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

Matthew B. Russell, Anthony W. D’Amato, Michael A. Albers, Christopher W. Woodall, Klaus J. Puettmann, Michael R. Saunders, and Curtis L. VanderSchaaf

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
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, Bauge 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 (Regniere 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.

### 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 of 0.2 (Saunders and Puettmann 2000). Thinnings 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 1. Site characteristics for white spruce plantations in northern Minnesota thinned 10 years previously.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Ownership</th>
<th>Stand age (yr)</th>
<th>Date thinned</th>
<th>Site index (m at 50 yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aitkin County</td>
<td>Private</td>
<td>36</td>
<td>Fall 1999</td>
<td>23</td>
</tr>
<tr>
<td>Johnson Landing</td>
<td>Public</td>
<td>48</td>
<td>Winter 2000</td>
<td>15</td>
</tr>
<tr>
<td>Larson Lake</td>
<td>Public</td>
<td>42</td>
<td>Winter 2000</td>
<td>12</td>
</tr>
<tr>
<td>Power Line</td>
<td>Public</td>
<td>56</td>
<td>Winter 2000</td>
<td>16</td>
</tr>
<tr>
<td>Plantation Road</td>
<td>Public</td>
<td>40</td>
<td>Fall 1998</td>
<td>20</td>
</tr>
<tr>
<td>Smith Creek</td>
<td>Private</td>
<td>39</td>
<td>Fall 1999</td>
<td>18</td>
</tr>
<tr>
<td>Sam Welch’s</td>
<td>Public</td>
<td>45</td>
<td>Summer 1999</td>
<td>20</td>
</tr>
<tr>
<td>Spruce Alley</td>
<td>Public</td>
<td>36</td>
<td>Summer 2002</td>
<td>20</td>
</tr>
<tr>
<td>Taconite Trail</td>
<td>Public</td>
<td>51</td>
<td>Winter 2001</td>
<td>18</td>
</tr>
<tr>
<td>Warba</td>
<td>Private</td>
<td>35</td>
<td>Winter 2002</td>
<td>21</td>
</tr>
</tbody>
</table>
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 (≥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 HT 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 (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 (ΔDBHEMULT and ΔHTMULT) for trees of ≥12.7 cm, depending on thinning and SBW defoliation level

\[
\Delta DBH_{MULT} = \frac{\Delta DBH}{\Delta DBH_{FVS-LS}} \tag{1}
\]

\[
\Delta HT_{MULT} = \frac{\Delta HT}{\Delta HT_{FVS-LS}} \tag{2}
\]

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 ±25% (Pokharel and...
In thinned stands with 20–32% SBW defoliation to applying aged SBW defoliation. Although equivalence tests with a null hypothesis averaging stands, mean live crown ratio was 0.46 (initial measurement to 0.37 (Table 3; Figure 1). The difference in particularly in stands affected by greater levels of SBW defoliation was as high as 7.23 m² ha⁻¹ in thinned stands with 0–5% SBW defoliation and as low as 5.92 m² 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 m² 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 non-modified 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, Hennig 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 from thinned stands with 0–5% SBW defoliation to applying aged SBW defoliation. Although equivalence tests with a null hypothesis averaging stands, mean live crown ratio was 0.46 (initial measurement to 0.37 (Table 3; Figure 1). The difference in particularly in stands affected by greater levels of SBW defoliation was as high as 7.23 m² ha⁻¹ in thinned stands with 0–5% SBW defoliation and as low as 5.92 m² 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 m² ha⁻¹ for all stands when FVS-LS multipliers were used, an improvement of 52% compared with that for FVS-LS.

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## Table 3. Results of equivalence tests of dissimilarity 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Thinning</th>
<th>SBW DEFOL (%)</th>
<th>n</th>
<th>Mean difference ± SE</th>
<th>Result</th>
<th>Mean difference ± SE</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>ΔBA (m² ha⁻¹)</td>
<td>Unthinned</td>
<td>0–5</td>
<td>9</td>
<td>−4.41 ± 1.25</td>
<td>NE</td>
<td>−3.54 ± 1.15</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5–20</td>
<td>19</td>
<td>−5.57 ± 1.01</td>
<td>NE</td>
<td>−1.62 ± 0.69</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20–32</td>
<td>3</td>
<td>−5.59 ± 1.37</td>
<td>NE</td>
<td>−2.37 ± 0.89</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td>Thinned</td>
<td>0–5</td>
<td>12</td>
<td>−1.07 ± 0.86</td>
<td>NE</td>
<td>−1.68 ± 0.99</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5–20</td>
<td>12</td>
<td>−0.79 ± 0.71</td>
<td>NE</td>
<td>−1.00 ± 0.73</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20–32</td>
<td>7</td>
<td>−2.01 ± 0.51</td>
<td>NE</td>
<td>−0.49 ± 0.33</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td>All plots</td>
<td></td>
<td>62</td>
<td>−3.53 ± 0.68</td>
<td>NE</td>
<td>−1.70 ± 0.37</td>
<td>NE</td>
</tr>
<tr>
<td>ΔDBH (cm)</td>
<td>Unthinned</td>
<td>0–5</td>
<td>171</td>
<td>−1.44 ± 0.21</td>
<td>NE</td>
<td>−1.22 ± 0.20</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5–20</td>
<td>367</td>
<td>−2.03 ± 0.26</td>
<td>NE</td>
<td>−0.74 ± 0.22</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20–32</td>
<td>69</td>
<td>−1.42 ± 0.12</td>
<td>NE</td>
<td>−0.66 ± 0.11</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td>Thinned</td>
<td>0–5</td>
<td>77</td>
<td>−0.89 ± 0.40</td>
<td>NE</td>
<td>−1.29 ± 0.42</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5–20</td>
<td>30</td>
<td>−2.66 ± 0.73</td>
<td>NE</td>
<td>−0.94 ± 0.68</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20–32</td>
<td>81</td>
<td>−0.67 ± 0.43</td>
<td>NE</td>
<td>−0.82 ± 0.43</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td>All trees</td>
<td></td>
<td>795</td>
<td>−1.40 ± 0.10</td>
<td>NE</td>
<td>−0.87 ± 0.09</td>
<td>NE</td>
</tr>
<tr>
<td>ΔHT (m)</td>
<td>Unthinned</td>
<td>0–5</td>
<td>171</td>
<td>0.46 ± 0.19</td>
<td>E</td>
<td>−0.65 ± 0.14</td>
<td>E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5–20</td>
<td>367</td>
<td>−0.48 ± 0.23</td>
<td>E</td>
<td>−0.31 ± 0.17</td>
<td>E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20–32</td>
<td>69</td>
<td>0.40 ± 0.27</td>
<td>NE</td>
<td>−0.19 ± 0.12</td>
<td>E</td>
</tr>
<tr>
<td></td>
<td>Thinned</td>
<td>0–5</td>
<td>77</td>
<td>0.53 ± 0.14</td>
<td>NE</td>
<td>−0.17 ± 0.19</td>
<td>E</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5–20</td>
<td>30</td>
<td>0.37 ± 0.18</td>
<td>NE</td>
<td>−0.16 ± 0.24</td>
<td>NE</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20–32</td>
<td>81</td>
<td>1.10 ± 0.11</td>
<td>NE</td>
<td>0.64 ± 0.27</td>
<td>E</td>
</tr>
<tr>
<td></td>
<td>All trees</td>
<td></td>
<td>795</td>
<td>0.42 ± 0.07</td>
<td>E</td>
<td>−0.21 ± 0.07</td>
<td>E</td>
</tr>
</tbody>
</table>

---

*Critical threshold was ±25%.*

*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).*
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 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.
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 \( \Delta DBH \) for white spruce using Forest Inventory and Analysis data from Michigan. Our results confirm these findings, given the overprediction of 10-year \( \Delta B A \) and \( \Delta DBH \) 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 \( \Delta DBH \) and \( \Delta HT \) 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 \( \Delta DBH \) 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 modifications 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**


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