OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

The Role of Forest Tent Caterpillar Defoliations and Partial Harvest in the Decline and Death of Sugar Maple

HENRIK HARTMANN* and CHRISTIAN MESSIER

Département des Sciences biologiques, Centre d'Étude de la Forêt (CEF), Université du Québec à Montréal, C.P.8888, succursale Centre-ville, Montréal, Québec, Canada H3C 3P8

• *Background and Aims* Natural and anthropogenic disturbances can act as stresses on tree vigour. According to Manion's conceptual model of tree disease, the initial vigour of trees decreases as a result of predisposing factors that render these trees more vulnerable to severe inciting stresses, stresses that can then cause final vigour decline and subsequent tree death. This tree disease model was tested in sugar maple (*Acer saccharum*) by assessing the roles of natural and anthropogenic disturbances in tree decline and death.
• *Methods* Radial growth data from 377 sugar maple trees that had undergone both defoliations by insects and partial harvest were used to estimate longitudinal survival probabilities as a proxy for tree vigour. Radial growth rates and survival probabilities were compared among trees subjected to different levels of above- and below-ground disturbances, between periods of defoliation and harvest, and between live and dead trees.
• *Key Results* Manion's tree disease model correctly accounts for vigour decline and tree death in sugar maple; tree growth and vigour were negatively affected by a first defoliation, predisposing these trees to death later during the study period due to a second insect outbreak that initiated a final vigour decline. This decline was accelerated by the partial harvest disturbance in 1993. Even the most severe anthropogenic disturbances from partial harvest did not cause, unlike insect defoliation, any growth or vigour declines in live sugar maple.
• *Conclusions* Natural disturbances acted as predisposing and inciting stresses in tree sugar maple decline and death. Anthropogenic disturbances from a partial harvest at worst accelerated a decline in trees that were already weakened by predisposing and inciting stresses (i.e. repeated insect defoliations). Favourable climatic conditions just before and after the partial harvest may have alleviated possible negative effects on growth resulting from harvesting.

Key words: Manion, tree disease model, disturbance, *Acer saccharum*, tree mortality, tree vigour.

INTRODUCTION

Tree decline is a gradual process that can take several years or even decades before tree death occurs (Pedersen, 1998*b*). Manion (1981) developed a conceptual model of tree disease that relates initial tree condition (i.e. vigour) to stress vulnerability and decline. According to this model, long-lasting predisposing factors such as soil compaction, genetic potential, or air pollutants reduce initial tree vigour and predispose affected trees, now less resistant against further disturbance, to more severe inciting stresses such as defoliating insects or drought. These stresses cause sharp and irreversible vigour declines. While contributing stresses, such as secondary pathogens or unfavourable climatic conditions, may accelerate this process and act as the 'coup de grâce' for declining trees, their role in decline may not be essential (Muller-Dumbois, 1987; Pedersen, 1998*b*).

Tree vigour is a somewhat arbitrary concept describing a tree's genetic capacity to survive subsequent stresses. It is often used synonymously with tree vitality, the status of tree health at any one time in response to environmental stresses (Shigo, 1986). Generally, tree vigour is estimated in the field based on visual criteria, such as crown condition, stem characteristics or pathological symptoms (Ouellet and Zarnovican, 1988; Millers *et al.*, 1991; Ontario Ministry of Natural Resources, 2004). More empirically, radial growth

rates can be interpreted as an integrative measure of tree physiological condition (Gehrig, 2004), carbon balance (Givnish, 1988) and tree vigour (Dobbertin, 2005). Tree-ring chronologies can then be used to estimate survival probabilities for the entire lifespan of trees (Bigler and Bugmann, 2004). Because longitudinal survival probabilities are estimated for the entire period covered by tree-ring chronology, they can be a valuable tool to evaluate the impact of past stresses on tree vigour (Hartmann *et al.*, 2008).

Stress factors in sugar maple decline, an ecologically and economically important tree species in north-eastern North America (Godman *et al.*, 1990), can result from natural disturbances such as droughts or insect defoliations (Allen *et al.*, 1992; Parshall, 1995; Kolb and McCormick, 1993; Payette *et al.*, 1996). Sugar maple is among the principal hosts of the forest tent caterpillar (FTC, *Malacosoma distria*; Fitzgerald, 1995). Repeated heavy defoliations over two or more years can cause a severe reduction in radial growth, branch and twig mortality, and weaken trees by exhausting carbon reserves from repeated refoliation (Wargo *et al.*, 1972; Wargo, 1981). This process makes trees more susceptible to subsequent stresses such as droughts (Renaud and Mauffette, 1991; Canadian Forest Service, 2001) or pathogens (Wargo and Houston, 1974).

While the impact of natural stresses on sugar maple growth and survival has been well studied (e.g. Gross, 1991; Payette *et al.*, 1996; Duchesne *et al.*, 2002, 2003), studies on the impacts of partial harvest disturbance have

* For correspondence. E-mail henrik333@sympatico.ca

investigated only growth release or tree physiology (e.g. Singer and Lorimer, 1997; Jones and Thomas, 2004, 2007) and not considered tree survival or vigour.

Residual trees near skid trails may suffer from a combination of soil compaction and root damage (Kozlowski, 1999; Rönnberg, 2000; Ouimet *et al.*, 2005; Nadezhdina *et al.*, 2006) that reduce water availability and uptake, respectively (Starsev and NcNabb, 2001; Komatsu *et al.*, 2007). Sudden canopy opening, on the other hand, may cause severe post-disturbance water stress due to increased water demand from fully exposed leaves (Bréda *et al.*, 1995). These stresses affect vigour of residual trees and may be important stress-inciting factors that cause growth reductions and mortality (Murphy, 1983; Helms and Hipkin, 1986).

The aim of the study was to investigate the influence of insect defoliation and harvest disturbance on radial growth and tree vigour of sugar maple (*Acer saccharum*) by asking the following questions: (*a*) Is observed tree decline driven, as predicted by Manion (1981), by an interaction of predisposing, inciting and contributing stresses, and can these stresses be associated with growth declines and decreases in survival probability? (*b*) How is growth and vigour of residual trees affected by disturbances from partial harvests? (*c*) Do FTC defoliations and harvest disturbances have a similar impact on tree radial growth and vigour?

MATERIALS AND METHODS

Study region

This study focused on sugar maple (*Acer saccharum* Marsh.) trees in forests near Temiscaming in western Quebec, Canada (46°43′N, 79°04′W). The forests of this region are part of the western sugar maple-yellow birch bioclimatic domain (Robitaille and Saucier, 1998). Mean annual temperatures range from 2·5 to 5·0 °C, the growing season spans 170–180 d, and mean annual precipitation is 800–1000 mm, with snowfall comprising roughly 25 % of total precipitation (Gosselin *et al.*, 2000). Soils of the region originate mainly from glacial tills (Robitaille and Saucier, 1998).

Study plots

In 2004 and 2005, 19 plots (26 × 56 m) were established in stands that had undergone a partial harvest in either 1993 or 1994. The partial harvest aimed at removing individual trees of low growth potential by reducing the pre-harvest average stand density of 27 m^2 ha^{-1} to 21 m^2 ha^{-1}. Sugar maple was the most abundant tree species (approx. 68 % of total post-harvest basal area), followed by yellow birch (*Betula alleghaniensis*, approx. 18 %), and red oak (*Quercus rubra*, approx. 3·5 %), and then others (e.g. *Fagus grandifolia*, *Thuja occidentalis*, *Tsuga canadensis*, *Abies balsamea*, *Picea glauca* and *Acer rubrum*) in smaller proportions.

The diameter was measured and the position of all live and dead trees >9·1 cm in diameter at breast height (dbh, 1·3 m above ground), together with all stumps (dsh, ≈0·5 m above ground) from the 1993/1994 harvest, was mapped. Mapping involved laying out a virtual grid on the forest floor. The plot centre line provided the *y* coordinates and perpendicular distances from this line (*x* co-ordinates) were measured using a Hägloff Vertex III® hypsometer (Haglöf Sweden AB). Also mapped were skid trail networks from the 1993/1994 partial harvest using soil disturbance, tree positions and regeneration as indicators for the original path. Path width was assumed to be 4 m, a conservative estimate of the original width of the skid trail.

Tree growth data

Growth data for live trees were obtained from increment cores (three per tree at 1·3 m above ground) taken from trees within the 19 plots. Recently dead trees (1993 or later) had to be searched for throughout the entire area harvested in 1993 and 1994. Presence of bark and fine branches and absence of advanced trunk decay were used as selection criteria for recently dead trees (Sénécal *et al.*, 2003).

To preclude growth-independent factors from influencing the parameter estimates of the growth-driven model of survival probability (see below), cross-sections of tree trunks at 1·3 m above ground level were collected only from dead trees without any evidence of obvious causes of instantaneous death (uprooting, bole breakage, etc.).

A total of 321 live and 56 dead trees were growth-sampled, distributed roughly uniformly among dbh classes (19·1–29·0 cm, 29·1–39·0 cm, 39·1–49·0 cm). These diameter limits (≥19·0 cm and ≤49·0 cm at 1·3 m above ground) were imposed to prevent heavily suppressed (i.e. smaller diameter) and senescent (i.e. large diameter) trees from being sampled, since both suppression and senescence can strongly influence growth.

Increment cores and cross-sections were progressively sanded (down to grain 400) to make the final cell layer in each tree-ring clearly visible. Tree-rings were then measured using a microscope equipped with a computer-assisted micrometer (0·001 mm precision). In most cases, at least two cores per tree were readable. For the dead trees, two radii per tree were measured on cross-sections for radial growth measurements. These tree-level measurements were averaged to account for intra-tree variability of radial increment due to growing conditions or leaning (Kienholz, 1930; Peterson and Peterson, 1995), thereby obtaining a single growth chronology per tree.

Twenty-nine dominant live trees were subsampled to construct a master chronology by using the COFECHA software (Holmes, 1983) to progressively add highly correlated tree-ring series to the already existing ones. We considered *r*-values ≥0·3 as good cross-correlations with the master chronology (Tardif *et al.*, 2001), which had a final overall cross-correlation coefficient of 0·479. Tree-rings with calendar years were matched by cross-dating live and dead tree-ring series based on (*a*) visual examination of marker years (principally a severe growth decline in 1971 and 1988) and (*b*) cross-correlation coefficients of chronology segments with the master chronology. COFECHA assisted in detecting missing or false rings in individual segments of tree-ring series. In suspect cases, false or missing rings on the cores or cross-sections were identified, and these added (with zero growth) or removed from the series. Corrected series were then run again in COFECHA to verify the cross-correlation with the master chronology.

Also collected were data from 90 live yellow birch trees from within the plots and a yellow birch chronology constructed by the means described above. The resulting chronology contained data from 20 individual trees and had a cross-correlation coefficient of 0·392. This chronology helped identify defoliation events in maple since yellow birch is not a host species of the FTC (see below).

Tree-ring series were standardized by dividing each individual tree-ring series by its growth trend estimate using a cubic smoothing spline. This procedure was done after visually checking the adequacy of the growth trend estimate (i.e. a close match was present between the growth trend estimate and the growth chronology) and produced dimensionless ring-width indices that can adequately be compared among trees of different ages and from different sites. Standardizing was done using the i.detrend function from the contributed R package dplR (Bunn, 2007) in R software (version 2·6·0; R Development Core Team, 2007).

Natural disturbances

Periods of FTC outbreaks were identified by subtracting a non-host (yellow birch) chronology of growth indices from chronologies of growth indices from sugar maples (Swetnam *et al.*, 1985). Residuals from the mean of the yellow birch (By) series were first rescaled to the variance of the host series to obtain predicted residual indices (PRI) that were then subtracted from the raw sugar maple (Ms) indices to produce the corrected sugar maple indices (CI; Swetnam and Lynch, 1989):

$$\text{PRI} = (\text{SD}_{\text{Ms}}/\text{SD}_{\text{By}}) \times (\text{Index}_{\text{By}} - \text{Mean}_{\text{By}}) \qquad (1)$$

$$\text{CI} = \text{Index}_{\text{Ms}} - \text{PRI} \qquad (2)$$

Periods were inferred as insect outbreaks when corrected indices were negative for at least three consecutive years because FTC outbreaks typically last about 2–4 years (Fitzgerald, 1995). Moreover, at least one of these indices had to be at least one standard deviation (SD) below the series mean. This stipulation allowed a close match between the inferred frequency of outbreak and the approximate average frequency of FTC outbreaks observed in this region (9+ years; Ministère des Ressources naturelles, de la Faune et des Parcs du Québec, 2002).

Measures of harvest disturbance

In the study stands, disturbance from logging (i.e. machinery traffic causing soil compaction and root damage or major canopy removal) did not occur until the 1993/1994 selection cut (D. Boileau, MRNFQ, Canada, pers. comm.).

Sudden exposure to higher light levels due to partial cutting. Because harvesting occurred 11 years prior to the field work in the present study, changes in light levels following partial harvest were simulated using a light-driven, spatially explicit model of stand dynamics, SORTIE (Pacala *et al.*, 1993, 1996). The simulation involved converting our diameter at stump height estimates to dbh using standard conversion tables (Ministère des Ressources naturelles, de la Faune et des Parcs du Québec, 2003). These dbh estimates were then used to 'resurrect' harvested trees (see below) and create maps of pre-harvest dbh that were then used as input to SORTIE to estimate light availability for individual trees.

SORTIE was parameterized with region-specific parameters of tree species allometry and species-specific light extinction coefficients (Canham *et al.*, 1994; Poulin and Messier, 2007; Lefrançois *et al.*, 2008; M. Beaudet, UQAM, Montreal, Canada, unpubl. res.). SORTIE then modelled tree and crown dimensions for each tree in the stand and computed their light availability as the seasonally averaged percentage of full sun (Canham, 1988). This routine was initially run on the plots, with the inclusion of harvested and recently dead trees, and then with residual trees only, viz. the actual post-harvest plots. Light availability was estimated individually for each tree at the centre of the simulated crowns at 0·75 × crown height. The ratio of post- to pre-harvest light availability was then computed as the measure of changes in light.

Soil disturbance in the proximity of trees. Based on the assumptions that (*a*) tree crown dimensions can be predicted from tree diameter and (*b*) tree crown dimensions are a proxy for the areal coverage of the root system (Tubbs, 1977), a circular 'influence zone' was estimated around each tree. These estimates were based on species-specific parameters of diameter–crown relationships that in turn yielded diameter-dependent influence zones with radii $(m) = 0\cdot100 \times$ dbh (cm) for sugar maple (Beaudet *et al.*, 2002). The intersection of these influence zones with the mapped skidding trails yielded a proportion of the influence zone disturbed by machinery traffic. This proportion, expressed as a percentage of the total area of the influence zone, was our measure of soil disturbance close to trees.

Longitudinal survival probability estimation

Longitudinal survival probabilities served as the proxy for tree vigour. Of the 321 live trees, a number equivalent to the sample size of dead trees ($n = 56$) were randomly selected and used to parameterize the survival probability model. Longitudinal logistic regression (Bigler and Bugmann, 2004), an approach that uses growth data from the entire lifespan of the trees, was used. Predictor variables (e.g. mean values and linear regression coefficients) were computed within a moving window of n years across the time-series. Data points containing the last year of growth of a dead individual are marked as 'dead'. All other data points are marked as 'live'.

In a companion study (Hartmann, *et al.*, 2008), the model best supported by the data from a set of candidate models composed of different predictor variables based on Akaike's Information Criterion (Burnham and Anderson, 2002) was selected. This model was:

$$P(survival) = \frac{e^{-7\cdot115+2\cdot017av3\log+0\cdot006slp5}}{1 + e^{-7\cdot115+2\cdot017av3\log+0\cdot006slp5}} \qquad (3)$$

where *P(survival)* is the probability that an individual survives, *av3*log is the log-transformed average over the previous 3 years of radial growth and *slp5* is the linear trend over the previous 5 years of radial growth.

R was used for parameter estimation using maximum likelihood methods. Non-parametric confidence intervals for the parameter estimates were computed with the bootcov bootstrap resampling procedure from the Design library (Harrell, 2005), based on 1000 iterations, with the 25th and the 975th quantiles serving as interval limits.

Model performance was estimated with Somer's D_{XY} index (Somers, 1962). This index indicates a model's discriminative ability and is closely related to the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Engelmann *et al.*, 2003). The bootstrap resampling procedure validate.lrm (Harrell, 2005) was used to account for over-optimistic classification measures when validating models on training data (data specificity). The validate.lrm procedure eliminates overfitting-induced optimism of D_{XY} and produces a more conservative estimate of the model's discriminative ability (Harrell, 2001). The model used in this study had a D_{XY} value of 0·783, corresponding to an AUC of 0·892 and indicating excellent model performance (Manel *et al.*, 1999; Table 1).

Interpretation of survival probabilities

The above procedure leads to an unbalanced data distribution (i.e. many live data points and few dead data points) and yields, based on logistic regression, survival probability estimates biased to the more abundant group (Fielding and Bell, 1997). Hence, survival probability estimates were all very close to unity and could not be directly interpreted as absolute measure of probability of survival unless adjustments were made for the unbalanced data distribution. However, in the present study, survival probabilities were interpreted only as a relative measure of tree vigour among groups of trees (see below), making threshold adjustments unnecessary.

Comparison of growth indices and survival probabilities among disturbance classes and dead trees

Live trees with available growth data were grouped into four classes of anthropogenic disturbance: (1) trees with neither machinery disturbance in their proximity nor a substantial ($>50\%$) increase in post-harvest light levels (N = no disturbance, $n = 134$), (2) trees with machinery

disturbance in their proximity, but no substantial increases in light levels (M = machinery, $n = 71$); (3) trees without machinery disturbance, but showing a substantial ($>50\%$) increases in post-harvest light levels (L = light, $n = 28$); and (4) trees with both machinery disturbance and substantial ($>50\%$) increases in post-harvest light (L&M = light and machinery, $n = 16$). Of the 321 live trees, 249 fell within these classes, with the remainder being trees with either no machinery disturbance but light increases $\leq 50\%$ ($n = 51$), or trees with machinery disturbance but only small increases ($\leq 50\%$) in light levels ($n = 21$).

Since ring-width measurement and survival probabilities are usually not normally distributed, the non-parametric Kruskal–Wallis test was used for annual comparisons of ring-width indices among disturbance classes and with dead trees in the years prior to and following harvest (1990–2004). A non-parametric simultaneous rank test procedure was employed for multi-comparisons using the npmc function from the R package npmc (Helms and Munzel, 2008). This procedure is based on estimations of simultaneous relative effects and variance among pairs, and does not assume continuity of the underlying distribution functions thereby allowing arbitrary ties. The procedure can be applied to all relevant multiple testing problems in the one-way layout and derives the test statistic (W_N^{BF}) and *P*-values with the Behrens–Fisher test (Munzel and Hothorn, 2001). Survival probabilities were analysed with the same procedure described above.

To test for differences between natural (FTC defoliation) and anthropogenic (partial harvest) disturbances, corrected growth indices were used as these are likely to be free of the effects of climate and other environmental factors on growth (Swetnam *et al.*, 1985). As the natural disturbance source, the 1986–92 FTC outbreak was selected, which had the strongest influence on growth rates among all inferred and documented FTC outbreaks. The within-tree-averaged growth indices were compared over the 1986–92 period with those over the 1994–98 post-harvest period (and just before the onset of the next FTC outbreak in 1999), within each disturbance class and within dead trees. Since observations were compared within growth chronologies of the same trees, a Wilcoxon signed-rank test was used. This test requires equal sample sizes between the two groups, a condition that was not met for dead trees for the 1994–98 period due to mortality dropout. Therefore data were compared from this period with a random subsample (without replacement) of the 1986–92 period, a Wilcoxon signed-rank test on this balanced sample was applied, this procedure repeated 1000 times and test *P*-values averaged.

Definition of stresses on tree growth and vigour

The factors that influence initial vigour and predispose trees to subsequent stress (Manion, 1981) are difficult to assess since an unambiguous benchmark for the absence of stress needs to be defined. However, predisposing factors have a diffuse impact on tree vigour, allowing trees to survive with modified vital functions (Waring, 1987). In this study, predisposing factors were defined as stresses

TABLE 1. *Parameter estimates, bootstrapped 95 % confidence intervals (CI), AUC (ROC) and optimism-corrected D_{XY} of the logistic survival probability model*

| Variables | Estimate | CI (95 %) | | D_{XY} | AUC |
		Lower	Upper		
Intercept	−7·115	−8·974	−5·337	0·783	0·892
*av3*log	2·017	1·713	2·375		
*slp*5	0·006	0·004	0·007		

with a moderate impact on tree vitality, i.e. as measured by radial growth. These stresses decrease radial growth levels but do not lead ultimately to tree death.

In contrast, according to Manion (1981), inciting factors are severe stresses, such as defoliations or drought, that cause severe declines in vigour and lead to tree death. This definition was used with respect to radial growth and survival probabilities. In an accompanying study, trees with survival probabilities permanently <0·987 eventually died (H. Hartmann, unpubl. data). Hence, this value was considered as a threshold for definite vigour decline and a benchmark for inciting stresses.

Contributing stresses may not play an essential role in tree decline (Muller-Dumbois, 1987; Pedersen, 1998*b*) but can deal the death blow to declining trees by accelerating their decline. Contributing stresses were defined as decreases in survival probabilities when these probabilities were already below the threshold of definite vigour decline.

Summer climate data as indicator of growth conditions

An indicator of growth conditions was computed based on mean summer monthly precipitation and temperature (April–August) using climate data from the two closest (approx. 60 km) weather stations (Environment Canada, http://climate.weatheroffice.ec.gc.ca).

RESULTS

Growth dynamics of undisturbed trees

Sugar maple trees undisturbed by the 1993/1994 partial harvest showed a sudden increase in growth in the late 1950s (Fig. 1A), a pattern evident for trees both live and dead at the time of sampling. Shortly after this increase, in

about 1960, growth rates of dead trees deviated from those of live trees. In 1971, a major drop in growth rates of both live and dead trees occurred, followed by a continuous growth decline for both groups. In 1988, another major drop in growth rates occurred for both live and dead trees (Fig. 1A). The 1993/1994 harvest was followed by a temporary increase in growth rates of dead trees, but these subsequently declined and died. In live trees, the 1988 growth decline was followed by a growth increase after the partial harvest that was then maintained until 2004.

Average ring-width indices do not show the difference between live and dead tree growth patterns as clearly as ring-width measurements, at least for earlier years. Until 1965, although standardized growth rates of dead trees were more variable than live tree growth indices, they oscillated around the same values (Fig. 1B). From 1965 to 1995, growth indices of live and dead trees were almost identical and both groups experienced a major drop in 1988, followed by an increase. From 1995 onwards, shortly after the 1993/1994 harvest (Fig. 1B), growth indices of dead trees declined whereas those of live trees maintained increased growth levels until 2004.

Yellow birch had a different pattern of growth from that of sugar maple during several periods, especially in the 1930s, 1940s and 1960s (Fig. 2A). Corrected sugar maple ring-width indices showed that growth of dead trees was affected more than that of live trees by FTC defoliations between the 1930s and mid-1940s, but dead trees exhibited higher growth rates from about 1945 until 1965 (Fig. 2B). Decreases in growth rates of dead trees lasted longer than those of live trees during the 1986–92 outbreaks (Fig. 2B). Although dead trees achieved a small, brief increase in growth rates in 1994 and 1995, growth declined again shortly after harvest in 1996 (Fig. 2B) and trees died shortly afterwards.
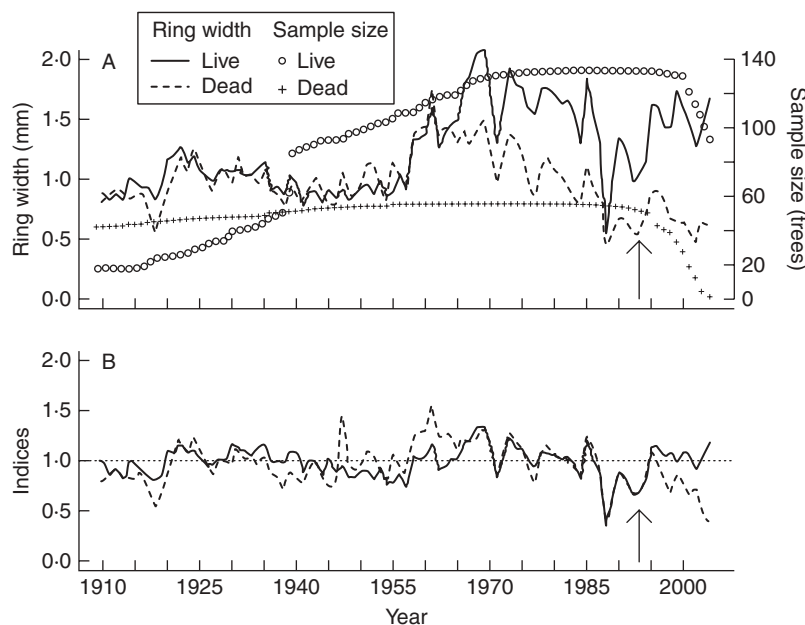

FIG. 1. (A) Average ring-width (mm) and sample size (trees) chronologies (1910–2003) of live and dead trees. (B) Average growth index chronologies (1910–2003) of live and dead sugar maple trees undisturbed by harvest. Arrows indicate the year of the selection harvest.
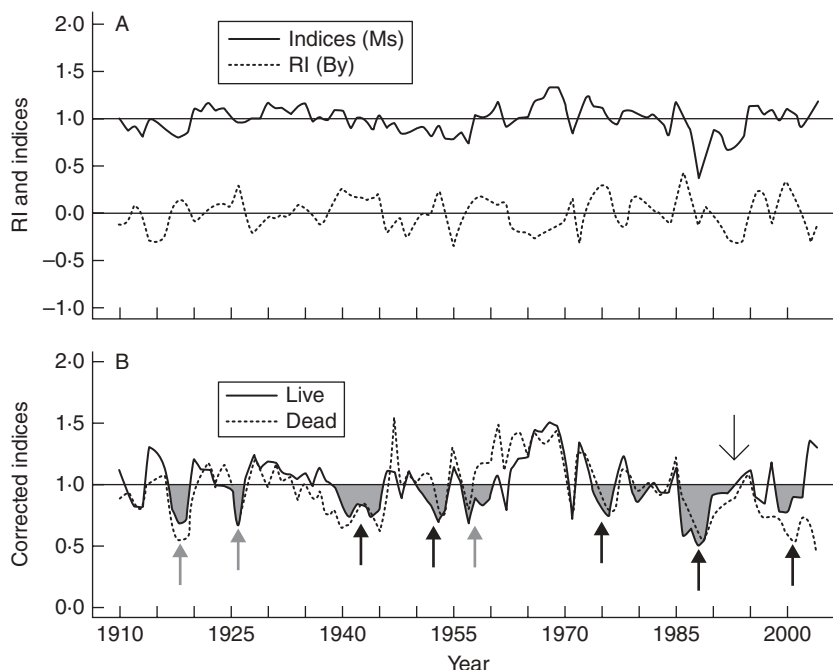
FIG. 2. (A) Averaged ring-width indices (1910–2003) of sugar maple (Ms) trees undisturbed by harvest (*n* = 134, as in Fig. 1B) and rescaled indices (RI) of yellow birch (By) trees (*n* = 20), a non-host species of the forest tent caterpillar. (B) Corrected ring-width indices of sugar maple trees obtained by subtracting RI in (A) from the host species (sugar maple) indices in (A). Shaded areas in (B) are periods of inferred (grey arrows) or documented (black arrows) FTC defoliations (see text for details). The downward-pointing arrow in (B) indicates the year of the selection harvest.

Eight insect outbreaks were identified between 1910 and 2004, with an average outbreak cycle of 11·75 years and an average outbreak length of 4·6 years (data not shown). All but the 1957–60 FTC outbreak could be confirmed by MRNFQ survey data (1938–2002). However, the Ministry survey indicated a continuous occurrence of FTC defoliations from 1950 until 1956, suggesting that both the 1950–54 and 1957–60 growth declines were caused by this single FTC outbreak.

Growth dynamics of disturbed trees

To evaluate the impact of partial harvest disturbance on radial growth, growth indices were examined between 1990 and 2004, i.e. from 3 years prior to until 10 years after partial harvest. In 1990, growth of dead trees was significantly lower than that of undisturbed live trees only (Table 2). From 1991 until 1994, there were no significant differences in growth indices among disturbance classes. Indices of dead trees were significantly different from all live trees in 1998, 2001 and 2003, from L, M and N trees in 1999 and 2000, from L and L&M trees in 1995, 1996, 1997 and 1998 and from N trees in 1995 (Table 2). Among live trees only, the growth indices of L trees were different from those of M trees in 1995 and 1997 and from N trees in 1995 (Table 2).

The FTC outbreak had a greater impact on growth of live sugar maple than any of the harvest disturbance types but this was not the case for dead sugar maple. Means of the averaged corrected indices during the natural disturbance (1986–92) varied between 0·627 for L trees and 0·727 for N trees (Table 3). During the anthropogenic disturbance

(1994–1998), corrected indices were consistently higher for all trees, ranging from 0·809 (D) to 1·267 (L) (Table 3). Differences in average corrected indices between periods of natural and anthropogenic disturbance were highly significant ($P < 0.001$) within disturbance classes of all live trees, but not significant for dead trees (Table 3).

As indicated by survival probabilities, dead trees exhibited the first signs of vigour decline in 1977, following the FTC outbreak in 1974–76 (Fig. 3). Vigour of dead trees was lower before the 1986–92 FTC outbreak than vigour of live trees. Also, vigour of dead trees declined more severely during the 1986–92 FTC outbreak than vigour of live trees. Dead trees never regained their pre-FTC outbreak vigour and their vigour stayed below that of live trees (Fig. 3). Multiple comparisons (Behrens–Fisher tests) indicated that survival probabilities of dead trees were significantly different from those of all four disturbance classes from 1992 until 2001 (Fig. 3, table inset). In the post-harvest period (1994 onwards), no differences of survival probabilities among disturbance classes were detected (Fig. 3).

Mean summer temperatures were only slightly above the long-term average (1910–2003) in the years following harvest (1994–97) while mean summer precipitation was above average in 1994, on average in 1995 and again above average in 1996 (Fig. 4).

DISCUSSION

The nature of predisposing and inciting stresses and their interaction

In the present study, dead trees were predisposed to inciting stresses by a first FTC outbreak in 1974–76 that initially

TABLE 2. *Behrens–Fisher tests on relative effect estimates of ring-width indices (1990–2003) between disturbance classes using a non-parametric simultaneous rank test*

Year	Comparison	n	Relative effect estimate					W_N^{BF}	P
			Effect	CI (lower)	CI (upper)	Var.	s.e.		
1990	D vs. N	189	0·648	0·518	0·778	0·382	0·045	3·290	0·021
1995	D vs. L	78	0·759	0·592	0·927	0·251	0·057	4·571	0·002
	D vs. L&M	66	0·719	0·531	0·906	0·267	0·064	3·441	0·019
	D vs. N	184	0·669	0·506	0·832	0·563	0·055	3·057	0·040
	L vs. M	99	0·296	0·106	0·487	0·413	0·065	−3·155	0·035
	L vs. N	162	0·281	0·091	0·471	0·671	0·064	−3·403	0·020
1996	D vs. L	71	0·694	0·512	0·877	0·273	0·062	3·133	0·034
	D vs. L&M	59	0·725	0·524	0·926	0·275	0·068	3·301	0·024
1997	D vs. L	69	0·748	0·575	0·921	0·242	0·059	4·189	0·003
	D vs. L&M	57	0·729	0·537	0·920	0·245	0·066	3·485	0·015
	L vs. M	99	0·302	0·112	0·492	0·420	0·065	−3·035	0·039
1998	D vs. L	67	0·799	0·638	0·960	0·202	0·055	5·455	0·000
	D vs. L&M	55	0·747	0·551	0·942	0·244	0·067	3·705	0·010
	D vs. M	110	0·681	0·502	0·861	0·412	0·061	2·965	0·047
	D vs. N	172	0·729	0·566	0·893	0·534	0·056	4·115	0·004
	L vs. M	99	0·259	0·082	0·435	0·359	0·060	−4·012	0·005
1999	D vs. L	62	0·777	0·593	0·962	0·242	0·062	4·441	0·002
	D vs. M	105	0·692	0·502	0·883	0·437	0·065	2·979	0·047
	D vs. N	165	0·715	0·534	0·895	0·615	0·061	3·519	0·016
2000	D vs. L	55	0·749	0·545	0·953	0·261	0·069	3·611	0·014
	D vs. M	99	0·737	0·543	0·932	0·428	0·066	3·610	0·013
	D vs. N	159	0·728	0·540	0·917	0·646	0·064	3·584	0·014
2001	D vs. L	45	0·749	0·520	0·978	0·267	0·077	3·234	0·030
	D vs. L&M	34	0·754	0·503	1·005	0·243	0·085	3·009	0·046
	D vs. M	89	0·767	0·557	0·977	0·445	0·071	3·775	0·010
	D vs. N	141	0·758	0·550	0·965	0·688	0·070	3·688	0·012
2003	D vs. L	30	0·872	0·572	1·172	0·168	0·075	4·973	0·022
	D vs. L&M	20	0·880	0·556	1·204	0·130	0·081	4·708	0·027
	D vs. M	72	0·845	0·558	1·132	0·368	0·072	4·822	0·024
	D vs. N	113	0·870	0·629	1·111	0·407	0·060	6·174	0·009

Only significant ($P < 0.05$) tests are shown.

TABLE 3. *Mean, standard error (s.e.) and range of averaged corrected indices during FTC outbreak (1986–1992) and harvest disturbances (1994–1998)*

Disturbance class	FTC outbreak			Harvest disturbance			P
	Mean	s.e.	Range	Mean	s.e.	Range	
N	0·727	0·185	0·260−1·281	1·033	0·255	0·561−2·048	<0·001
M	0·704	0·177	0·329−1·230	0·972	0·248	0·260−1·664	<0·001
L	0·627	0·234	0·223−1·022	1·267	0·372	0·495−2·047	<0·001
L&M	0·687	0·151	0·283−0·876	1·156	0·292	0·614−1·752	<0·001
D	0·688	0·247	(0·189)−1·252	0·809	0·419	0·132−1·859	0·352

P-values refer to a Wilcoxon signed-rank test between periods.
Negative values are in parenthesis.

decreased their vigour. The 1986–92 FTC outbreak acted then as a second inciting stress, having a longer lasting and more severe negative effect on growth rates and vigour of dead trees than the 1974–76 outbreak. Although growth rates and survival probabilities of dead trees temporarily recovered shortly after partial harvest, their decline resumed and accelerated drastically from 1997 onwards (Fig. 3). Partial harvest disturbances may have acted as a contributing stress in these already weakened trees.

Successive defoliation events can deplete carbon reserves, readily weaken sensitive trees and trigger sugar maple decline (Parker and Houston, 1971; Kolb and McCormick, 1993; Payette *et al.*, 1996). The severe defoliation in 1986–92 may have acted as an inciting stress in the decline of already weakened trees (Horsley *et al.*, 2002). In the live trees, abundant carbon reserves may explain their greater potential for recovery than in dead trees, since these reserves allow trees to quickly rebuild leaf area after defoliation and, subsequently, their photosynthetic apparatus (Landhäusser and Lieffers, 2002).

Sugar maple tree decline and death was driven by an interaction between predisposing and inciting stresses, as
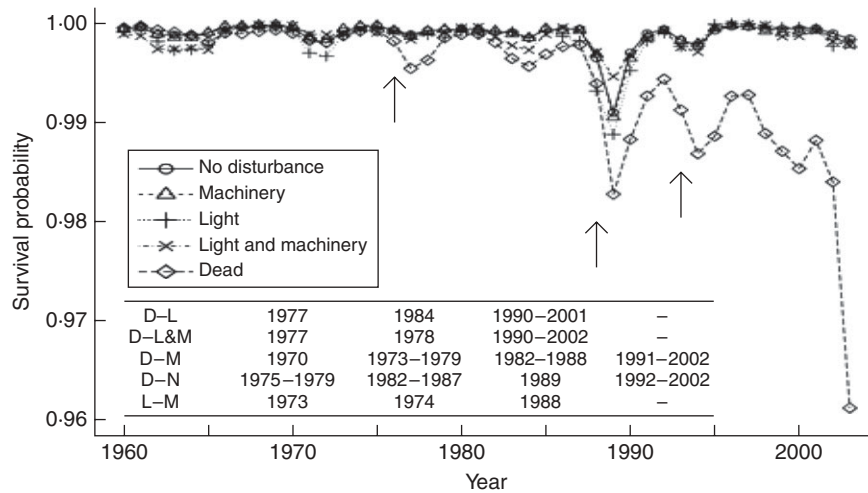
FIG. 3. Average survival probabilities of live and dead sugar maple trees from 1960–2003. The table specifies years of significant differences ($P < 0.05$) between pairs of disturbance classes and dead trees and among disturbance classes. Arrows indicate the most severe years of FTC outbreaks (1974–76, 1986–92) and the partial harvest (1993). The horizontal line indicates a critical probability threshold [$P(Y = 1) = 0.987$] for a definite vigour decline (see text for details).
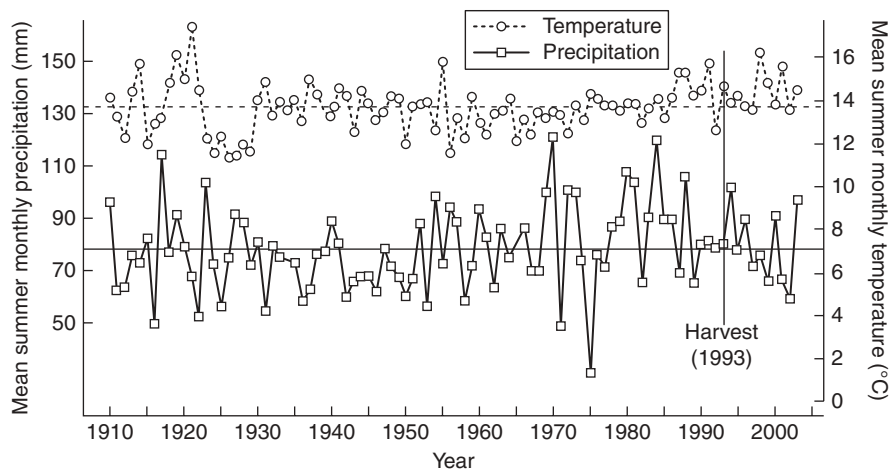

FIG. 4. Mean summer (April–August) monthly precipitation and temperature computed from climate data covering the years 1910–2003. Horizontal lines indicate the long-term mean precipitation and temperature across these years. The vertical line indicates the year of the partial harvest (1993).

suggested by Manion's conceptual tree disease model (Manion, 1981). Similarly, Hogg *et al.* (2002) found that FTC defoliation combined with other environmental stresses led to reduced growth and crown dieback in trembling aspen (*Populus tremuloides*). The present results are in general agreement with other findings that identified defoliating insects (Payette *et al.* 1996), fungal pathogens (Cherubini *et al.*, 2002; Marçais and Bréda, 2006) or drought (Pedersen, 1998*a*; Suarez *et al.*, 2004) as inciting stresses in tree decline and death.

Impact of partial harvest on tree growth and vigour

Radial growth rates of live trees in all partial harvest disturbance classes quickly regained or even surpassed pre-disturbance growth levels after partial harvest. None of these trees showed a growth stagnation known as 'thinning shock' (e.g. Staebler, 1956; Harrington and Reukema,

1983). On the contrary, trees experiencing strong increases in light showed the greatest increases in post-disturbance growth, increases that lasted in some cases until 1998 (Table 2). Although photoinhibitive effects of significant and sudden increases in light have been observed in seedlings of shade-tolerant beech (*Fagus sylvatica*; Tognetti *et al.*, 1997) and in saplings of shade-tolerant sugar maple (Naidu and DeLucia, 1997), this photoinhibition was not the case for adult sugar maple trees in the present study, even though mean increases in light levels were remarkably high (>600 %, data not shown). Hence, sudden changes in light availability from partial harvest did not act as a stress causing growth declines.

Soil disturbance is thought to negatively impact radial growth of trees (Clayton *et al.*, 1987). The impacts occur through disturbance effects on soil physical properties (Kozlowski, 1999) or potential damage to the root system (Wästerlund, 1992) but also through fungal infections of

the root system (Nadezhdina *et al.*, 2006). However, growth of trees that experienced machinery disturbance was only lower than those of trees with increased light, but not significantly different from those of undisturbed trees (Table 2). This finding is surprising since these trees had a mean soil disturbance of 34·7 % (data not shown). The coarse soil texture in the study plots (either sandy, sandy loam or, in one plot, rocky) may explain the absence of negative effects of machinery disturbance on growth since these soils are not compacted easily (Horn, 1988; McBride and Joosse, 1996). Furthermore, the dense root network of the abundant woody understorey vegetation (mostly tree regeneration, beaked hazel, *Corylus cornuta*, and hobblebush, *Viburnum lantanoides*) in the humus layer of the maple stands studied may have increased soil strength and thus resistance to mechanical forces from logging equipment (Wästerlund, 1989). Machinery disturbance apparently did not cause fungal infections of the tree root systems and associated severe growth declines, as has been observed, for example, in trees infected with root rot (Mallet and Volney, 1999; Cherubini *et al.*, 2002).

Impacts of insect outbreaks and partial harvest on radial growth and tree vigour

As indicated by the average corrected growth indices, tree growth was lower during natural disturbance than during the post-harvest period (Table 3), meaning FTC defoliation had a stronger negative effect on growth rates than any harvest disturbance. These results show that disturbances from partial harvest, even in their most severe form, had no significant negative effect on the growth of the trees sampled. However, trees that had incurred obvious damage from harvest (uprooting, bole breakage, girdling, etc.) were not sampled. This type of 'disturbance' would most probably cause growth reduction and has been found to cause high post-harvest tree mortality (Nyland, 1994).

Conclusions

The present findings showed that FTC defoliations acted as both predisposing and inciting stresses on maple, whereas partial harvest acted, at worst, as contributing stresses and only in already declining trees. Since the full range of above- and below-ground disturbance severity caused by a partial harvest was sampled, it is concluded that partial harvest disturbances did not contribute to maple decline and death. However, the rather favourable climatic conditions found in the post-harvest period could have reduced any negative impact of partial harvesting through its positive effect on tree growth (Hanson *et al.*, 2001).

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