Sugar Maple Decline after Defoliation by Forest Tent Caterpillar

Dustin Wood, Ruth Yanai, Douglas Allen, and Sandra Wilmot

ABSTRACT

Defoliation is a significant stressor of forest stands that may incite decline disease of sugar maple (*Acer saccharum*: Marsh). The recent outbreak (2002–2007) of forest tent caterpillar (FTC; *Malacosoma disstria*: Hübner) in the northeastern United States offered the opportunity to assess the effects of defoliation and site conditions on sugar maple health. We measured 51 North American Maple Project stands in New York and Vermont in the summer of 2007. Dieback ($P = 0.07$) and mortality ($P = 0.04$) were both worse in stands defoliated by FTC. Low growing–season soil moisture during the outbreak, indicated by Palmer's Z-index; cool mean temperature during the outbreak; and concave microrelief were also important predictors of forest damage. We present the results of our multiple regression equations for stand dieback ($R^2 = 0.71$) and mortality ($R^2 = 0.64$) in tables that can be used by forest managers to evaluate the vulnerability of their sugar maple stands to decline after defoliation by FTC.

Keywords: NAMP, dieback, vigor, forest health, vulnerability

The recent outbreak (2002–2007) of forest tent caterpillar (FTC; *Malacosoma disstria* Hubner) has affected millions of acres of northern hardwoods in the northeastern United States and Canada, especially in New York and Vermont. In 2006, about 1.2 million ac were defoliated by FTC in New York, with another 343,000 ac of FTC defoliation in Vermont. The FTC can be particularly damaging to trees, because it is active early in the growing season (Allen 1987).

Sugar maple (*Acer saccharum* Marsh.) is the preferred host of FTC in the Northeast and is one of the most economically and ecologically important trees in the region. Sugar maple is a keystone species of the northern hardwood ecosystem, supports a variety of wildlife, and may reach 300–400 years of age (Godman et al. 1990). Recent Forest Inventory Analysis data indicate that it is also increasing in abundance (Allen 1996). Its strong, lightly colored wood has a variety of structural and aesthetic uses. Sugar maple is also important to the maple syrup industry. A report from the New England Regional Climate Variability and Change Assessment (2001) estimated that 75% of US maple sugar is produced in the Northeast.

Defoliation is a significant stressor of forest stands that has been known to incite decline disease in sugar maple, interacting with predisposing (site, stand, and climate) or contributing (secondary organisms) factors (Manion 1991, Houston 1992). Defoliation reduces the amount of active leaf surface for photosynthesis and subsequent storage of carbohydrate reserves (starches) in roots (Parker 1970, Parker and Houston 1971). Carbohydrate storage is further depleted when trees refoliate within a growing season (Wargo et al. 1972); refoliation is

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Received June 3, 2008; accepted October 14, 2008.

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more likely after early season defoliation (Allen 1987). Defoliation and subsequent refoliation also increase tree susceptibility to invasion by secondary organisms (Wargo 1972).

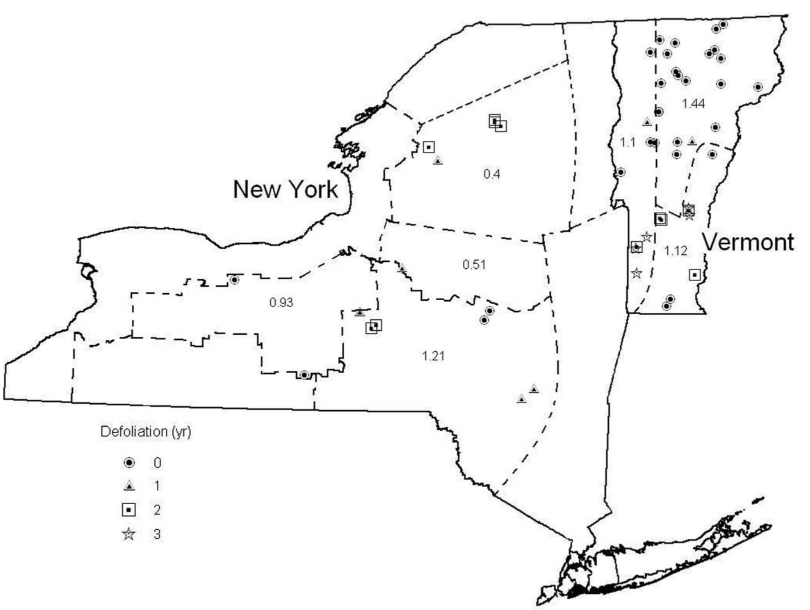

Figure 1. Northern hardwood stands visited in 2007, coded by the number of FTC defoliation events. Dashed lines inside of the state boundaries indicate US climate division boundaries, and the values indicate the mean Palmer Z-index during the outbreak (2002–2006). Higher values indicate greater average soil moisture.

Because of these stress-induced changes, defoliated trees can exhibit crown dieback and loss in vigor and may eventually die. These changes have been referred to as symptoms of decline. In some cases, a single stress such as defoliation may trigger these decline symptoms (Houston 1999, Horsley et al. 2002). The FTC was strongly related to sugar maple decline in Ontario in the mid-1970s (Hendershot and Jones 1989), although there were probably other contributing factors (Gross 1991).

Some sugar maple stands in the Northeast have been less resilient to the recent FTC defoliation than others. A common hypothesis is that the number or severity of defoliations is related to the amount of damage, but stands with similar defoliation histories have differed in their response to this stress. Also, some stands have significant crown dieback and mortality after only one season of FTC defoliation. It is likely that there are some predisposing, inciting, or contributing factors (Manion 1991, Houston 1992) interacting with defoliation in these stands that explain their different responses.

Extreme climatic conditions have been associated with past sugar maple declines (Horsley et al. 2002). Growing season drought and resulting soil moisture deficiency are common inciting and predisposing factors. Declines in the 1950s in Wisconsin (Skilling 1964), in the late 1970s and 1980s in Pennsylvania (Kolb and McCormick 1993), and in the 1980s in New York (Allen 1987) and southern Québec (Payette et al. 1996) were associated with prolonged periods of dry weather.

Stand structure has been an important predisposing factor to sugar maple declines in Wisconsin, Vermont, and New York (Skilling 1964, Bauce and Allen 1991, Allen 1996). In Vermont, mortality and dieback were especially prevalent in pole and small sawtimber–sized sugar maple stands (Teillon et al. 1982). Gross (1991) found that damage was significantly greater on intermediate and suppressed trees in even-aged stands. Similarly, average annual mortality in sugar maple stands over a 9-year period was significantly greater in intermediate and suppressed trees (Allen et al. 1999). Intermediate and suppressed trees on even-aged northern hardwood stands are usually weak trees of poor vigor and poor genetic potential (Nyland 2002).

Stand history and anthropogenic disturbance are important to forest health. Some cases of sugar maple decline occurred on or near the fringes of the natural range for northern hardwoods (i.e., northwestern Pennsylvania and Wiconsin; Nyland 1999, Whitney 1999), where other forest types had previously dominated. A poor adaptation of sugar maple to marginal sites in these cases may have predisposed sugar maple to decline (Houston 1999, Nyland 1999).

Soil chemistry has been an important factor in many of the previous sugar maple declines. In northwestern Pennsylvania, declining sugar maple stands were deficient in important base cations (Ca, Mg, and K), had excesses of antagonistic base cations (Al and Mn), and had experienced heavy insect defoliation (Kolb and McCormick 1993, Wilmot et al. 1996, Long et al. 1997, Horsley et al. 2000, Bailey et al. 2004). Soil chemistry is undoubtedly critical to sugar maple health. We did not include soil chemistry in this study, however, because forest managers commonly do not have this information when they forecast the health of their stands.

The recent outbreak of FTC offered the opportunity to test climatic and site factors and their interactions with FTC defoliation within the natural range of northern hardwoods using stands monitored under the North American Maple Project (NAMP). The NAMP is a regional program established in 1988 that monitored sugar maple health across 10 states and 4 Canadian provinces (Millers et al. 1991). Using new and previously monitored NAMP stands, the objectives of this study were to (1) examine the health and condition of sugar maple stands in New York and Vermont, (2) determine if damage was significantly greater in stands defoliated by FTC, and (3) identify factors that may exacerbate forest damage after defoliation by FTC. Important factors were incorporated into a vulnerability rating index that can be used by forest managers to predict forest damage. Tables such as these can provide managers with a basis for prioritizing management tasks, scheduling and implementing treatments, and preventing timber value loss (Hyland 1983).

Methods

Design. During summer 2007, we visited 18 northern hardwood stands in New York using NAMP field methods (Millers et al. 1991). Ten of the 18 stands were previously monitored under the NAMP but had not been visited since 1998. The other eight stands were newly established. The new stands were sited in areas where extensive damage after FTC defoliation had been reported by foresters. An additional 33 NAMP stands have been measured annually by the Vermont Department of Forests, Parks, and Recreation (VTDFPR; Figure 1).

Table 1. Sugar maple crown condition variables (51 stands) and predictor variables (47 stands) used to assess vulnerability to forest tent caterpillar (FTC) defoliation, and their Pearson correlation coefficient (*R*).

			Correlation (*R*)	
Variable	Units	Explanation	Dieback	Mortality
Dependent variables				
Crown dieback	%	Average tree dieback in each stand	—	—
Mortality	%	2007 Assessment of recent death (not a rate)	—	—
Defoliation	Class	1 (not defoliated); 2 (defoliated)	—	—
Defoliation in 2002	Class	1 (not defoliated); 2 (defoliated)	−0.10	0.16
Defoliation in 2004	Class	1 (not defoliated); 2 (defoliated)	−0.14	−0.15
Defoliation in 2005	Class	1 (not defoliated); 2 (defoliated)	**0.33**	**0.35**
Defoliation in 2006	Class	1 (not defoliated); 2 (defoliated)	**0.26**	**0.36**
Defoliation events	yr	No. of years defoliated by FTC	0.18	0.27
Defoliation severity index	—	Sum of defoliation events × severity (1 = moderate, 2 = heavy)	0.08	0.11
Tree crown position	1–4	1 (dominant); 2 (codominant); 3 (intermediate); 4 (suppressed)	−0.18	−0.15
Quadratic stand dbh	in.		−0.19	−0.12
Basal area/acre all spp.	ft2		−0.22	−0.03
Basal area/acre sugar maple	ft2		−0.22	−0.12
Percent sugar maple	%		−0.01	−0.06
Crown closure	Class	1 (open); 2 (moderate); 3 (full)	−0.24	−0.19
Crown structure	Class	1 (single story); 2 (two story); 3 (multistory)	−0.2	−0.16
Elevation	m		−0.04	−0.01
Slope	%		0.01	0.05
Terrain	Class	1 (flat); 2 (hilly); 3 (mountainous)	0.14	0.16
Predictor variables				
Landform type	Class	1 (headslope); 2 (sideslope); 3 (noseslope); 4 (flat); 5 (ridgetop); 6 (spur ridge); 7 (cove); 8(draw)	0.24	0.23
Slope position	Class	1 (backslope); 2 (footslope); 3 (terrace); 4 (shoulder); 5 (flat); 6 (summit); 7 (floodplain)	0.01	0.05
Topographic position	Class	1 (mid); 2 (upper/lower)	0.07	0.09
Soil drainage	Class	1 (well drained); 2 (poorly drained)	−0.09	0.03
Microrelief	Class	1 (concave); 2 (planar); 3 (convex)	**−0.46**	**−0.51**
Site rockiness	Class	1 (no large rocks); 2 (2–10 large rocks in plot); 3 (>10 large rocks or bedrock exposed)	0.11	0.08
Soil texture	Class	1 (silt/clay); 2 (fine sand); 3 (med. sand); 4 (coarse sand); 5 (fine gravel)	−0.06	−0.12
Site aspect	Class	1 (east); 2 (south); 3 (west); 4 (north)	−0.04	−0.09
Annual mean precipitation	in.		0.09	0.02
Summer (May–September) mean precipitation	in.		0.04	0.01
Outbreak mean precipitation	in.		0.1	0.13
Annual mean temperature	°F		**−0.48**	**−0.38**
Outbreak mean temperature	°F		**−0.34**	−0.22
Annual minimum temperature	°F		**−0.40**	−0.25
Annual maximum temperature	°F		**−0.44**	**−0.44**
Outbreak mean Z-index	—	May—September average during outbreak years (2002–2006)	**−0.53**	**−0.43**

Dieback and mortality values in bold indicate a significant correlation ($\alpha = 0.05$).

The FTC defoliation was the most important recent source of damage to these stands. A few (7%) of the stands in Vermont were affected by the 1998 ice storm, with most trees having less than 10% crown damage (US Forest Service 1998). Bruce spanworm (*Operophtera bruceata* Hulst) defoliated 40% of Vermont plots in 2002 and 2003 and 11% of New York plots in 2006.

Stand defoliation by FTC was recorded by aerial sketch mapping, where the observer threshold for noticeable defoliation is around 25% of leaf area removed. Whenever possible, we relied on the accounts of state foresters who ground-truthed the defoliated areas that were identified by the sketch maps to confirm that the defoliation was accurately located from the air and indeed was caused by FTC. For areas not ground-truthed, we relied on the aerial sketch maps. Defoliation intensity was determined for every stand, on a rating scheme of 1 = moderate (25–50% of trees defoliated) and 2 = severe (>50% of trees defoliated).

Stands chosen for study were in the northern hardwood cover type, where sugar maple represents 50% or more of the stand. The most common overstory associates were American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.) black cherry (*Prunus serotina* Ehrh.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.). None of the stands had been managed or disturbed in the previous 15 years, and most stands were even-aged and greater than 100 years old as estimated by state foresters. As part of the NAMP, a cluster of five 1/10 ac subplots was laid out at each stand, with a 66-ft buffer between subplots and a 330-ft buffer from nonforested areas (Millers et al. 1991). Each subplot had similar species composition and site characteristics.

Dependent Variables. At each stand, we assessed the crown health and condition of an average of 70 sugar maple trees greater than 4 in. dbh, following NAMP protocol (Millers et al. 1991). To assure consistency and accuracy in crown rating, all field crews participated in the VTDFPR annual training in 2007. Crown dieback was estimated

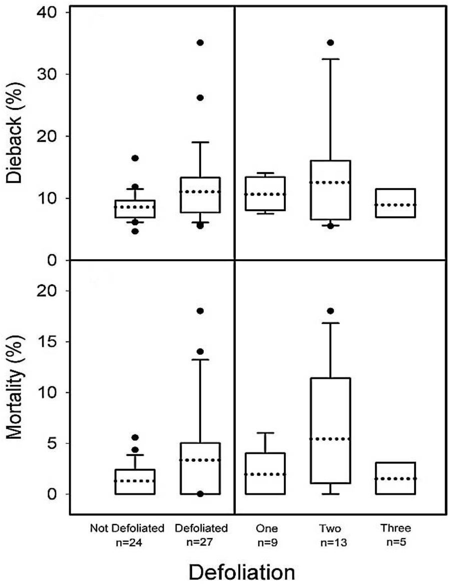

Figure 2. Dieback (P = 0.07) and mortality (P = 0.04) were both greater in defoliated (n = 27) than nondefoliated (n = 24) stands (P = 0.07). Dotted lines of the box plot indicate the mean value. Lines represent the 25th percentile and 75th percentile. Whiskers represent 99% of the sample distribution and outliers are represented by *x*.

from two perpendicular sides of each tree as the percentage of the crown with fine twig mortality on branches less than 4 in. in diameter. In the New York sites, dead sugar maple trees that still had fine twigs were tallied to assess recent mortality. Fine twig loss probably occurs within 2 or 3 years after tree death. Tree mortality in the Vermont sites was assessed annually. To create a measure comparable with the New York sites, we used the sum of mortality from 2005 to 2007.

Predictor Variables. We assessed a suite of tree, stand, and site characteristics at most stands (n = 47; Table 1). For four stands in Vermont, records for site and stand characteristics were missing; these stands were used only for crown health comparisons between defoliated and nondefoliated stands. The tree variables we measured include dbh and crown position. Stand variables include assessments of crown closure and structure. Other stand descriptors such as quadratic stand diameter and basal area were calculated using the tallied tree data. Site variables included assessments of microsite physiography, topography, and soils.

Regional climate variables for each site were obtained from the National Climatic Data Center (National Climatic Data Center 2007). We acquired temperature and precipitation data from the closest meteorological stations to each site, as well as annual means of precipitation and temperature during the FTC outbreak (2002–2006). Some stands were geographically close enough to each other that they shared meteorological stations. We also used Palmer's Z-index, a short-term measure of regional drought (Palmer 1965) to characterize the average growing season (May–September) soil moisture during the FTC outbreak at each stand. As with temperature and precipitation, some of the stands shared the same Z-index.

Data Analysis. Dieback ratings were averaged for all the sugar maple trees in the stand, because the stand was the experimental unit. Mortality in each stand was expressed as a percentage of all trees. Pearson correlation coefficients were used to compare dieback and mortality for all stands (n = 51). We also used t-tests to analyze the difference in means for dieback and mortality between defoliated (n = 27) and nondefoliated (n = 24) stands. Then, with the stands that had the full suite of site information (n = 47), we used Pearson correlation coefficients to determine the relationship between the predictor variables (Table 1) and dieback and mortality.

A multiple regression of the predictor variables was used to identify empirical models for dieback and mortality. We represented FTC defoliation as a variable in the regression, using four different approaches: (1) defoliated or not defoliated during the outbreak (at least once or not at all); (2) four variables describing defoliation in 2002, 2004, 2005, or 2006 (defoliation was not detected at any of the stands in 2003); (3) the number of defoliation events; and (4) the defoliation severity index (DSI). The DSI is the product of the number of years of defoliation times the intensity of those defoliations, on a scale of one to two, as defined previously. The models were chosen by identifying combinations of predictor variables that maximized the model R^2 and minimized the value of Akaike's information criterion (AIC), a measure of the goodness-of-fit of a statistical model. Although the model with the lowest value for AIC is preferred, it does not distinguish the best model from others if the difference in their AIC value is less than or equal to two (Akaike 1974).

We analyzed residuals using the chi-square test for heteroscedasticity (nonconstant variance), which would violate the assumptions of regression (Freund and Littell 2000). To validate each selected model, we used data splitting (Snee 1977). An estimation data set is used to estimate model coefficients, while a prediction data set is used to measure the prediction accuracy, such as the mean absolute error (MAE), mean error (ME), root mean squared error (RMSE), and R^2 of the estimated model and coefficients. In this case, we used a random subset of 20 stands as the prediction data set and the remaining 27 stands were used as the estimation data set. We compared the model prediction accuracy between the estimation and prediction data sets to assess the accuracy of each full model.

Models were then incorporated into two vulnerability rating tables modeled after a rating table by Hyland (1983), which classified southern pine stands into vulnerability classes from very high to very low after southern pine beetle infestation. Based on our best regression models with five predictor variables, we classified stands as high,

Table 2. Correlation matrix for forest tent caterpillar defoliation.

	2002 Defoliation	2004 Defoliation	2005 Defoliation	2006 Defoliation	Defoliation Severity Index	Defoliation (0, 1)
2004 Defoliation	−0.07					
	0.65					
2005 Defoliation	−0.09	0.46				
	0.5	***<0.001***				
2006 Defoliation	0.16	0.32	0.35			
	0.26	***0.02***	***0.01***			
Defoliation severity index	−0.02	0.82	0.68	0.68		
	0.88	***<0.001***	***<0.001***	***<0.001***		
Defoliation (1 = no; 2 = yes)	0.13	0.44	0.64	0.82	0.77	
	0.35	***<0.001***	***<0.001***	***<0.001***	***<0.001***	
Defoliation events	0.14	0.69	0.73	0.8	0.9	0.87
	0.34	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***

Most of the defoliation variables are significantly correlated (P-values are in italic, significant P-values are in bold).

Table 3. Significant predictor variables included in the sugar maple dieback and mortality multiple regression models.

Model and Candidates	R^2	AIC	Chi-square
Dieback			
2006 Defoliation; microrelief; outbreak mean temperature; outbreak mean Z-index; defoliation events	0.71	108	$P = 0.26$
2006 Defoliation; microrelief; outbreak mean temperature; outbreak mean Z-index; DSI	0.71	109.2	
2006 Defoliation; 2004 defoliation; microrelief, outbreak mean temperature; outbreak mean Z-index	0.68	112.7	
2006 Defoliation; 2005 defoliation; microrelief; outbreak mean temperature; outbreak mean Z-index	0.68	113.8	
Crown structure; microrelief; outbreak mean temperature; outbreak mean Z-index; outbreak mean precipitation	0.66	115.9	
Mortality			
2006 Defoliation; microrelief; outbreak mean temperature; outbreak mean Z-index; defoliation severity index	0.64	89.5	$P = 0.08$
2006 Defoliation; 2004 defoliation; microrelief, outbreak mean temperature; outbreak mean Z-index	0.62	91	
2006 Defoliation; microrelief; outbreak mean temperature; outbreak mean Z-index; defoliation events	0.6	94.2	
2006 Defoliation; tree crown position; microrelief; outbreak mean temperature; outbreak mean Z-index;	0.6	94.4	
2004 Defoliation; microrelief; outbreak mean temperature; outbreak mean Z-index; defoliation events	0.59	94.6	

The candidates are arranged by their Akaike's information criterion values; the top candidate for each model was chosen for the vulnerability rating tables.

medium, or low in vulnerability to dieback and mortality.

Results

Defoliation by FTC. Twenty-seven of the 51 stands in New York and Vermont had been defoliated at least once by FTC. Several stands in St. Lawrence County, New York, and Windsor and Rutland Counties in Vermont were defoliated twice, and a few stands in these areas were defoliated three times. Most of the stands that were defoliated more than once were defoliated in consecutive years.

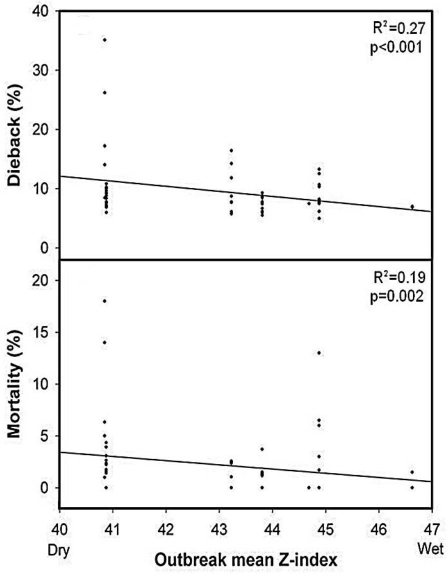

Figure 3. Relationships between outbreak mean Z-index and sugar maple dieback and mortality. Stands were healthier in wetter sites.

Defoliated versus Nondefoliated Stands. Dieback (percent of sugar maple crown dieback averaged by stand) across all stands was low (9.9 ± 5.2%), but 15 of the 51 stands exhibited more than 10% dieback. Eleven of the 15 stands with more than 10% dieback were defoliated during the outbreak. Dieback was 2.6% greater in defoliated stands than in nondefoliated stands ($P = 0.07$; Figure 2a). Dieback increased by about 2% up to 2 years duration, but in stands defoliated for 3 years ($n = 5$), dieback was only slightly higher than in nondefoliated stands (Figure 2a).

Mortality (recently dead sugar maple trees as a percentage of all sugar maple trees) across all stands averaged 2.3 ± 3.8%. Three stands had more than 10% mortality; all three were defoliated during the outbreak. Mortality was significantly ($P = 0.04$) higher in defoliated stands than in nondefoliated stands (Figure 2b). Mortality was highest in stands defoliated twice (5%), but, surprisingly, was the same for stands defoliated three times compared with nondefoliated stands.

The Pearson correlation coefficient was significant between dieback and mortality ($P < 0.001$; $r = 0.77$). However, the relationship between these variables was evident only when all stands (defoliated and nondefoliated) were included in the analysis. In nondefoliated stands, the correlation was not significant ($r = 0.43$). Dieback and mortality are not interchangeable indicators of damage but describe different aspects of stand health.

Site, Stand, and Tree Relationships with Dieback and Mortality. Defoliation can be represented in several ways, not all of them independent. Most of the variables used to represent defoliation were significantly correlated with one another (Table 2). Two of the correlations were above $r = 0.85$. Defoliation (at least once) during the outbreak was highly correlated with defoliation duration ($r = 0.87$), which is not surprising, because nondefoliated stands have a duration of zero. Defoliation duration was highly correlated with the DSI ($r = 0.90$), which increases with additional years of defoliation. Correlations between years of defoliation (2002 and 2004–2006) were not as strong; mathematically, these variables are independent, although stands defoliated during an outbreak are likely to be defoliated again.

Many predictor variables were significantly correlated with both dieback and mortality (Table 1). Specifically, stands with low soil moisture, cooler temperatures, and recent defoliation by FTC were likely to have high dieback and mortality (Table 1). Stands that had poor site drainage (concave microrelief) or that were defoliated in 2005 also had significantly higher dieback and mortality (Table 1). The significant correlation with 2005 defoliation (in addition to the significant correlation with 2006 defoliation, described previously) relates to the fact that 5 of the 16 stands defoliated in 2005 were not defoliated in 2006. This finding suggests that stands that were defoliated in 2005 still showed damage (dieback and mortality) when we measured them in 2006.

Empirical Models for Dieback and Mortality. Many significant predictor variables were identified in the regression models describing dieback and mortality (Table 3). Most candidate models had two common variables: outbreak mean Z-index, which describes drought (Table 1; Figure 3), and 2006 defoliation. Microrelief (Figure 4), outbreak mean temperature, defoliation duration, and DSI were also commonly significant.

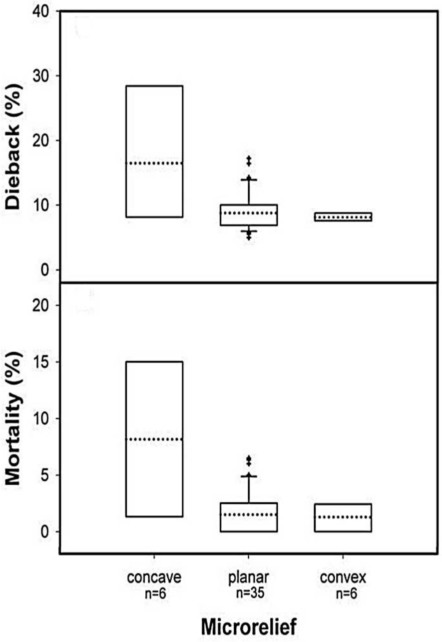

Figure 4. Relationships between site microrelief and sugar maple dieback and mortality. Stands were healthier on convex microrelief.

The superior regression models were easier to identify for mortality than for dieback, because the R^2 and AIC values clearly showed their superior statistical power (Table 3). The two best dieback regression models had the same R^2 and did not differ by more than two in their AIC values, implying that they explained almost the same amount of information in their predictions.

Two defoliation variables appeared in the best candidate models for dieback and mortality (Table 3). These variables had a significant, but not high, correlation with each other. The addition of the second variable improved the variation explained by 8% for dieback and 9% for mortality. More highly correlated variables do not appear as predictors in a single model, because they are not likely to explain much more variation in damage among stands.

Model Validation and Vulnerability Rating. The chi-square test for heteroscedasticity for the best dieback and mortality models (Table 3) showed that the residuals had constant variance, although the residuals for mortality approached heteroscedasticity ($P = 0.08$). A nonnormal distribution of mortality is not surprising because many stands had zero mortality (defined by the number of recently dead sugar maple on the plot).

Data splitting of the best candidate models for dieback and mortality revealed that the estimation data set accurately depicted the model coefficients (Table 4). The MAE and ME of the dieback prediction data set showed that the predictions (MAE) were accurate to within 3%; the positive value for the ME indicates that the predictions were overestimated more than underestimated. The RMSE for dieback was within 4%, although the full model with all stands had an RMSE of 3%, as would be expected with a larger data set. Mortality predictions were accurate to 3% as well (Table 4). The RMSE and MAE values were both within 3.2%, and the ME indicates that the predictions were slightly overestimated.

Table 4. Accuracy of the prediction data set ($n = 20$) using coefficients from the estimation data set ($n = 27$), for the best models of sugar maple dieback and mortality.

Model	R^2	RMSE	MAE	ME
Dieback	0.64	3.93	2.99	0.66
Mortality	0.46	3.22	2.18	0.31

The rating tables for dieback (Table 5) and mortality (Table 6) rate stands for their vulnerability to decline. The tables present a range of conditions for a typical northern hardwood stand. Individual relationships between a predictor variable and a dependent variable are not depicted in these tables, because the coefficients of each predictor variable in the regression model depend on what the other variables in the model can explain. The relationship between individual predictor variables and damage variables should be made based on the correlation coefficients (Table 1).

Discussion

Defoliation was a powerful predictor of mortality in northern Minnesota (Churchill et al. 1964), dieback in Ontario (Gross 1991), and dieback and mortality in New York (Bauce and Allen 1991, Wink and Allen 2007) and may be sufficient to cause decline by itself (Houston 1999). We found that forest damage (dieback and mortality) was significantly higher in stands defoliated by FTC compared with nondefoliated stands (Figure 2). Defoliation was the most important predictor of damage in our vulnerability models (Table 3).

Drought is an important predictor of damage, and there are several ways of representing it. The Z-index we obtained for our stands more accurately reflects short-term regional conditions than other drought measures, but it could not be assessed independently for each stand (Table 1). Similarly, Drohan et al. (2002) found that the Palmer drought severity index (a similar measure to the Z-index that better reflects long-term drought) was not a significant predictor of decline in northwestern Pennsylvania, because their stands did not have independent soil moisture data.

In our study, low soil moisture during the growing season (Palmer's Z-index) was the second most important factor in predicting forest damage. Although there were no prolonged, regionwide droughts during the outbreak, drought would likely exacerbate damage. Drought in combination with defoliation was especially devastating to maple sugar bushes in New York in the early 1980s (Allen 1987) and stands in southern Québec (Payette et al. 1996) and Pennsylvania (Horsley et al. 2000) in the late 1980s and early 1990s. The biochemical changes in sugar maple caused by drought are similar to the changes caused by insect defoliation (Parker 1970), and the combination of these stress factors may leave trees exceptionally vulnerable to decline (Houston 1999).

Site microrelief was also an important predictor of damage after FTC defoliation in our models. The healthiest sugar maple trees were on sites with convex microrelief, which are likely well drained. In contrast, Auchmoody (1987) suggested that northern hardwood site quality is worst on convex microrelief, because soils tend to be shallower and rockier; concave sites accumulate more nutrients. Other landscape variables, such as slope position and landform position, were not significant in our models, although sugar maple decline in the Allegheny plateau is limited to upper landscape positions (Horsley et al. 2002).

Mean annual temperature during the FTC outbreak was important in our models. Specifically, dieback and mortality were higher in stands with colder temperatures (measured at the nearest meteorological station). Several factors may be linked with lower mean annual temperatures, including late-spring frost, which may cause defoliation and mortality (Horsley et al. 2002). Both the monthly and the mean annual temperatures were above normal for New York and Vermont during the outbreak, but May 2005 was an exceptionally cold month, with temperatures at least 9°F below normal. At the three sites in the Adirondacks with the highest sugar maple mortality, the average

Table 5. 2006 defoliation. The vulnerability rating table for sugar maple dieback, as depicted by the equation: dieback = 91.2 + 6.8 (2006 defoliation) − 10.2 (forest tent caterpillar outbreak mean Z-index) − 3.8 (microrelief) − 1.5 (outbreak mean temperature) − 2.6 (defoliation events).

	Microrelief								
	Concave			Planar			Convex		
	Annual temperature (°F) during outbreak (2002–06)								
Vulnerability of dieback in sugar maple stands	39–41	42–44	45–47	39–41	42–44	45–47	39–41	42–44	45–47
Z-index and No. of defoliation events									
Defoliated									
Dry, Z = 0.35–0.74									
1	High	High	High	High	High	High	High	High	High
2	High	High	High	High	High	High	High	High	High
3	High	High	High	High	High	High	High	High	Medium
Mid, Z = 0.75–1.14									
1	High	High	High	High	High	High	High	High	High
2	High	High	High	High	High	High	High	High	Medium
3	High	High	High	High	High	Medium	High	Medium	Medium
Moist, Z = 1.15–1.40									
1	High	High	High	High	High	Medium	High	High	Medium
2	High	High	High	High	High	Medium	High	Medium	Medium
3	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
Not Defoliated									
Dry, Z = 0.35–0.74									
0	High	High	High	High	High	High	High	Medium	Medium
1	High	High	High	High	High	High	High	Medium	Medium
2	High	High	High	High	High	Medium	High	Medium	Medium
3	High	High	High	High	High	Medium	High	Medium	Medium
Mid, Z = 0.75–1.14									
0	High	High	High	High	High	High	High	Medium	Medium
1	High	High	High	High	High	Medium	High	Medium	Medium
2	High	High	Medium	High	High	Medium	High	Medium	Low
3	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
Moist, Z = 1.15–1.40									
0	High	High	High	High	High	Medium	High	Medium	Medium
1	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
2	High	High	Medium	High	Medium	Low	Medium	Medium	Low
3	High	Medium	Medium	Medium	Medium	Low	Medium	Low	Low

R^2 = 0.71. Rating (damage): low (≤7% dieback); medium (7–15% dieback); high (>15% dieback).

daily low temperature in May is 39°F (National Oceanic and Atmospheric Administration 2002). In addition, April 2005 was a particularly warm month, with temperatures 4.5–6°F above normal; in the absence of snowpack, root freezing during an unusually cold May could be a source of stress. Several stands in New York and Vermont also experienced drought in May, June, and July of the same year. A study by Auclair et al. (1996) found that dieback was correlated with drought stress (low soil moisture), but only after forests were affected by root freezing events. Similarly, root freezing in combination with defoliation preceded a major sugar maple decline in southern Québec in the early 1980s (Hendershot and Jones 1989). Detailed, onsite climatic accounts for each stand throughout an outbreak, including measures of soil moisture, are needed to test these hypotheses.

It was no surprise that defoliation measured in 2006 was a very significant variable in the models. The assessments of dieback and mortality that we used from 2007 are one-time measurements of the stand's response to predisposing conditions and stress, so it could be expected that the most recent defoliation would be most important. But mortality may represent stand health over a relatively long period of time (Hallett et al. 2006), and other stressors may have affected the stands in the years before measurement. In contrast, dieback is a short-term stand health assessment (Hallett et al. 2006). Our measurements of dieback in 2007 probably most strongly reflect a response to defoliation in 2006. Dieback in response to earlier defoliation events is no longer visible after branches recover or die and drop off. Gross (1991) found that sugar maple trees with less than 40% dieback were able to recover within 2 years. Similarly, Allen et al. (1995) showed that dominant and codominant sugar maples with as much as 35% crown dieback recovered to less than 15% within a single year. Other indicators of physiological condition such as leaf development may also return to normal within 2 years (Churchill et al. 1964).

Although this study was able to explain many important factors involved in tree decline after defoliation, additional measurements may be needed to explain why the five stands that were defoliated three times showed less dieback and mortality than stands defoliated fewer times. These stands may be especially resilient to defoliation because of other factors not measured in this study, such as soil chemistry.

Dieback is commonly reported as the percentage of trees with high dieback (at least 15% of the crown). Using that metric, our stands had an average of 10.1% dieback. This is high compared with previous results from NAMP stands. From 1988 to 1994, stands across the region averaged less than 7% dieback, except during a pear thrips outbreak in 1988, when average dieback approached 8% (Allen et al. 1995). In our analysis of forest vulnerability, we analyzed sugar maple dieback as the average dieback

Table 6. 2006 defoliation. The vulnerability rating table for sugar maple mortality, as depicted by the equation: mortality = 48.6 + 4.28 (2006 defoliation) − 5.4 (outbreak mean Z-index) − 3.2 (microrelief) − 0.8 (outbreak mean temperature) − 1.0 defoliation severity index.

	Microrelief								
	Concave			Planar			Convex		
	Annual temperature (°F) during outbreak (2002–2006)								
Mortality in sugar maple stands	39–41	42–44	45–47	39–41	42–44	45–47	39–41	42–44	45–47
Z-index and defoliation severity index									
Defoliated									
Dry, Z = 0.35–0.74									
1	High	High	High	High	High	High	High	High	Medium
2	High	High	High	High	High	Medium	High	Medium	Medium
3	High	High	High	High	High	Medium	High	Medium	Medium
4	High	High	High	High	High	Medium	Medium	Medium	Low
5	High	High	High	High	Medium	Medium	Medium	Medium	Low
6	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
Mid, Z = 0.75–1.14									
1	High	High	High	High	High	Medium	High	Medium	Medium
2	High	High	High	High	High	Medium	Medium	Medium	Low
3	High	High	High	High	Medium	Medium	Medium	Medium	Low
4	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
5	High	High	Medium	Medium	Medium	Medium	Medium	Low	Low
6	High	High	Medium	Medium	Medium	Low	Medium	Low	Low
Moist, Z = 1.15–1.40									
1	High	High	High	High	Medium	Medium	Medium	Medium	Low
2	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
3	High	High	Medium	Medium	Medium	Low	Medium	Low	Low
4	High	Medium	Medium	Medium	Medium	Low	Medium	Low	Low
5	High	Medium	Medium	Medium	Medium	Low	Low	Low	Low
6	Medium	Medium	Medium	Medium	Low	Low	Low	Low	Low
Not defoliated									
Dry, Z = 0.35–0.74									
0	High	High	High	High	Medium	Medium	Medium	Medium	Low
1	High	High	Medium	High	Medium	Medium	Medium	Medium	Low
2	High	High	Medium	High	Medium	Medium	Medium	Low	Low
3	High	High	Medium	Medium	Medium	Low	Medium	Low	Low
4	High	Medium	Medium	Medium	Medium	Low	Medium	Low	Low
5	High	Medium	Medium	Medium	Medium	Low	Low	Low	Low
6	Medium	Medium	Low	Medium	Low	Low	Low	Low	Low
Mid, Z = 0.75–1.14									
0	High	High	Medium	High	Medium	Medium	Medium	Low	Low
1	High	High	Medium	Medium	Medium	Low	Medium	Low	Low
2	High	Medium	Medium	Medium	Medium	Low	Medium	Low	Low
3	High	Medium	Medium	Medium	Medium	Low	Low	Low	Low
4	Medium	Medium	Low	Medium	Low	Low	Low	Low	Low
5	Medium	Medium	Low	Medium	Low	Low	Low	Low	Low
6	Medium	Medium	Low	Low	Low	Low	Low	Low	Low
Moist, Z = 1.15–1.40									
0	High	Medium	Medium	Medium	Medium	Low	Medium	Low	Low
1	High	Medium	Medium	Medium	Low	Low	Low	Low	Low
2	Medium	Medium	Low	Medium	Low	Low	Low	Low	Low
3	Medium	Medium	Low	Medium	Low	Low	Low	Low	Low
4	Medium	Medium	Low	Low	Low	Low	Low	Low	Low
5	Medium	Low	Low	Low	Low	Low	Low	Low	Low
6	Medium	Low	Low	Low	Low	Low	Low	Low	Low

R^2 = 0.64. Rating (damage): low (≤5% mortality); medium (5–10% mortality); high (>10% mortality).

of all sugar maple trees in the stand, because this measure better represents the health of the stand.

Mortality in our stands accounted for 2.3% of all sugar maple trees, with nondefoliated stands averaging 1.2% (Figure 2). Healthy stands have an annual mortality rate of 0.5 to 1% (Kelley and Eav 1987, Kelley et al. 1992); our rates should be about twice the annual mortality rate (in Vermont, we used 2 years of annual mortality, but in New York, which had not been monitored annually, we tallied recently dead trees based on the presence of fine twigs). The average of our defoliated stands (3.2%) thus seems higher than expected in healthy stands. Our three worst stands had an average mortality of 15%, clearly an abnormal rate.

Manion (1991) and Houston (1992) described forest decline as a disease complex that involves a set of predisposing, inciting, and/or contributing factors that exacerbate the progressive deterioration of tree health, ultimately leading to mortality. Based on our results and the firsthand reports of local foresters, many of the stands we visited are declining. We have assembled suites of factors that explain the decline symptoms to a reasonable degree in our stands and they identify FTC defoliation as a main inciting factor for decline. Additional research could improve the predictive power of our vulnerability models. Some factors worthy of investigation include the role of *Armillaria*, a root-rot fungus, in tree mortality after damage; land-use history, including silviculture and logging; and soil factors such as acidity and nutrient availability.

Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19(6):716–723.

Allen, D.C. 1987. Insects, declines, and general health of northern hardwoods: Issues relevant to good forest management. P. 252–285 in *Proc. of Silvi. Symp. On Managing northern hardwoods*, SUNY Coll. Environ. Sci. and For., Syracuse, NY, June 23–25, 1986, SUNY-ESF Fac., Nyland, R.D. (ed.). For. Misc. Publ. 13 (ESF 87-002).

Allen, D.C. 1996. Using FIA data to assess forest health. P. 82–90. in *Proc. of conf. of The empire forest—Changes and challenges*, Nov. 13–15, 1995, SUNY Coll. Environ. Sci. and For., Syracuse, NY.

Allen, D.C., A.W. Molloy, R.R. Cooke, D. Lachance, and C. Barnett. 1995. *North American Maple Project, seven year report*. US For. Ser., Northeast State and Private For. Stn. 57 p.

Allen, D.C., A.W. Molloy, R.R. Cooke, and B.A. Pendrel. 1999. A ten-year regional assessment of sugar maple mortality. P. 27–45 in *Proc. of an Int. Symp. on Sugar maple ecology and health*, June 2–4, 1998, Warren, PA, Horsley, S.B., and R.P. Long (eds.). US For. Serv. GTR NE-261.

Auchmoody, L.R. 1987. Soil-site relations for northern hardwoods. P. 14–24 in *Proc. of Silvi. Symp. On Managing northern hardwoods*, June 23–25, 1986, SUNY Coll. Environ. Sci. and For., Syracuse, NY, Nyland, R.D. (ed.). SUNY-ESF Fac. For. Misc. Publ. 13 (ESF 87-002).

Auclair, A.N.D., J.T. Lill, and C. Revenga. 1996. The role of climate variability and global warming in the dieback of northern hardwoods. *Water Air Soil Pollut.* 91:163–186.

Bailey, S.B., S.B. Horsley, R.P. Long, and R.A. Hallett. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau. *Soil Sci. Soc. Am. J.* 68:243–252.

Bauce, E., and D.C. Allen. 1991. Etiology of a sugar maple decline. *Can. J. For. Res.* 21(5): 686–693.

Churchill, G.B., H.H. John, D. P. Duncan, and A.C. Hodson. 1964. Long-term effects of defoliation on aspen by the forest tent caterpillar. *Ecology* 45(3):630–633.

Drohan, P.J., S.L. Stout, and G.W. Petersen. 2002. Sugar maple (*Acer saccharum* Marsh.) decline during 1979–1989 in northern Pennsylvania. *For. Ecol. Manag.* 170:1–17.

Freund, R.J., and R.C. Littell. 2000. *SAS system for regression*, 3rd Ed. SAS Publishing, Cary, NC.

Godman, R.M., H.W. Yawney, and C.H. Tubbs. 1990. *Acer saccharum* Marsh. Sugar maple. P. 78–91 in *Silvics of North America, Vol. 2., Hardwoods*, Burns, R.M., and B.H. Honkala (eds.). US For. Serv. Agric. Handbk. 250.

Gross, H.L. 1991. Dieback and growth loss of sugar maple associated with defoliation by the forest tent caterpillar. *For. Chron.* 67(1):33–42.

Hallett, R.A., S.W. Bailey, S.B. Horsley, and R.P. Long. 2006. Influence of nutrition and stress on sugar maple at a regional scale. *Can. J. For. Res.* 36:2235–2246.

Hendershot, W.H., and A.R.C. Jones. 1989. Maple decline in Quebec: A discussion of possible causes and the use of fertilizers to limit damage. *For. Chron.* 65:280–287.

Horsley, S.B., R.P. Long, S.W. Bailey, R.A. Hallett, and T.J. Hall. 2000. Factors associated with the decline disease of sugar maple on the Allegheny plateau. *Can. J. For. Res.* 30(9):1365–1378.

Horsley, S.B., R.P. Long, S.W. Bailey, R.A. Hallett, and P.M. Wargo. 2002. Health of eastern North American sugar maple forests and factors affecting decline. *North. J. Appl. For.* 19(1):34–44.

Houston, D.R. 1992. A host-saprogen model for forest dieback-decline diseases. P. 3–25 in *Forest decline concepts*, Manion, P.D., and D. Lachance (eds.). APS Press, New York.

Houston, D.R. 1999. History of sugar maple decline. P. 19–26 in *Proc. of an Int. Symp. On Sugar maple ecology and health*, Warren, PA, June 2–4, 1998, Horsley, S.B., and R.P. Long (eds.). US For. Serv. GTR NE-261.

Hyland, J.R. 1983. Hazard rating-a strategy for battle against beetle. *Ala. Treasur. For.* 2(1): 26–28.

Kelley, R.S., and B. Eav. 1987. *Vermont hardwood tree health survey 1986.* Vermont Department of Forests, Parks and Recreation, Waterbury, VT. 30 p.

Kelley, R.S., L. Smith, and S.M. Cox. 1992. *Vermont hardwood tree health in 1991 compared to 1986.* Vermont Department of Forests, Parks and Recreation, Waterbury, VT. 25 p.

Kolb, T.E., and L.H. McCormick. 1993. Etiology of sugar maple decline in four Pennsylvania stands. *Can. J. For. Res.* 23(11):2395–2402.

Long, R.P., S.B. Horsley, and P.R. Lilja. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. *Can. J. For. Res.* 27:1560–1573.

Manion, P.D. 1991. *Tree disease concepts*. Prentice-Hall, Englewood Cliffs, NJ. 399 p.

Millers, I., D. Lachance, W.G. Burkman, and D. C. Allen. 1991. *North American sugar maple decline project: Organization and field methods.* US For. Serv., Gen. Tech. Rep. NE-154, Northeastern Forest Exp. Stn., Radnor, PA. 30 p.

National Climatic Data Center (NCDC). 2007. *Annual climatological summaries for years 2002–2006.* Available online at www.ncdc.noaa.gov/oa/ncdc.html; last accessed June 29, 2007.

National Oceanic and Atmospheric Administration (NOAA). 2002. *Climatography of the United States No. 81.* Monthly station normals of temperature, precipitation, and heating and cooling degree days 1971–2000. NOAA National Climatic Data Center, Asheville, NC. 36 p.

New England Regional Assessment Group. 2001. *The Assessment of the Potential Consequences of Climate Variability Report*. US Global Change Research Program. Univ. of New Hampshire. 96 p.

Nyland, R.D. 1999. Sugar maple: Its characteristics and potentials. P. 1–13 in *Proc. of an Int. Symp. on Sugar maple ecology and health*, Warren, PA, June 2–4, 1998, Horsley, S.B., and R.P. Long (eds.). US For. Serv. GTR NE-261.

Nyland, R. D. 2002 *Silviculture: Concepts and applications*, 2 Ed. McGraw-Hill, New York. 704 p.

Palmer, W.C. 1965. *Meteorological drought*. Res. Pap. 45, US Weather Bureau, NOAA Library and Information Services Division, Washington, DC. 58 p.

Parker, J. 1970. *Effects of defoliation and drought on root food reserves in sugar maple seedlings.* US For. Serv. Res. Pap. NE-169, Northeastern Forest Exp. Stn., Upper Darby, PA. 8 p.

Parker, J., and D.R. Houston. 1971. Effects of repeated defoliation on root and root collar extractives of sugar maple trees. *For. Sci.* 17: 91–95.

Payette, S., M.J. Fortin, and C. Morneau. 1996. The recent sugar maple decline in southern Québec: Probable causes deduced from tree rings. *Can. J. For. Res.* 26(6):1069–1078.

Skilling, D.D. 1964. *Part 5. Ecological factors associated with maple blight.* Univ. of Wisconsin Res. Bull. 250. Univ. of Wisconsin, Madison, WI. 15 p.

Snee, R.D. 1977. Validation of regression models: Methods and examples. *Technometrics* 19(4):415–428.

Teillon, H.B., B.S. Burns, and R.S. Kelley. 1982. *Forest insect and disease conditions in Vermont*. Vermont Department of Forestry, Parks, and Recreation, Montpelier, VT. 22 p.

US Forest Service. 1998. *Status report, Ice Storm 1998.* US For. Serv., Northeast State and Private Forestry Station, Durham, NH. 36 p.

Wargo, P.M. 1972. Defoliation-induced chemical changes in sugar maple roots stimulate growth of *Armillaria mellea. Phytopathology* 62: 1278–1283.

Wargo, P.M., Parker J., and Houston, D.R. 1972. Starch content in roots of defoliated sugar maple. *For. Sci.* 18:203–204.

Wilmot, T.R., D.S. Ellsworth, and M.T. Tyree. 1996. Base cation fertilization and liming effects on nutrition and growth of Vermont sugar maple stands. *For. Ecol. Manag.* 84:1123–1134.

Whitney, G.G. 1999. Sugar maple: Abundance and site relationships in the pre- and post-settlement forest. P. 14–18 in *Proc. of an Int. Symp. on Sugar Maple ecology and health*, Warren, PA, June 2–4, 1998, Horsley, S.B., and R.P. Long (eds.). US For. Serv. GTR NE-261.

Wink, R.A., and D.C. Allen. 2007. The combined effects of defoliation and modified timber stand improvement on hardwoods in the tug hill region of New York. *North. J. Appl. For.* 24(1):43–51.