-1})	QMD (cm)	Dbh (cm)	HT (m)
Aitkin County	UT	3	6.6	1,417 (137)	48.99 (4.91)	20.98 (0.27)	18.9 (0.8)	13.2 (0.7)
	T	3	11.6	729 (75)	36.81 (0.57)	25.55 (1.33)	24.9 (0.8)	15.8 (0.3)
Johnson Landing	UT	3	11.7	979 (104)	38.38 (4.74)	22.30 (0.18)	17.4 (1.2)	13.4 (0.9)
	T	3	6.7	854 (137)	37.29 (3.27)	23.93 (1.95)	21.6 (1.1)	15.5 (0.7)
Larson Lake	UT	4	9.9	1,531 (158)	23.29 (1.53)	14.03 (0.74)	13.6 (0.6)	7.7 (0.6)
	T	4	21.6	594 (90)	15.31 (2.77)	18.26 (1.47)	17.4 (1)	10.7 (0.5)
Power Line	UT	3	5.0	2,208 (150)	49.27 (3.06)	16.91 (0.95)	13.1 (0.5)	9.8 (0.5)
	T	3	5.0	833 (182)	23.38 (4.37)	19.07 (0.97)	18.1 (1.3)	11.9 (1.5)
Plantation Road	UT	3	13.3	1,271 (150)	39.03 (5.77)	19.72 (0.45)	15.5 (0.9)	12 (0.9)
	T	3	5.0	542 (55)	22.66 (1.17)	23.22 (1.03)	22.4 (0.8)	16.9 (0.4)
Smith Creek	UT	3	28.3	1,583 (137)	47.72 (1.16)	19.68 (0.68)	16.2 (0.7)	10 (0.7)
	T	3	31.7	583 (21)	20.50 (2.41)	21.07 (1.13)	20.7 (0.6)	13.7 (0.9)
Sam Welch's	UT	3	6.6	1,083 (91)	42.55 (3.85)	22.35 (0.29)	19.4 (0.9)	12.8 (0.9)
	T	3	3.3	583 (55)	29.20 (1.10)	25.36 (0.80)	24.7 (1)	17.4 (0.4)
Spruce Alley	UT	3	3.3	1,333 (185)	34.82 (5.57)	18.23 (0.93)	21 (0.6)	14.1 (1)
	T	3	0.0	708 (75)	24.13 (2.39)	20.85 (0.43)	21.1 (1.1)	12.9 (1.4)
Taconite Trail	UT	3	0.0	854 (205)	31.37 (2.63)	22.31 (1.83)	21.2 (0.7)	13.9 (0.7)
	T	3	0.0	583 (21)	24.13 (1.50)	22.94 (0.64)	26.5 (1)	16.1 (0.6)
Warba	UT	3	0.0	1,646 (116)	64.20 (3.26)	22.32 (0.36)	15.4 (0.8)	8.7 (0.7)
	T	3	0.0	896 (110)	43.29 (3.24)	25.15 (2.30)	19.6 (1.1)	12.7 (0.6)
All sites	UT	31	8.5	1,395 (77)	41.4 (2.27)	20.0 (0.56)	16.6 (0.3)	11.2 (0.2)
	T	31	8.5	688 (34)	27.3 (1.69)	22.4 (0.59)	21.7 (0.4)	14.4 (0.3)

Data are means (SE). *n*, number of measurement plots within each thinned/unthinned portion; TPH, number of trees per ha; BA, basal area; QMD, quadratic mean diameter; HT, tree height; SBW DEFOL, mean current-year defoliation from SBW over 10 years; UT, unthinned; T, thinned.

one of three defoliation classes: none to very light (0–5%), light (5–20%), and moderate (20–32%). The moderate defoliation class corresponds roughly with cumulative defoliation measures in which SBW impacts are predicted to become substantial (e.g., growth reductions of 20%; Erdle and MacLean 1999). Tree measurements included dbh, total tree height (HT), and live crown ratio. Variables of interest provided by FVS-LS were 10-year basal area increment (ΔBA; stand-level) and ΔDBH and ΔHT (tree-level).

FVS-LS Simulations

FVS-LS (download date Dec. 23, 2014) (Dixon and Keyser 2008), a distance-independent individual tree growth-and-yield model, was used to simulate the development of these stands. The core of the FVS-LS model was originally developed in 1993 from the TWIGS model (Miner et al. 1988) and was reformulated in 2006 to improve model performance (Dixon and Keyser 2008). In brief, the ΔDBH submodel for large trees ($\geq$12.7 cm) in FVS-LS comprises three components: a potential growth equation (Hahn and Leary 1979), a modified growth equation (Holdaway 1984), and an adjustment factor (Holdaway 1985). This potential-modifier approach is similarly used for predicting large tree ΔHT in FVS-LS. First, ΔHT is modeled by estimating a growth effective age using the equations of Carmean et al. (1989) to quantify potential increment. Then ΔHT is reduced using a modifier equation (Dixon and Keyser 2008).

Sample plots, comprising nearly 100% white spruce, were simulated as individual stands (Ray et al. 2009) for unthinned (initial measurement) and thinned portions (measurement occurring immediately after thinning). Short-term projections (1 10-year interval) were carried out using a site-specific estimate of site index for white spruce (Table 1) for the Chippewa National Forest (geographic location code = 903) without record tripling of the tree list (NOTRIPLE); i.e., an appropriate number of trees were available for input into FVS-LS. The initial tree list was specified by using the observed species, dbh, HT, and live crown ratio. Ten-year ΔBA, ΔDBH, and ΔHT were compiled for each tree. These stand and tree attributes were subsequently compared with the observed values measured 10 years after thinning.

SBW Multipliers for FVS-LS

The performance of individual tree increment equations within FVS has been shown to display bias throughout both the US Lake States (e.g., Pokharel and Froese 2008) and Canada (e.g., Lacerte et al. 2004, 2006, Pokharel and Froese 2009). Specifically in our study area, FVS-LS predictions may be improved by incorporating stand treatment and disturbance history in the form of multipliers applied to individual tree increment predictions. Hence, we calculated multipliers (i.e., Figure 1 in Ray et al. 2009) following the FVS-LS simulations to adjust ΔDBH and ΔHT estimates (ΔDBH_{MULT} and ΔHT_{MULT}) for trees of $\geq$12.7 cm, depending on thinning and SBW defoliation level

$$\Delta DBH_{MULT} = \frac{\Delta DBH}{\Delta DBH_{FVS\text{-}LS}} \quad (1)$$

$$\Delta HT_{MULT} = \frac{\Delta HT}{\Delta HT_{FVS\text{-}LS}} \quad (2)$$

where the numerator of the multiplier is the observed 10-year increment and the denominator is the FVS-LS-predicted 10-year increment. Multipliers were averaged for all trees occurring at each level of thinning (i.e., thinned and unthinned) and SBW defoliation level (i.e., 0–5%, 5–20%, and 20–32%). Modified predictions were subsequently made by applying the multipliers to the original estimates produced by FVS-LS.

To assess the performance of FVS-LS with and without SBW multipliers, we conducted equivalence tests comparing observed and predicted values of ΔBA, ΔDBH, and ΔHT using two one-sided tests (Wellek 2003). Equivalence tests are commonly applied in the forest science literature and are advantageous in that they can be used in model validation by assuming a null hypothesis of dissimilarity (Robinson and Froese 2004). Dissimilarity in the equivalence test was specified using a threshold of $\pm$25% (Pokharel and

Table 3. Results of equivalence tests of dissimilarity[a] indicating equivalence (E) or no equivalence (NE) comparing observed values with 10-year predictions from FVS-LS for white spruce plantations in northern Minnesota 10 years postthinning.

				FVS-LS		FVS-LS modified	
Variable[b]	Thinning	SBW DEFOL (%)	n	Mean difference ± SE	Result	Mean difference ± SE	Result
ΔBA ($m^2\ ha^{-1}$)	Unthinned	0–5	9	−4.41 ± 1.25	NE	−3.54 ± 1.15	NE
		5–20	19	−4.57 ± 1.01	NE	−1.62 ± 0.69	NE
		20–32	3	−8.59 ± 1.37	NE	−2.37 ± 0.89	NE
	Thinned	0–5	12	−1.07 ± 0.86	NE	−1.68 ± 0.99	NE
		5–20	12	−0.79 ± 0.71	NE	−1.00 ± 0.73	NE
		20–32	7	−2.01 ± 0.51	NE	−0.49 ± 0.33	NE
	All plots		62	−3.53 ± 0.68	NE	−1.70 ± 0.37	NE
ΔDBH (cm)	Unthinned	0–5	171	−1.44 ± 0.21	NE	−1.22 ± 0.20	NE
		5–20	367	−2.03 ± 0.26	NE	−0.74 ± 0.22	NE
		20–32	69	−1.42 ± 0.12	NE	−0.66 ± 0.11	NE
	Thinned	0–5	77	−0.89 ± 0.40	NE	−1.29 ± 0.42	NE
		5–20	30	−2.66 ± 0.73	NE	−0.94 ± 0.68	NE
		20–32	81	−0.67 ± 0.43	NE	−0.82 ± 0.43	NE
	All trees		795	−1.40 ± 0.10	NE	−0.87 ± 0.09	NE
ΔHT (m)	Unthinned	0–5	171	0.46 ± 0.19	E	−0.65 ± 0.14	E
		5–20	367	−0.48 ± 0.23	E	−0.31 ± 0.17	E
		20–32	69	0.40 ± 0.27	NE	−0.19 ± 0.12	E
	Thinned	0–5	77	0.53 ± 0.14	NE	−0.17 ± 0.19	E
		5–20	30	0.37 ± 0.18	NE	−0.16 ± 0.24	NE
		20–32	81	1.10 ± 0.11	NE	0.64 ± 0.27	E
	All trees		795	0.42 ± 0.07	E	−0.21 ± 0.07	E

[a] Critical threshold was ±25%.
[b] Variables are: 10-year basal area increment (ΔBA); 10-year diameter increment (ΔDBH); 10-year height increment (ΔHT); number of plots (n); mean difference (observed-predicted); mean current-year defoliation from spruce budworm over 10 years (SBW DEFOL).

Froese 2008) to permit a moderate amount of disagreement between observed and predicted values. Root mean square error (RMSE) and bias were also computed to assess improvements in ΔBA, ΔDBH, and ΔHT using the SBW multipliers.

Results

Performance of FVS-LS and Modifications

Ten years after treatment, basal area in thinned and unthinned stands averaged 41.3 ± 2.49 (mean ± SE) and 37.5 ± 2.04 $m^2\ ha^{-1}$, respectively (Table 2). Live crown ratio steadily decreased in unthinned stands during the study period (from 0.43 ± 0.01 at the initial measurement to 0.37 ± 0.01 after 10 years). For thinned stands, mean live crown ratio was 0.46 ± 0.01 after 10 years.

The FVS-LS simulations overpredicted ΔBA after 10 years, particularly in stands affected by greater levels of SBW defoliation (Table 3; Figure 1). The difference in ΔBA (observed − predicted) averaged −3.53 $m^2\ ha^{-1}$ for all stands, primarily due to overprediction of tree ΔDBH. Mean bias ranged from −8.59 $m^2\ ha^{-1}$ in unthinned stands with 20–32% SBW defoliation to −0.79 $m^2\ ha^{-1}$ in thinned stands with 5–20% SBW defoliation. The RMSE was as high as 7.23 $m^2\ ha^{-1}$ in unthinned stands with 0–5% SBW defoliation and as low as 5.92 $m^2\ ha^{-1}$ in thinned stands with 0–5% SBW defoliation. Although equivalence tests with a null hypothesis of dissimilarity and a threshold of ±25% were not rejected in all stands for ΔBA for both FVS-LS and modified FVS-LS predictions, applying ΔDBH multipliers resulted in less bias in the analysis of modified FVS-LS predictions. The difference in ΔBA averaged −1.70 $m^2\ ha^{-1}$ for all stands when FVS-LS multipliers were used, an improvement of 52% compared with that for FVS-LS.

Equivalence tests were rejected in all stands for ΔDBH using FVS-LS and modified predictions. The difference in ΔDBH averaged −1.40 cm for all trees, and mean bias ranged from −2.66 cm in thinned stands with 20–32% SBW defoliation to −0.67 cm in thinned stands with 5–20% SBW defoliation. The RMSE was as high as 4.75 cm in thinned stands with 20–32% SBW defoliation and as low as 2.67 cm in unthinned stands with 5–20% SBW defoliation. Multipliers for ΔDBH predictions provided by FVS-LS were generally the smallest (i.e., <1) for unthinned stands with greater SBW defoliation, ranging from 0.65 to 1.07 (Figure 2). Application of ΔDBH multipliers resulted in less bias than nonmodified FVS-LS predictions. The difference in ΔDBH averaged −0.87 cm for all stands with use of FVS-LS multipliers, an improvement of 38% compared with FVS-LS.

Differences in observed and FVS-LS-predicted ΔHT averaged 0.42 m for all trees, and mean bias ranged from −0.48 m in unthinned stands with 20–32% SBW defoliation to 1.10 m in thinned stands with 5–20% SBW defoliation. The RMSE was as high as 2.62 m in thinned stands with 5–20% SBW defoliation and as low as 1.28 m in thinned stands with 20–32% SBW defoliation. Multipliers for ΔHT predictions provided by FVS-LS were generally >1 (ranging from 0.94 to 1.38) (Figure 2), indicating underprediction of ΔHT for trees in most stand conditions. Applying ΔHT multipliers resulted in less bias than in the original FVS-LS predictions, particularly for thinned stands. Differences in observed and FVS-LS-modified ΔHT averaged −0.21 m for all trees, and equivalence tests were not rejected for most stand conditions.

Discussion

Eastern SBW is the most damaging forest insect across northeastern North America in terms of yield reductions and economic losses (Hardy et al. 1983, Gray 2013). Despite substantial research on SBW and its role in shaping future forest structure with varying economic implications (e.g., MacLean et al. 2001, Hennigar et al. 2011), much of the work has occurred at large spatial scales that consider severe outbreak scenarios. Much less research has focused on the basic stand and tree responses in managed stands that result

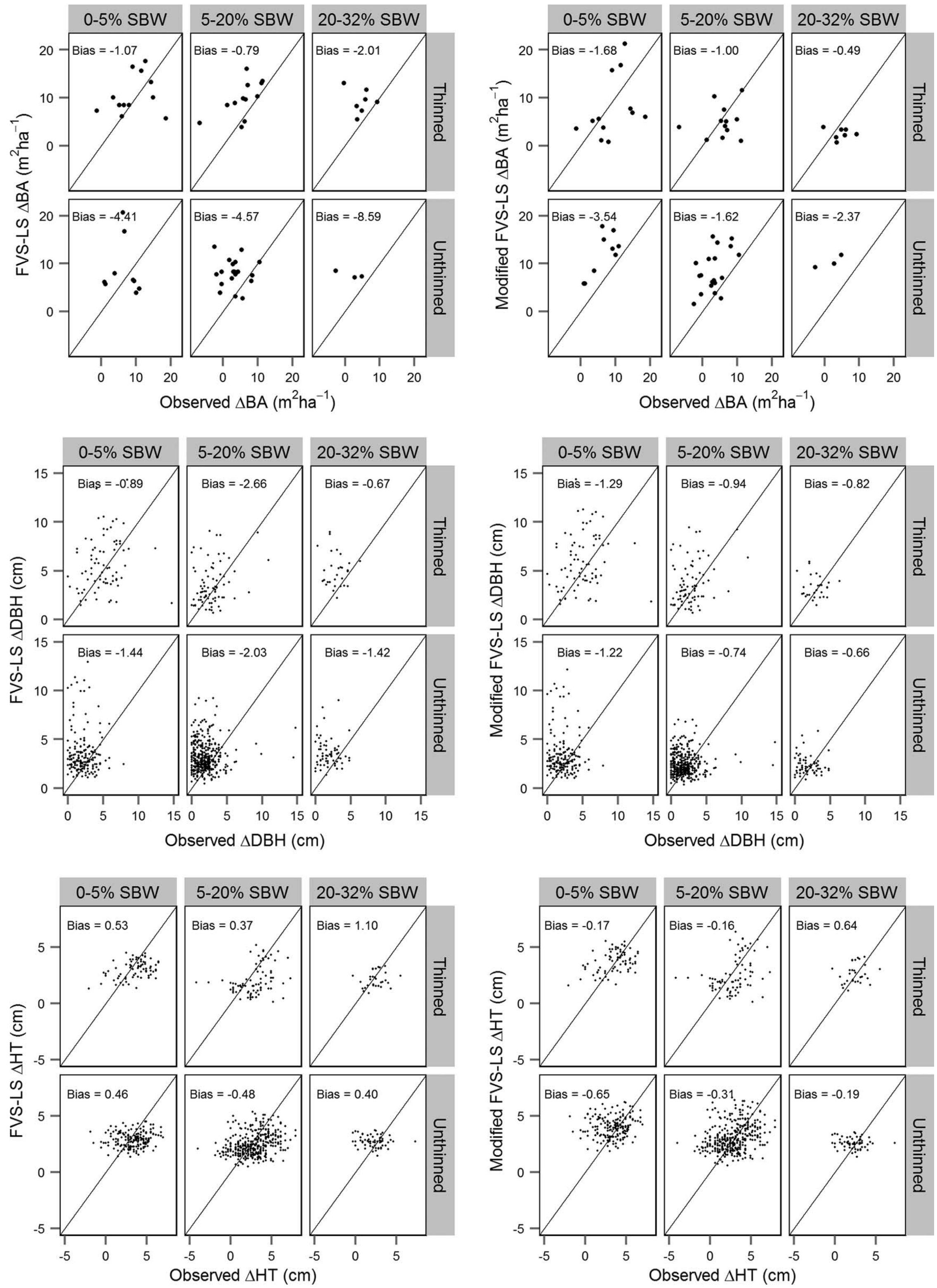

Figure 1. Performance of FVS-LS and modifications for representing plot and tree attributes for white spruce plantations for the corresponding classes of mean current-year defoliation from SBW over the past 10 years in northern Minnesota, with corresponding 1:1 lines.

from light to moderate SBW defoliation and particularly how these processes are represented in simulation models.

The overprediction of stand-level basal area growth by FVS-LS underscores the increasing importance of accounting for the impacts of biotic disturbances to generate realistic productivity expectations from managed stands (Woods and Coates 2013). Understanding the growth-mortality tradeoffs of growth simulators and their relationship with tree characteristics such as crown dimensions will be needed as modelers seek to refine the accuracy and performance of forest growth models.

Mortality is an important growth model component to be considered in future model evaluations because simulations indicate that it is most sensitive to changes in future climate regimes, such as increases in drought severity and duration (Crookston et al. 2010).

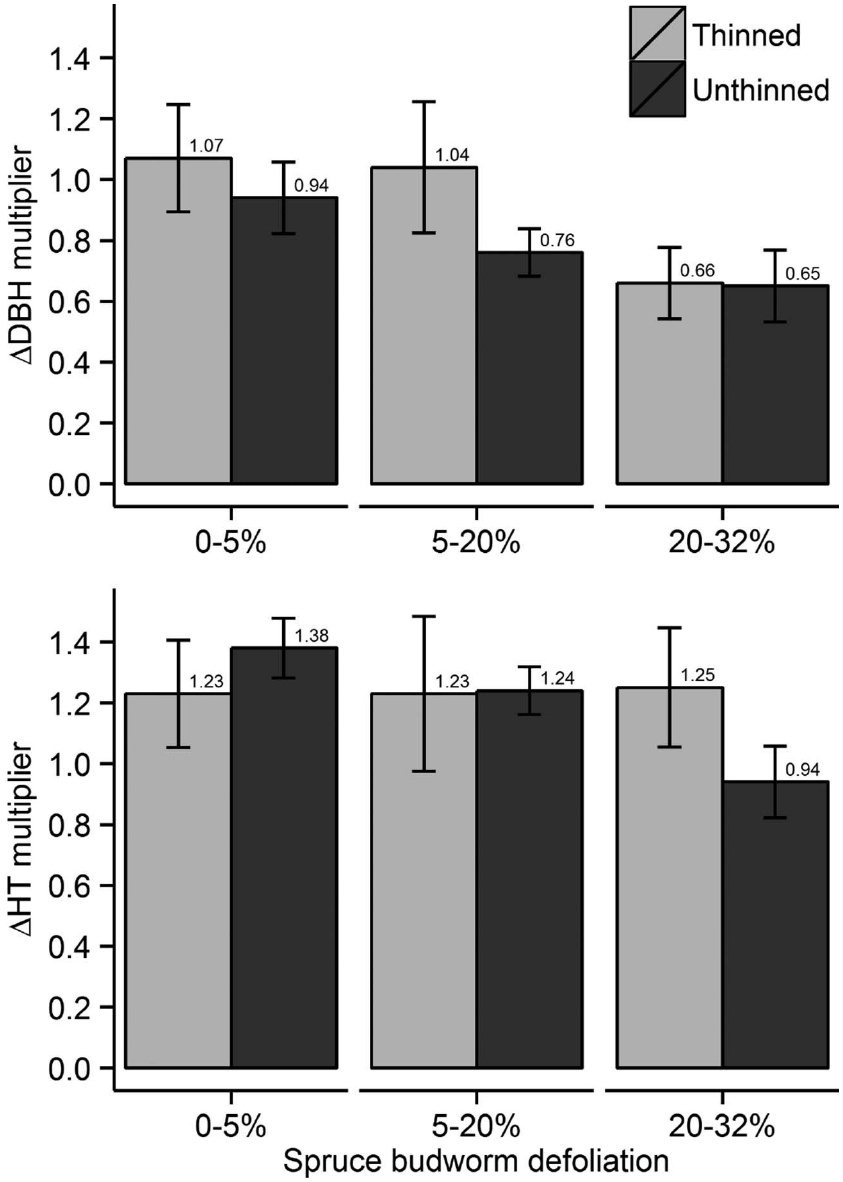

Figure 2. Growth multipliers (Equations 1 and 2) for FVS-LS predictions based on data from white spruce plantations with SBW activity. Multipliers with values of >1 indicate that the model is predicting slower rates of growth than observed in the data. Error bars denote 95% confidence limits.

Further investigations into the dynamics of these plantations are also complicated by separation of mortality components that may be attributed to self-thinning or SBW defoliation. Mortality related to SBW has been observed in stands with similar defoliation patterns (<35%), at least for balsam fir (Pothier and Mailly 2006). Future work might focus on comparing the growth and yield of these low to moderately defoliated stands with those experiencing more severe SBW infestations. However, such study sites for comparison may need to be found outside of this study area, given the large areas of light to moderate defoliation that are currently found throughout Minnesota (MNDNR 2011, 2012). Similarly, it will be critical to monitor deadwood dynamics from SBW-related mortality compared with that for other modes of tree death, given the importance of these processes to understanding forest carbon dynamics in these systems (e.g., insect-killed versus windthrow versus suppression; Taylor and MacLean 2007) with various impacts on disparate forest carbon pools (e.g., aboveground live versus forest floor; Woodall et al. 2013).

In terms of monitoring the health of individual trees, there are perhaps no metrics more effective than crown attributes (Innes 1993, Randolph 2013), given that they serve as surrogates for photosynthetic capacity (Assmann 1970). In managing these white spruce plantations, D'Amato et al. (2011) suggested maintaining live crown ratios in excess of 0.40 to sustain high levels of individual tree growth. Ten years after treatment, thinned stands on average continue to maintain this target. Ultimately, decreased rates of crown recession along with increased ΔDBH indicate that growth continues to be sustained with increased individual tree volume rates in these stands through 10 years postthinning.

The ability of forest growth-and-yield models to accurately depict stand and tree growth responses in areas with insect and disease outbreaks has not been quantified throughout the region to our knowledge. Hence, benchmarking the performance of a model such as FVS-LS is essential because of its widespread use by forest managers and attempts by researchers to calibrate the predictive ability of the model in both the United States (e.g., Pokharel and Froese

2008) and Canada (e.g., Lacerte et al. 2004, 2006, Pokharel and Froese 2009). At the tree level, Pokharel and Froese (2008) observed tremendous overprediction (134%) of 10-year ΔDBH for white spruce using Forest Inventory and Analysis data from Michigan. Our results confirm these findings, given the overprediction of 10-year ΔBA and ΔDBH across all stands (i.e., both thinned and unthinned stands both with and without SBW defoliation). One potential reason for disparities between model predictions and observations is that data used in the original TWIGS model formulation (i.e., the foundation of FVS-LS) probably did not include measurements from stands where disturbances were noted in favor of representing "the average species growth and mortality" (Miner et al. 1988). Furthermore, we could not identify documentation of whether or not white spruce plantations were a component of the original TWIGS model parameterization. Given the improvement in predictions using the ΔDBH and ΔHT multipliers, benchmarking the performance of forest growth simulators while simultaneously refining growth predictions of disturbed stands may help to improve model output used in projection systems for forest management planning. Because the volume growth of large trees is primarily driven by ΔDBH in FVS (Crookston and Dixon 2005), this kind of model benchmarking provides insight into the reliability of predictions for managed stands subject to repeated low-severity disturbances. Simple modifications to the suite of tree mortality functions within FVS could result in improved precision for estimating future number of trees (e.g., Radtke et al. 2012). However, such modifications will require refining existing models with extensive data sets that include a range of conditions of stands, especially those affected by natural disturbances (e.g., insects and diseases).

Incorporating stand and tree responses to insects and diseases in combination with management scenarios such as thinning will be integral as we seek to adopt silvicultural strategies for mitigating the potential effects of forest health threats. Insect and disease addfiles are available in some variants of the FVS model (e.g., Crookston et al. 1990, Marsden et al. 1993); however, few are currently offered for the species and current forest health threats in eastern North America (e.g., SBW). Interested users of FVS-LS may implement the modifiers presented here (i.e., Figure 2) following the model run if the interest lies in a refined estimate of individual tree growth in stands affected by SBW. Specifically for SBW, climate variables that reflect the phenology of the insect may aid in quantifying the susceptibility and subsequent tree and stand response to defoliation, such as the cumulative number of degree-days in April–May (Gray 2013). Such analyses that incorporate disturbances are needed to assess productivity and mortality trends under future global change scenarios (Crookston et al. 2010, Gunn et al. 2014). Detailed studies that monitor individual tree response to such disturbances along with assessment of indicators of forest health at regional and/or national scales will be essential in determining the role that silviculture can play in mitigating the effects from these threats.

Literature Cited

AMIRO, B.D., A.G. BARR, J.G. BARR, T.A. BLACK, R. BRACHO, M. BROWN, J. CHEN, ET AL. 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res. Biogeosci.* 115(G4):G00K02.

ASSMANN, E. 1970. *The principles of forest yield study*. Pergamon Press, Oxford, UK. 506 p.

BAUCE, E. 1996. One and two years impact of commercial thinning on spruce budworm feeding ecology and host tree foliage production and chemistry. *For. Chron.* 72(4):393–398.

CARMEAN, W.H., J.T. HAHN, AND R.D. JACOBS. 1989. *Site index curves for forest tree species in the eastern United States*. USDA For. Serv., Gen. Tech. Rep. NC-128, North Central Experiment Station, St. Paul, MN. 142 p.

CROOKSTON, N.L., J.J. COLBERT, P.W. THOMAS, K.A. SHEEHAN, AND W.P. KEMP. 1990. *User's guide to the western spruce budworm modeling system*. USDA For. Serv., Gen. Tech. Rep. INT-274, Intermountain Research Station, Ogden, UT. 75 p.

CROOKSTON, N.L., AND G.E. DIXON. 2005. The Forest Vegetation Simulator: A review of its applications, structure, and content. *Comput. Electron. Agr.* 49(1):60–80.

CROOKSTON, N.L., G.E. REHFELDT, G.E. DIXON, AND A.R. WEISKITTEL. 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. *For. Ecol. Manage.* 260(7):1198–1211.

D'AMATO, A.W., S.J. TROUMBLY, M.R. SAUNDERS, K.J. PUETTMANN, AND M.A. ALBERS. 2011. Growth and survival of *Picea glauca* following thinning of plantations affected by eastern spruce budworm. *North. J. Appl. For.* 28(2):72–78.

DALE, V.H., L.A. JOYCE, S. MCNULTY, R.P. NEILSON, M.P. AYRES, M.D. FLANNIGAN, P.J. HANSON, ET AL. 2001. Climate change and forest disturbances. *BioScience* 51(9):723–734.

DIXON, G.E., AND C.E. KEYSER. 2008. *Lake States (LS) variant overview—Forest Vegetation Simulator*. Revised July 2013. USDA For. Serv., Int. Rep., Forest Management Service Center, Fort Collins, CO. 44 p.

ERDLE, T.A., AND D.A. MACLEAN. 1999. Stand growth model calibration for use in forest pest impact assessment. *For. Chron.* 75(1):141–152.

EX, S.A., AND F.W. SMITH. 2014. Evaluating Forest Vegetation Simulator performance for trees in multiaged ponderosa pine stands, Black Hills, USA. *For. Sci.* 60(2):214–221.

FETTES, J.J. 1950. *Investigations of sampling techniques for population studies of spruce budworm on balsam fir in Ontario*. Forest Insect Lab., Ann. Tech Rep. 4, Sault Ste. Marie, ON. 209 p.

GRAY, D.R. 2013. The influence of forest composition and climate on outbreak characteristics of the spruce budworm in eastern Canada. *Can. J. For. Res.* 43(12):1181–1195.

GUNN, J.S., M.J. DUCEY, AND A.A. WHITMAN. 2014. Late-successional and old-growth forest carbon temporal dynamics in the Northern Forest (Northeastern USA). *For. Ecol. Manage.* 312:40–46.

HAHN, J.T., AND R.A. LEARY. 1979. Potential diameter growth functions. P. 22–26 in *A generalized forest growth projection system applied to the Lake States region*. USDA For. Serv., Gen. Tech. Rep. NC-49, North Central Forest Experiment Station, St. Paul, MN.

HANN, D.W., D.D. MARSHALL, AND M.L. HANUS. 2003. *Growth rate, 5-year height-growth rate, 5-year mortality rate. and maximum size-density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest*. Res. Cont. 40, Forest Research Laboratory, Oregon State Univ., Corvallis, OR. 83 p.

HARDY, Y., A. LAFOND, AND L. HAMEL. 1983. The epidemiology of the current spruce budworm outbreak in Quebec. *For. Sci.* 29(4):705–725.

HENNIGAR, C.R., AND D.A. MACLEAN. 2010. Spruce budworm and management effects on forest and wood product carbon for an intensively managed forest. *Can. J. For. Res.* 40(9):1736–1750.

HENNIGAR, C.R., J.S. WILSON, D.A. MACLEAN, AND R.G. WAGNER. 2011. Applying a spruce budworm decision support system to Maine: Projecting spruce-fir volume impacts under alternative management and outbreak scenarios. *J. For.* 109(6):332–342.

HOLDAWAY, M.R. 1984. *Modeling the effect of competition on tree diameter growth as applied in STEMS*. USDA For. Serv., Gen. Tech. Rep. NC-94, North Central Forest Experiment Station, St. Paul, MN. 9 p.

Holdaway, M.R. 1985. *Adjusting STEMS growth model for Wisconsin forests.* USDA For. Serv., Res. Pap. NC-267, North Central Forest Experiment Station, St. Paul, MN. 8 p.

Innes, J.L. 1993. *Forest health: Its assessment and status*. CAB International, London, UK. 687 p.

Kurz, W.A., G. Stinson, G.J. Rampley, C.C. Dymond, and E.T. Neilson. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proc. Natl. Acad. Sci. USA* 105(5):1551–1555.

Lacerte, V., G.R. Larocque, M. Woods, W.J. Parton, and M. Penner. 2004. Testing the Lake States variant of FVS (Forest Vegetation Simulator) for the main forest types of northern Ontario. *For. Chron.* 80(4):495–506.

Lacerte, V., G.R. Larocque, M. Woods, W.J. Parton, and M. Penner. 2006. Calibration of the forest vegetation simulator (FVS) model for the main forest species of Ontario, *Can. Ecol. Model.* 199(3):336–349.

MacLean, D.A., T.A. Erdle, E.E. Mackinnon, K.B. Porter, K.P. Beaton, G. Cormier, and M. Budd. 2001. The Spruce Budworm Decision Support System: Forest protection planning to sustain long term wood supply. *Can. J. For. Res.* 31(10):1742–1757.

MacLean, D.A., and H. Piene. 1995. Spatial and temporal patterns of balsam fir mortality in spaced and unspaced stands caused by spruce budworm defoliation. *Can. J. For. Res.* 25(6):902–911.

Magnusson, S., R.I. Alfaro, and P. Boudewyn. 2005. Survival-time analysis of white spruce during spruce budworm defoliation. *Silva Fenn.* 39:177–189.

Marsden, M.A., B.B. Eav, and M.K. Thompson. 1993. *User's guide to the Douglas-fir beetle impact model*. USDA For. Serv., Gen. Tech. Rep. RM-250, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 9 p.

McKinnon, L.M., G.J. Kayahara, and R.G. White. 2006. *Biological framework for commercial thinning even-aged single-species stands of jack pine, white spruce, and black spruce in Ontario*. Ontario Ministry of Natural Resources, Tech. Rep. TR-046, Science and Information Branch, Northeast Science and Information Section, South Porcupine, ON, Canada. 127 p.

Miner, C.L., N.R. Walters, and M.L. Belli. 1988. *A guide to the TWIGS program for the North Central United States*. USDA For. Serv., Gen. Tech. Rep. NC-125, North Central Forest Experiment Station, St. Paul, MN. 105 p.

Minnesota Department of Natural Resources (MNDNR). 1994. *Forest development manual*. Minnesota Department of Natural Resources, Division of Forestry, St. Paul, MN. 164 p.

Minnesota Department of Natural Resources (MNDNR). 2011. *Minnesota forest health annual report.* Division of Forestry, Minnesota Department of Natural Resources, St. Paul, MN. 63 p.

Minnesota Department of Natural Resources (MNDNR). 2012. *Minnesota forest health annual report*. Division of Forestry, Minnesota Department of Natural Resources, St. Paul, MN. 83 p.

Minnesota Department of Natural Resources (MNDNR). 2013. *Minnesota's forest resources 2012*. Minnesota Department of Natural Resources, Division of Forestry, Resource Assessment, Grand Rapids, MN. 68 p.

Mitchell, R.G., R.H. Waring, and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *For. Sci.* 29(1):204–211.

Petrova, M., J.D. Bakker, and E.C. Turnblom. 2014. Ten-year periodic diameter model for uneven-aged ponderosa pine stands in the Southwest reduces long-term error propagation. *For. Sci.* 60(6):1148–1155.

Piene, H. 1991. The sensitivity of young white spruce to spruce budworm defoliation. *North. J. Appl. For.* 8:168–171.

Piene, H. 2003. Growth recovery in young, plantation white spruce following artificial defoliation and pruning. *Can. J. For. Res.* 33(7): 1267–1275.

Pokharel, B., and R.E. Froese. 2008. Evaluating alternative implementations of the Lake States FVS diameter increment model. *For. Ecol. Manage.* 255(5–6):1759–1771.

Pokharel, B., and R.E. Froese. 2009. Representing site productivity in the basal area increment model for FVS-Ontario. *For. Ecol. Manage.* 258(5):657–666.

Pothier, D., and D. Mailly. 2006. Stand level prediction of balsam fir mortality in relation to spruce budworm defoliation. *Can. J. For. Res.* 36(7):1631–1640.

Radtke, P.J., N.D. Herring, D.L. Loftis, and C.E. Keyser. 2012. Evaluating Forest Vegetation Simulator predictions for southern Appalachian upland hardwoods using a modified mortality model. *South. J. Appl. For.* 36(2):61–70.

Randolph, K.C. 2013. Development history and bibliography of the US Forest Service crown-condition indicator for forest health monitoring. *Environ. Monit. Assess.* 185(6):4977–4993.

Rauscher, H.M. 1984. *Growth and yield of white spruce in the Lake States (a literature review).* USDA For. Serv., Res. Pap. NC-253, North Central Experiment Station, St. Paul, MN. 46 p.

Ray, D.G., M.R. Saunders, and R.S. Seymour. 2009. Recent changes to the northeast variant of the Forest Vegetation Simulator and some basic strategies for improving model outputs. *North. J. Appl. For.* 26(1):31–34.

Régnière, J., and M. You. 1991. A simulation model of spruce budworm (Lepidoptera: Tortricidae) feeding on balsam fir and white spruce. *Ecol. Model.* 54(3–4):277–297.

Robinson, A.P., and R.E. Froese. 2004. Model validation using equivalence tests. *Ecol. Model.* 176(3–4):349–358.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana. Ecol. Monogr.* 54(4):429–462.

Saunders, M.R., and K.J. Puettmann. 2000. *A preliminary white spruce density management diagram for the Lake States.* Staff Pap. Ser. No. 145, Department of Forest Resources, Univ. of Minnesota, St. Paul, MN. 15 p.

Seymour, R.S. 1992. The red spruce-balsam fir forest of Maine: Evolution of silvicultural practice in response to stand development patterns and disturbances. P. 217–244 in *The ecology and silviculture of mixed-species forests*, Kelty, M.J., B.C. Larson, and C.D. Oliver (eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Taylor, S.L., and D.A. MacLean. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. *Can. J. For. Res.* 37(4):750–762.

Tkacz, B., K. Riitters, and K.E. Percy. 2013. Forest monitoring methods in the United States and Canada: An overview. P. 49–73 in *Developments in environmental science*, Marco, F., and F. Richard (eds.). Elsevier, New York.

Turner, M. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.

Waring, K.M., and K.L. O'Hara. 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. *For. Ecol. Manage.* 209(1–2): 27–41.

Wellek, S. 2003. *Testing statistical hypotheses of equivalence.* Chapman and Hall, London, UK. 304 p.

Wisconsin Department of Natural Resources. 2006. *Silviculture handbook.* Wisconsin Department of Natural Resources, Madison, WI. 551 p.

Woodall, C.W., M.C. Amacher, W.A. Bechtold, J.W. Coulston, S. Jovan, C.H. Perry, K.C. Randolph, et al. 2011. Status and future of the forest health indicators program of the United States. *Environ. Monit. Assess.* 177(1–4):419–436.

Woodall, C.W., G.M. Domke, K. Riley, C.M. Oswalt, S.J. Crocker, and G.W. Yohe. 2013. Developing a framework for assessing global change risks to forest carbon stocks. *PLoS One* 8(9):e73222.

Woods, A., and K.D. Coates. 2013. Are biotic disturbance agents challenging basic tenets of growth and yield and sustainable forest management? *Forestry* 86(5):543–554.