Forest Ecology and Management 256 (2008) 1771–1779

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Using longitudinal survival probabilities to test field vigour estimates in sugar maple (*Acer saccharum* Marsh.)

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A R T I C L E I N F O

Article history:
Received 22 March 2007
Received in revised form 29 November 2007
Accepted 28 February 2008

Keywords:
Selection cut
Radial growth
Survival model
Logistic model

A B S T R A C T

Tree mortality is a major force driving forest dynamics. To foresters, however, tree mortality is often considered a loss in productivity. To reduce tree mortality, silvicultural systems, such as selection cuts, aim at removing trees that are more likely to die. In order to identify trees with higher risks of mortality, field classifications are employed that assess vigour based on external characteristics of trees. We used a novel longitudinal approach for estimating survival probabilities based on ring-width measurements, initially developed by Bigler and Bugmann [Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. Ecol. Appl. 14 (3), 902–914], to parameterize a survival probability model for sugar maple (*Acer saccharum* Marsh.) and to test whether field-assessed tree vigour classes are corroborated by survival probabilities determined from radial growth history. Data from 56 dead and 321 live sugar maples were collected in stands in western Quebec (Canada) that had undergone a selection cut ≈10 years prior to sampling. Our results showed that tree vigour established from external defects and pathological symptoms, using the classification of Boulet [Boulet, B., 2005. Défauts externes et indices de la carie des arbres: guide d'interprétation. Publication du Québec, Sainte-Foy, Quebec. 291 pp.], is partially corroborated by growth-driven survival probabilities. Moribund trees had lower survival probabilities than vigorous trees over several years in the period prior to vigour assessment. Intermediate vigour classes showed less obvious tendencies, but this may be due to the growth-independent nature of some defects used for their classification. Although the timing of tree death may not be correctly predicted by the vigour classification (i.e., our results suggest that time of death generally was overestimated), its general agreement with survival probabilities determined from growth series make it a useful tool for tree selection in sugar maple stands under selection management.

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1. Introduction

Tree mortality is a major force driving forest dynamics and succession (Franklin et al., 1987; Pacala et al., 1996). It influences species composition, together with the size and age-structure of forest stands (Oliver and Larson, 1996), and is a key process in nutrient and biomass cycling (Brown and Schroeder, 1999). Knowledge of mortality rates is necessary for developing sustainable forest management practices (Davis et al., 2001). However, our understanding of the processes underlying tree mortality remains limited and warrants further investigation (Manion and Lachance, 1992; Hawkes, 2000).

In young stands undergoing canopy closure, trees die through self-thinning when increasing population densities limit resources for particular individuals (Yoda et al., 1963). Suppressed trees decrease their growth rates, which in turn reduce their competitive capacity under conditions of limited resources (Oliver and Larson, 1996). In mature stands, tree mortality rates may be indicators of environmental stresses (Brooks, 1994; Pedersen, 1999; Dobbertin, 2005), such as insect defoliation or drought, which may weaken individual trees until they die (Manion, 1981).

In forest management, tree mortality is often seen as a loss in forest productivity, and standing dead trees (snags) are considered a potential danger during logging operations, although more recently their ecological role has been recognized (e.g., DellaSala et al., 1995; Hunter, 1999). Nevertheless, most partial harvests, such as the selection system, attempt to remove low-vigour trees (Smith et al., 1997), thereby reducing future mortality losses while liberating resources for the residual trees. The residual stand therefore is expected to have a higher proportion of 'healthy' trees than before harvest, and to offer better growth conditions for residual trees, which should translate into lower mortality rates. However, to achieve this goal of decreasing post-harvest stand-level mortality rates, individual-level tree vigour must be

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doi:10.1016/j.foreco.2008.02.045

adequately assessed in the field prior to harvesting under operational conditions.

Several tree classification systems have been developed to assess tree vigour based on social, morphological and pathological qualities of the target trees (e.g., Ouellet and Zarnovican, 1988), crown characteristics (Millers et al., 1991) or bark characteristics (OMNR, 2004). Although these indicators may be adequate tools for tree selection, their use may have unintended consequences. For example, it has been observed that stands under industrial management had mortality rates 5 years after selection harvest that were higher than expected, based on previous experimental studies (Bédard and Brassard, 2002). These higher-than-expected mortality rates, which occurred among trees without obvious harvest damage (skidding wounds, crown damage from felling, etc.), might be a consequence of ambiguous or ineffective marking guidelines (Meunier et al., 2002) that rely on visual assessments of tree vigour. If inadequate criteria are used, low-vigour trees may be retained to in harvested stands. However, the link between tree classification and future mortality occurrence has not been empirically tested.

Other approaches for assessing tree vigour are based on measures of photosynthesis, gas exchange or nutrient content in leaves, transport rates of water or ions, as well as measurements of tree vital function such as radial growth (Gehrig, 2004). Radial growth of tree stems is assumed to be a low priority in carbon allocation; it varies with growth conditions (e.g., soil, climate, and competition) and has been used as a sensitive surrogate measure of the carbon balance of trees (Kobe et al., 1995; Kobe, 1997). It is also a potentially useful indicator of stress and tree vigour (Waring and Pitman, 1985; Pedersen, 1998). Radial growth increment has been used to assess survival probabilities of individual trees by comparing growth of live and dead trees (e.g., Monserud, 1976; Hamilton, 1986) and is considered a viable approach to assess tree vigour.

To date, most studies of tree mortality probabilities are based on a cross-sectional approach where the data consist of a single measurement of recent growth per tree. These data can take the form, for example, of the ring-width or basal area increment in the year prior to sampling or prior to the year of death, or some derived variable such as the mean growth rate over a given period of recent growth (e.g., Bigler and Bugmann, 2003). With this approach, predictions of tree status (dead or alive) are accurate only at one single point in time, namely the year when growth measurements are taken or the period for which the predictor variable was computed. Therefore, the cross-sectional approach cannot be used to predict mortality probabilities for other periods in a tree's life. More recent studies have used a longitudinal approach to model the probability of mortality over time, for example, for the entire life span of trees (Bigler and Bugmann, 2004; Bigler et al., 2004).

Unfortunately, radial increment cannot be easily measured in the field, since it requires repeated diameter measurements or increment core sampling. This repeated measurement precludes its use as a tool for vigour assessment and tree selection on an operational basis. However, radial growth can provide a powerful validation of existing vigour classifications by comparing survival probabilities of trees of different vigour classes (Bigler et al., 2004).

In this study, radial growth rates of sugar maple (*Acer saccharum* Marsh.) were used to parameterize a survival probability model for empirically estimating tree vigour. These survival probabilities were compared to field estimations of tree vigour using the classification system described in Boulet (2005). Sugar maple was selected for our study because it is a major, ecologically important North American tree species. It is shade tolerant and forms uneven-aged stands of great geographical extent spanning the northeastern USA and eastern Canada (Godman et al., 1990).

The objectives of this study were to: (1) develop a longitudinal survival probability model using radial growth series from sugar maple trees from stands in western Quebec, Canada, and (2) use this model to determine whether survival probabilities corroborate the visual classification of tree vigour used for tree marking.

2. Material and methods

2.1. Study area

The study sites are located in the Abitibi-Temiscamingue region of western Quebec, about 60 km southeast of the city of Temiscaming (46°43′ north, 79°04′ west). The region is part of the western sugar maple-yellow birch bioclimatic domain (Robitaille and Saucier, 1998). Mean annual temperature varies from 2.5 to 5.0 °C; growing season extent is 170–180 days, and mean annual precipitation ranges from 800 to 1000 mm, with about 25% of total precipitation falling as snow (Gosselin et al., 2000). Soils are derived principally from glacial till, with the remainder originating from fluvio-glacial deposits in the large valley bottoms, and peat-bogs in poorly drained depressions (Robitaille and Saucier, 1998).

In 2004 and 2005, 19 plots (26 m × 56 m) were established in uneven-aged sugar maple stands that had been harvested by selection cuts in 1993 or 1994. The studied stands had an average pre-harvest basal area of 27 m^2/ha, which was reduced by harvesting to an average 21 m^2/ha. On average, maximum canopy height reached 25–28 m. The entire area experienced two forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks (1971 and 1988), which caused heavy defoliation in sugar maple (MRNFP, 2002; MRNF, 2005), one of its host species (Fitzgerald, 1995).

In our plots, sugar maple made up 68% of total basal area, yellow birch (*Betula alleghaniensis* Britton) about 18%, red oak (*Quercus rubra* L.) 3.5%, and American beech (*Fagus grandifolia* Ehrh.), eastern white cedar (*Thuja occidentalis* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.) each constituting roughly 1.5% of the total. Other species such as balsam fir (*Abies balsamea* [L.] P. Mill.), white spruce (*Picea glauca* [Moench] Voss), and red maple (*Acer rubrum* L.) occurred in minor proportions (<1% of total basal area).

Plots were established at locations where site characteristics were considered representative of the greater region, i.e., on level ground or on gentle slopes with good to moderate drainage, and on podzols of glacial origin. In these plots the diameter at breast height (dbh, 1.3 m above ground level) and crown class (dominant, codominant, intermediate, suppressed) of all trees >10.0 cm dbh was determined. Also, tree vigour was assessed using a visual classification system (see below) and three increment cores for each live tree between 19.1 and 49.0 cm dbh were taken as a retrospective measure of radial stem growth. Trees <19.1 and >49.0 cm were excluded from sampling to avoid heavily suppressed or senescent individuals.

2.2. Tree vigour classification

The tree vigour classification that we used has been developed by the Quebec Ministry of Natural Resources (Boulet, 2005), and relies on pathological symptoms (e.g., presence of cankers and fungi), mechanical damage (e.g., cracks, leaning) and other visible features (e.g., improper branch shedding, crown openness) to assign trees to >200 vigour codes, which are then grouped into four main vigour classes. The classification system is considered a thorough framework for tree vigour assessment and, since it is based on symptoms of physiological vigour decline, can be regarded as an indicator of tree vigour beyond the geographical boundaries of where it was developed. The vigour classification takes into account wood properties, but also assigns tree survival probabilities until the next harvest entry, typically scheduled every 20–25 years (MRN, 1997).

The four vigour classes are described as follows. Trees of reserve stock (class 'R') are free of any symptoms of disease or damage and are considered 'healthy' trees with the highest probability of survival. Growing trees (class 'C' have minor defects but are not biologically declining and are expected to survive until the next harvest without risk of imminent wood decay. Low quality or defective trees (class 'S') are considered to be declining in terms of vigour, wood quality and volume increment, and are not expected to survive until the next harvest. Moribund trees (class 'M') show signs of either lethal pathological infection or severe damage with high risk of trunk breakage. Moribund trees are biologically declining (decreasing vigour, wood decay) and are assumed to have a high probability of mortality before the next harvest entry.

The vigour classification system has a hierarchical structure based on the assumed severity of observed defects. When assessing a tree's vigour, one should first determine whether the tree shows signs or symptoms of fungal infection (sporocarps, stroma) and, if present, this observation determines the vigour code. If the tree is free of fungal infection, then signs or symptoms of cambium necroses (cambial diseases) should be determined and, if present, they will determine the vigour code. The stepwise assessment procedure continues further using various types of criteria, in the following order: bole defects and bark mechanical injuries, root and butt wounds, bark fissures and bole cracks, woodworm and woodpecker damage (wood dust and bird-pecks), crown defects, and finally, branching defects.

Listing all possible defects for vigour classification is beyond the scope of this paper. However, typical fungal infections for sugar maple involve the northern tooth fungus (*Climacodon septentrionalis* [Fr.] P. Karst.), which causes severe crown dieback. In all cases, sugar maples showing signs of this fungal infection are classified as moribund. However, the mere presence of a pathogen does not automatically relegate the infected tree to moribund status. For example, latent stump decay incurred by the mossy maple conk (*Oxyporus populinus* [Schumach.] Donk [1933]) only leads to a 'C' code if present at or below 60 cm from the base of the stump. If the same pathogen is encountered higher on the trunk and is associated with necroses, cracks, and heart rot, the tree would be given an 'M' code. Similar complex ratings apply to necroses. For example, the presence of cankers such as *Neonectria* sp., *Eutypella* sp., or *Sirococcus* sp. would rate a 'C' code, if no or only superficial wood decay is visible. If heart wood decay (>5 cm in depth) is present but the necroses covers less than one apparent side of the trunk, the associated code is 'S.' However, if the necrosis spans over more than one apparent side of the trunk, the tree is then classified as moribund.

Other classification criteria, such as trunk deformations, bark cracks, and root or crown damage are more straightforward to identify than pathogen infections, but their inclusion adds to overall classification complexity as well. More details of the rating system can be found in the field guide (Boulet, 2005).

2.3. Tree growth data

While all growth data for live trees were obtained from increment cores taken from trees inside the study plots, the number of dead trees in the plots was insufficient for our analyses. We therefore had to extensively search for dead trees throughout the entire area of the 1993 and 1994 harvest blocks. However, we only sampled dead trees that were on sites and within stands similar to those where the initial live tree plots were located. Also, only trees with evidence of recent death (1993 or later) were selected, based on the presence of bark and fine branches, and on the absence of advanced trunk decay (Sénécal et al., 2003).

Dead tree growth data for parameterizing the survival probability model (see below) were collected from dead trees without any evidence of obvious causes of instantaneous death (uprooting, bole breakage, etc.). This was to exclude growth-independent factors from influencing the parameter estimates of the growth-driven survival probability model. Standing dead trees were felled and a cross section of the trunk at 1.3 m above ground level was sampled.

A total of 321 live and 56 dead trees were sampled, with a more or less uniform distribution among dbh classes (19.1–29.0, 29.1–39.0, and 39.1–49.0 cm). Increment cores and cross sections were progressively sanded down to grain 400 to allow a clear identification of the final cell layer in each tree-ring. Tree-rings were measured using a microscope equipped with a computer-assisted micrometer (0.001 mm precision). Of the three increment cores taken per live tree, at least two were readable in most cases, and were used for growth measurements. For the dead trees, two radii per tree were chosen from cross sections so that growth measurements could be undertaken. 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).

A subsample of dominant live trees was selected to construct a master chronology using the program COFECHA (version 6.06P, Holmes, 1983). Live and dead tree-ring series were then cross-dated based on the visual examination of marker years and correlation with the master chronology. All tree-ring series showed a severe growth decline in 1988 and this decline served as reliable marker year. After a visual dating with these marker years, COFECHA was used to detect missing or false rings in individual tree-ring series, which were then identified on the cores or cross sections. These missing or false rings were then added or removed from the series and COFECHA was run again to verify the cross-correlation with the master chronology. This procedure was repeated until good cross-correlations ($r \geq 0.3$, Tardif et al., 2001) with the master chronology were obtained. For live trees, the series covered calendar years from 1878 (healthy) or 1898 (moribund) to the year of sampling (2004), whereas the dead tree series (measured completely from cross sections) covered calendar years 1848–2003 or earlier, depending on the year of death of individual trees.

From the 321 live trees sampled in our plots, 56 individuals (i.e., a number equivalent to the sample size of dead trees) were randomly selected and used to parameterize the survival probability model. To assure that growth of selected trees (and the resulting survival probability model) had not been negatively influenced by direct harvest disturbance, live trees were selected only when our field assessment indicated absence of obvious harvest disturbance (i.e., trees not close to skid trails and not heavily thinned).

2.4. Logistic regression

Logistic regression was used to model survival probabilities as a function of radial growth, in the following form (Bigler and Bugmann, 2003):

$$P(Y = 1) = \frac{e^{\beta X}}{1 + e^{\beta X}} \tag{1}$$

where $P(Y = 1)$ is the probability that an individual tree survives given the matrix of independent variables X. The latter include three types of growth variables: (i) growth level (average growth over a specified period), (ii) growth trend (regression slopes of growth over a specified period) and (iii) growth sensitivity (average growth variability over the preceding 5 years, see below for details). The vector β of regression parameters is estimated in the analysis (Hosmer and Lemeshow, 2000; Quinn and Keough, 2002).

Table 1
Growth level, growth trend and growth sensitivity variables computed for different time windows used for logistic regression analysis of survival probabilities

Number of tree-rings to compute variable	Types of growth variables					
	Level[*]		Trend		Sensitivity	
	Variable name	*n*	Variable name	*n*	Variable name	*n*
1	rw-log	9727	–	–	–	–
3	av3-log	9722	slp3	9727		–
5	av5-log	9512	slp5	9504	sens5	9727
10	av10-log	9286	slp10	9283	–	–
25	–	–	slp25	8723	–	–

Shown are variable names and their respective number of observations, including live and dead measurements. Number of observations of dead measurements is constant across growth variables and equal the number of dead trees ($n = 56$).

[*] Log-transformed.

A manual stepwise procedure was used in the modelling process. First, only one growth level variable was included at a time. The growth level predictor variables that we considered were the log-transforms of the arithmetic mean over the preceding 3, 5 and 10 years of radial growth (Table 1). The log-transformation was applied to lower the weight of very high growth values. Using the Akaike Information Criterion (AIC, Burnham and Anderson, 2002), the D_{XY} and bootstrapped confidence intervals (see below) were used as the main decision criteria for selecting the 'best' univariate model, which was then used for further analysis. Second, growth trend variables were added individually to the best univariate model. The growth trend variables that we considered were the coefficients of the local linear regression over the preceding 3, 5, 10, and 25 years (Table 1). To avoid redundancy, only one growth trend and one growth level variable was allowed in the final model. Last, the mean sensitivity over the preceding 5 years was added to the best bivariate model. This variable represents the responsiveness of individuals to environmental signals, such as climate (Fritts, 1976). High sensitivity values have been associated with tree vigour decline because dying trees may exhibit higher variability in past growth rates (Ogle et al., 2000; Suarez et al., 2004). Interannual sensitivity was defined as (Fritts, 1976):

$$S_t = \frac{\mathrm{abs}(\mathrm{rw}_t - \mathrm{rw}_{t-1})}{\mathrm{abs}(\mathrm{rw}_t + \mathrm{rw}_{t-1})} \tag{2}$$

where S_t is the sensitivity in the year t, and rw is the ring-width measurement in the year t. We used the average sensitivity of the most recent 5 years, assuming that declining trees would exhibit growth variability during the period close to their death.

Parameter estimation was done with R software (version 2.4.0, R Development Core Team, 2005), using maximum log-likelihood. The model with the lowest AIC was retained for further analysis. Non-parametric confidence intervals for parameter estimates were computed using a bootstrap resampling procedure (*bootcov*) with 1000 repetitions and applying the 25th and the 975th quantile as interval limits. Longitudinal data from tree-rings are interannually correlated and, therefore, are not independent within an individual tree-ring series. This violation of independence will underestimate the true variance and confidence interval width. To correct for within-cluster (i.e., within-tree) correlation of the responses, the *bootcov* function was used, which allows substituting cluster sampling with replacement for the usual simple sampling with replacement. The resulting parameter estimates therefore can be regarded as unbiased and were considered significant when the confidence interval did not include zero; otherwise the model was rejected even if it had a lower AIC.

To obtain additional information on the gain in model performance when variables were added, Somer's D_{XY} index was used as another decision criterion (Somers, 1962). D_{XY} is indicative of the 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) and, as such, is independent of prevalence and classification thresholds (Swets, 1988). It ranges from -1 (indicating perfect status misclassification, where all live trees are classified as dead or vice versa) to 1 (perfect status classification); values >0.6 indicate good discrimination (see Manel et al., 1999). To account for over-optimistic classification measures when validating the model on the training data (data specificity), the bootstrap resampling procedure *validate.lrm* from the *R Design* library (Harrell, 2005) was used. This procedure eliminates the optimism of the D_{XY} due to overfitting and produces a more conservative estimate of the model's discriminative ability (Harrell, 2001).

2.5. Longitudinal survival probability estimations

Survival probabilities were estimated following a longitudinal approach to logistic regression developed by Bigler and Bugmann (2004). This method uses tree-ring data from live and dead trees to estimate survival probabilities over the life span of a tree. To do so, growth data from the entire life span of the trees must enter the modelling process. First, tree growth variables (e.g., mean values and trend coefficients over different periods) are computed as predictor variables. Variables containing the last year of growth of a dead individual are marked as 'dead' measurements. All measurements of dead trees, excluding those from the year of death, and all live tree-ring measurements are marked as 'live' measurements. The logistic regression model is then fitted to data points from the entire life span of all trees.

2.6. Comparisons of survival probabilities

Among the available tree growth series (321 live, 56 dead), the data were divided into five distinct groups according to the status (live or dead) and vigour code of live trees. Individual survival probabilities were computed for vigorous ('R', $n = 160$), growing ('C', $n = 87$), declining ('S', $n = 31$), moribund ('M', $n = 43$) and dead ('D', $n = 56$) trees, and compared among groups. A series of annual ANOVAs was applied to determine whether within-year differences in survival probabilities varied statistically ($P < 0.05$) among these five groups. For years with significant differences, Tukey's HSD adjustment for multiple comparisons was applied to obtain adjusted P-values for unplanned comparisons between pairs of groups (Quinn and Keough, 2002).

3. Results

In the first step of the regression analysis, the univariate model with the best fit (lowest AIC) contained the log-transformed averages over the last 3 years of growth (model 2, Table 2).

Table 2
Parameter estimates, bootstrapped 95% confidence intervals (CI), AIC, and optimism-corrected D_{XY} of logistic mortality models. Models in bold are the 'best' univariate or bivariate models

	Independent variables	Estimate	CI (95%)		AIC	D_{XY}
			Lower	Upper		
Univariate models						
Model 1	Intercept	−1.740	−5.379	0.053	587.1	0.772
	rw-log	1.093	0.799	1.721		
Model 2	**Intercept**	**−6.589**	**−8.422**	**−4.724**	**545.9**	**0.715**
	av3-log	**1.872**	**1.567**	**2.193**		
Model 3	Intercept	−7.088	−9.397	−4.424	567.1	0.634
	av5-log	1.923	1.476	2.335		
Model 4	Intercept	−8.153	−11.121	−4.974	586.3	0.563
	av10-log	2.052	1.547	2.551		
Bivariate models						
Model 5	Intercept	−7.623	−9.555	−5.792	519.5	0.798
	av3-log	2.082	1.779	2.440		
	slp3	0.004	0.002	0.005		
Model 6	**Intercept**	**−7.115**	**−8.974**	**−5.337**	**513.5**	**0.783**
	av3-log	**2.017**	**1.713**	**2.375**		
	slp5	**0.006**	**0.004**	**0.007**		
Model 7	Intercept	−6.278	−8.393	−4.242	540.9	0.707
	av3-log	1.826	1.493	2.202		
	slp10	0.003	−0.005	0.008		
Model 8	Intercept	−5.820	−7.943	−4.018	534.4	0.710
	av3-log	1.756	1.455	2.132		
	slp25	0.008	−0.007	0.017		
Trivariate model						
Model 9	Intercept	−5.951	−8.414	−3.508	510.0	0.793
	av3-log	1.904	1.536	2.302		
	slp5	0.005	0.003	0.007		
	sens5yr	−2.622	−5.154	0.420		

Although the log-transformed annual measurement (rw-log, model 1) yielded a model with a higher D_{XY} (0.772) than model 2 (0.715), its AIC was markedly higher (587.1) than that of model 2 (545.9, Table 2). The addition of the growth trend variable yielded bivariate models with consistently lower AICs than univariate models. However, the inclusion of 10- and 25-year slopes decreased the D_{XY} to 0.707 and 0.710, respectively (Table 2). Among the two models with lower AICs and higher D_{XY} values, the addition of the trend over 5 years yielded an AIC (513.5) well below the model including the 3-year slope (519.5, Table 2). Therefore model 6 ($D_{XY} = 0.783$) was considered for further analysis even if the D_{XY} was slightly greater for model 5 (0.798). The addition of the sensitivity variable to this model caused a slight decrease in the AIC (510.0) and little improvement in the D_{XY} (0.793), but the confidence interval of the parameter estimate spanned across zero, so this predictor was rejected as being significant (Table 2).

Table 3
Sample sizes (n), mean values and standard errors (S.E.) of the predictor variables av3-log [ln(3-year average growth (μm/yr) + 1)] and slp5 [5-year regression slope (μm/yr)] of live trees in different vigour classes and dead trees

	Vigour class	n	Predictors			
			av3-log		slp5	
			Mean	S.E.	Mean	S.E.
Live	R	160	6.999^{A}	0.627	5.654^{a}	183.167
	C	87	6.920^{B}	0.657	2.170^{ad}	177.333
	S	31	6.918^{B}	0.698	2.651^{ad}	183.857
	M	43	6.893^{B}	0.645	-4.956^{bd}	201.980
Dead	D	56	6.742^{C}	0.679	-4.570^{Cd}	142.456

Upper case letters, if different between vigour classes, indicate a significant difference at $P < 0.001$, lower case at $P < 0.05$, Tukey's HSD.

Table 4
Number of trees per defect type and their respective percentage distribution within each vigour class

Defect	Vigour class							
	R (vigorous)		C (growing)		S (declining)		M (moribund)	
	N	%	N	%	N	%	N	%
None	129	80.6	0	0.0	0	0.0	0	0.0
Sporocarps	0	0.0	3	3.4	1	3.2	11	25.6
Necroses	0	0.0	0	0.0	6	19.4	23	53.5
Bole	7	4.4	8	9.2	8	25.8	1	2.3
Root and butt	6	3.8	3	3.4	0	0.0	1	2.3
Cracks	8	5.0	36	41.4	4	12.9	6	14.0
Bird pecks	5	3.1	31	35.6	7	22.6	1	2.3
Crown	0	0.0	2	2.3	1	3.2	0	0.0
Branching	5	3.1	4	4.6	4	12.9	0	0.0
Total	160	100.0	87	100	31	100	43	100

Means of the growth level variable were similar among the intermediate vigour classes, which in turn differed significantly ($P < 0.001$) from the means for vigour class R and the dead trees (Table 3). Mean log-transformed growth over 3 years (av3-log) of live trees varied between 6.893 (vigour class M) and 6.999 (R) but was only 6.742 for dead trees (Table 3). Slopes over 5 years showed a direct relationship with vigour; mean regression slopes decreased with vigour and ranged from positive (5.654, R) to negative values (−4.956, M, Table 3). However, slopes were statistically different only between vigour class R and M ($P < 0.05$) and vigour class R and D ($P < 0.001$). Interestingly, regression slopes of moribund and dead trees (−4.570) were quite similar (Table 3).

More than 80% of vigorous trees had no defects, while the reminder had cracks (5.0%), bole (4.4%), root and butt defects (3.8%), or bird pecks and branching defects (both 3.1%, Table 4). These defective trees showed no signs of decay. Most defects of growing trees were bole cracks lacking signs of decay or bird pecks, which together affected more than 75% of trees in this class (Table 4). Declining trees were mostly affected by bole defects (25.8%), bird pecks (22.6%) and cambium necroses (19.4%). There was evidence of fungal infection in one individual in this class (Table 4). Moribund trees were mostly affected by sporocarps and stromata (26.6%), together with cambium necroses (52.4%) and decayed cracks (14.3%), which characterized more than 90% of trees in this class (Table 4).

For all vigour classes, there was a strong growth decline apparently due to disturbance in 1971 and 1988 (Fig. 1a). Average annual growth rates of vigorous trees (R) were consistently higher than growth rates of trees in other vigour classes, at least from the 1960s onwards, but showed a similar pattern (Fig. 1a). On the other hand, growth of dead trees (D) showed a distinct pattern of steady decline from 1960 onwards, with a small increase in the last year (Fig. 1a). This apparent recovery is likely due to the continued decrease in sample size of dead trees (Fig. 1b) and associated higher variability in dead tree data towards the end of the series (Fig. 1c).

Survival probabilities were compared from 1970 onwards for more than 30 years prior to vigour estimation. Survival probabilities of dead trees were statistically different ($P < 0.05$) from those of live trees (all vigour classes) in 1976 through 1978, 1985, and in every year from 1987 until 2003 (Fig. 2a). Differences among vigour classes were less apparent and did not cover longer periods

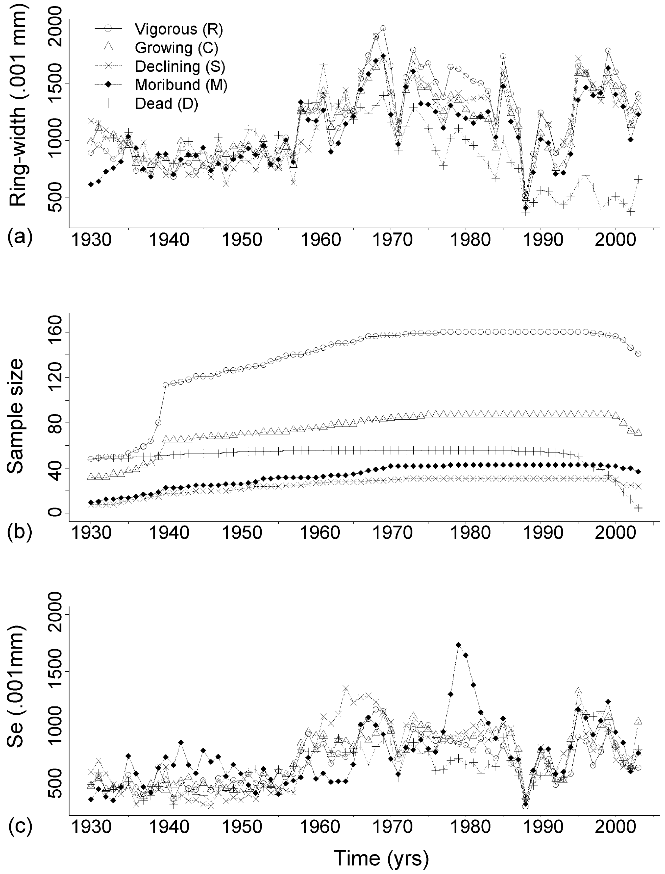

Fig. 1. Median annual ring-width (a), sample sizes (b), and standard errors (S.E.) of means (c) from 1930 to 2003 for vigorous (R), growing (C), declining (S), moribund (M) and dead (D) adult sugar maple trees. Ring-widths were measured to 0.001 mm precision. Note the strong decline in sample size of dead trees due to mortality related drop-out.

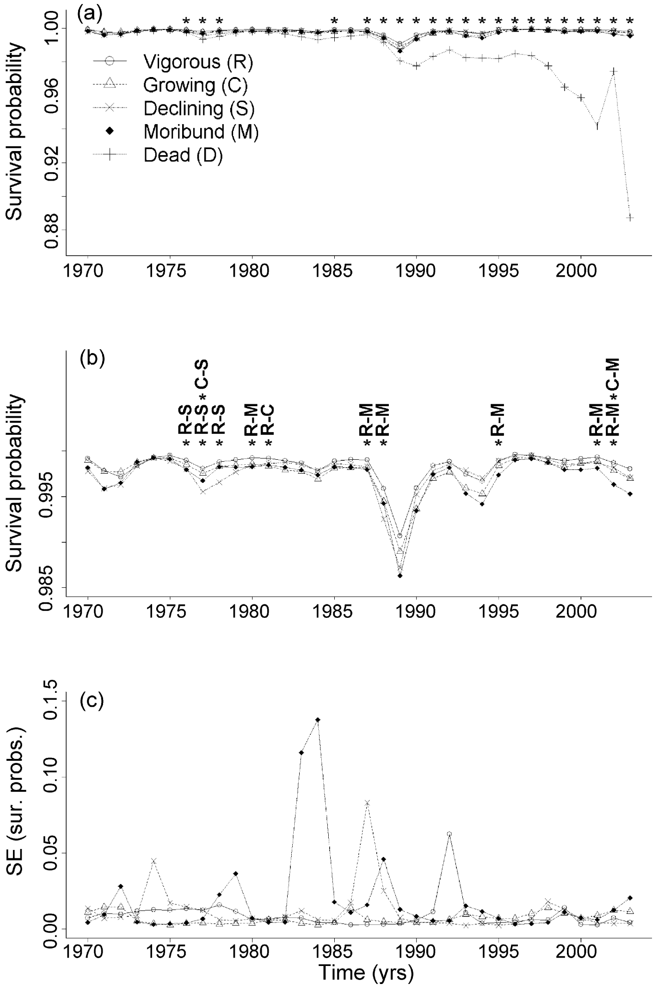

Fig. 2. Survival probabilities (a and b) and their corresponding standard errors (c) from 1970 to 2003. Panel a shows survival probabilities of vigorous (R), growing (C), declining (S), moribund (M), and dead (D) trees; panel b excludes dead trees. Asterisks (*) above the curves in (a) indicate the years of significant differences ($P < 0.05$, ANOVA) between dead and live (all vigour classes), in (b) asterisks indicate the years of significant differences ($P < 0.05$) between vigour classes based on Tukey's HSD tests for years with significant ($P < 0.05$) annual ANOVAs. Vigour classes that were significantly different from each other are listed in panel (b), with a dash separating significantly different groups.

(Fig. 2b). In the late 1970s survival probabilities of declining trees were significantly lower than those of vigorous (1976–1978) and growing (1977) trees (Fig. 2b). In 1989, which was the year following defoliation, survival probabilities dropped as markedly as radial growth in 1988 (Fig. 1a) but similarly among vigour classes. Another decline occurred in 1993–1994, the years when harvesting took place, but this trend was followed by a quick recovery (Fig. 2b).

Survival probabilities of vigorous trees were significantly higher than those of moribund trees in 1980, 1987, 1988, 1995, 2001, and 2002, and higher than those of growing trees in 1981 (Fig. 2b). Also in 2002, survival probabilities of growing trees were higher than those of moribund trees (Fig. 2b). Standard errors of the means were large for moribund (1983–1984, 1988), declining (1987) and vigorous (1992) trees, but low for most of the time before and especially after these brief periods (Fig. 2c).

4. Discussion

4.1. Linking field vigour estimates to retrospective survival probabilities

We used radial tree-ring series to estimate retrospectively survival probabilities for the entire life span of trees and used these probabilities to test the validity of a field vigour classification system. While the former methodology has been proven adequate (Bigler and Bugmann, 2004), the latter is more ambiguous especially if vigour was estimated at the very end of the tree-ring series. It is obvious that tracing back vigour estimates through time is challenging. At what point in time has a tree entered a vigour class estimated in 2004 and how did this influence radial growth rates?

Trees that were showing signs or symptoms of advanced lethal pathogen infection in 2004 (e.g., presence of perennial conks) had been already under attack for some time, in the case of the tinder fungus (*Fomes fomentarius* [L.] J.J. Kickx) up to 30 or more years (Schmidt, 2006). Also, it has been observed that pine trees (*Pinus mugo* Turra) were infected and killed by *Armillaria* spp. only if they were weakened by competition and this weakening translated into a gradual, several decades lasting decline of radial growth prior to death (Cherubini et al., 2002). These low growth rates were estimated as preconditioning to fungal attack and not as its result (Cherubini et al., 2002). Similarly, Pedersen (1998) found that oak trees (*Quercus* spp.) died several decades after an inciting drought stress and that these trees had lower growth rates than surviving trees during this period. Lower growth rates of dead trees prior to drought were considered indicative of the preconditioning of these trees to further decline (Pedersen, 1998). On the other hand, Davis et al. (1997) observed that heavily cankered (*Cryphonectria parasitica* [Murrill] Barr) scarlet oak trees (*Quercus coccinea* Münchh.) had higher growth rates (basal area increment) than moderately cankered individuals, but their growth rates were still lower than non-cankered trees. Potential mechanisms for this growth stimulation were attributed to callus formation close to the sites of infection and sampling, and thus, were considered worthy of further investigation (Davis et al., 1997). Whether or not slow growth rates are the cause or the consequence of fungal infection may still be an open question, but both phenomena often coincide. Also, declines due to fungal infection or other sources of stress are slow processes, which may last decades. Signs (sporocarps, stromata, cankers) or symptoms (wood decay, crown dieback) of fungal infection therefore can be assumed to be reliable criteria for estimating tree vigour in the field and can be linked to survival probabilities estimated from past radial growth rates.

Similarly, severe crown dieback, if chronic or induced by competition or drought, classifies a tree as moribund when >26% of the crown is dead in suppressed individuals and >51% of the canopy of trees with open, chlorotic and dwarf-leaved crowns is dead (Boulet, 2005). Although severe crown dieback (i.e., >40%) cannot not be supported by trees for very long periods (Gross, 1991), our data show (Fig. 1a) that a single severe crown defoliation caused by a forest tent caterpillar outbreak (1971) initiated severe declines in growth rates that persisted over decades in less vigorous trees. Similar results have been observed in trembling aspen (*Populus tremuloides* Michx.) where crown defoliations reduced radial growth rates and predisposed trees to attack by wood-boring insects and fungal pathogens (Hogg et al., 2002).

Structural defects, such as butt defects, bole cracks or strong leaning, reduce survival probabilities by increasing the risk of mechanical failure. The presence of deep cracks decreases the tree's mechanical resistance to external forces, such as wind, and increases the tree's risk to fall over (Smiley et al., 2007). These risks are unlikely to show in radial growth rates but the vigour classification system assigns a moribund code only to major structural defects (e.g., crack >1.5 m) that are accompanied by profound wood decay caused by fungal activity (Boulet, 2005). However, because fungal infections in this instance are a result of mechanical damage rather than one of reduced vigour, their linkage to radial growth rates may be difficult to detect. This decreases the potential of survival probabilities inferred from radial growth to reflect vigour classification in these cases.

4.2. Validating the field vigour estimates with growth-dependent survival probabilities

In this study, radial growth of dead and, to a lesser extent, moribund trees diverged from that of vigorous trees shortly after 1971 and onwards (Fig. 1a). This and a subsequent growth decline in 1988 can be linked to forest tent caterpillar defoliation, a disturbance recurring over about a 9-year cycle in the study region (MRNFP, 2002; MRNF, 2005). A comparison of growth rates in sugar maple (a host species) and yellow birch (a non-host species) clearly showed that birch did not incur the same growth reduction as sugar maple (Hartmann, unpublished data), supporting the hypothesis that the growth decrease observed among maples resulted from tent caterpillar defoliation and not from other disturbances (e.g., drought). Growth declines prior to death are consistent with Manion's tree decline model (Manion, 1981), where predisposing stresses reduce tree vigour and inciting factors cause a final decline and death. For dying trees, the first defoliation (although not a long-term stress, as stated in Manion's model) reduced tree vigour, i.e., growth rates and survival probabilities, and predisposed these trees to a second, more intense forest tent caterpillar defoliation, which led to an accelerated growth decline and to death (Fig. 1a). Average growth rates during these defoliations were (although not significantly) higher in vigorous than in moribund trees, possibly indicating that their greater carbon reserves allowed for quick foliage replacement and growth recovery (McLaughlin et al., 1980).

Survival probabilities corroborate, at least partially, the visual tree vigour classification used for tree marking. The different vigour classes that are used in Quebec (Boulet, 2005) are supposed to broadly predict tree survival probabilities. It is assumed that moribund trees will likely die before the next harvest (over the next 20–35 years), whereas declining trees should survive until the next harvest despite their decreasing vigour (and hence, survival probability). Growing and vigorous trees are assumed to have unconstrained life expectancy.

Although the average 5-year slope of moribund and now dead trees was negative (Table 3), survival probabilities of moribund trees showed no monotonic negative growth trend over the most recent 30 years (Fig. 2a), as has been observed in other studies (Bigler et al., 2004). This may be due to the fact that, in this study, vigour estimates were based on external signs and symptoms related to vigour but not on any actual measures of physiological activity. Bigler et al. (2004, p. 185) used cambial vitality, a measure that "correlated significantly with the number of cells produced by the cambium", for vigour estimations in European silver fir (*Abies alba* Mill.). Obviously, the number of cells produced by the cambium correlates well with tree ring-width. However, vigorous, growing and declining trees in this study had higher (positive) average growth trends computed over the entire tree-ring series than those of moribund and dead trees (negative, Table 3), indicating that moribund and now dead trees showed an overall growth decline over their life span.

In this study, mean survival probabilities of vigorous trees were greater than those of moribund or declining trees for most years from 1970 onwards, although not consistently throughout this period (Fig. 2a). The growth-driven survival probability model used in this study may not correctly predict survival probabilities in trees affected by growth-independent defects, such as bole cracks, which accounted for roughly 14% of moribund trees. Similarly, most growing (≈90%) and declining (≈61%) trees were classified based on bole injuries, root butt defects, cracks or bird pecks (Table 4). None of these defects is directly linked to radial growth rates, and therefore, their effects on tree vigour would be difficult to relate to survival probability estimated from retrospective growth series. This may also explain why no significant differences in survival probabilities between intermediate vigour classes have been detected.

4.3. Implications for forest management

The results of this study highlight the strengths and weaknesses of an elaborate visual field vigour classification system. In a context where partial harvesting is used, vigour estimation is a crucial step in assigning harvest priorities for tree marking if stand improvement is sought (OMNR, 2004). Tree classification systems have a long tradition, dating back to the 1840s (Rosznyay, 1979). Early classifications, such as that proposed by Kraft (1884), described trees in terms of their social position, and were later amended to include qualitative measures of bole quality (Heck, 1931). In 1956, Leibundgut defined the IUFRO (International Union of Forest Research Organizations) tree classification system, which combines social position, harvest priority and tree quality in a numeric code (Leibundgut, 1956).

Only much later did Waring et al. (1980) define a quantitative measure of tree vigour as the ratio of basal area growth to sapwood basal area representing the amount of stemwood produced per square meter of foliage. Instead of describing trees by visually evaluating their external condition, the 'Waring vigour' index described their overall vitality. Assuming that stem growth has a low priority in carbon allocation, the amount of stemwood produced, weighted by the size of a tree's photosynthetic apparatus, was considered indicative of tree vigour (Waring et al., 1980). Other vigour measures, such as crown transparency (Millers et al., 1991), nutrient content of needles or sapwood (Joos, 1997), electric cambial resistance (Torelli et al., 1996) or chlorophyll fluorescence (Lichtenthaler and Rinderle, 1988), also aimed at describing tree vigour (see Gehrig, 2004 for a comprehensive review). Among these vigour-based measures, only crown transparency can be easily assessed in the field. However, crown openness can be caused by several agents and stresses (Innes, 1993) that vary temporally, especially in broadleafed trees, and therefore, it may not be adequate as a criterion for tree removal.

The vigour classification used in this study may overestimate the time-to-tree death. If moribund trees were to die within 20–25 years following vigour estimation, one would expect their survival probabilities to decline in a fashion similar to those of dead trees. However, survival probabilities of dead trees were significantly lower than those of all vigour classes in most years from 1970 onwards and in every year from 1987 to 2003 (Fig. 2a). This indicates that moribund trees were not declining as rapidly as dead trees were prior to their death, at least for the most recent 16 years. It is therefore doubtful that these trees would die within the predicted period.

The classification system used in Quebec, which is based on vigour-related defects in trees, has the practicality of classical tree classifications and was able to discriminate between moribund and vigorous trees, the two extreme vigour classes. It did not discriminate among the intermediate vigour classes, which suggests that the various criteria used did not affect diameter growth. However, such field vigour classifications could not adequately predict the timing of tree death with any accuracy.

Acknowledgements

We thank Catherine Malo for her help during the long weeks of field work and dendrochronological analyses. We also thank Mr. Denis Boileau of the Quebec Ministry of Natural Resources for his help in explaining historical tree growth disturbances and Ronnie Drever for reviewing an earlier draft of this paper. We also thank Lana Ruddick and Bill Parsons for improving the linguistic quality of the manuscript. We would also like to thank Christof Bigler, an anonymous reviewer, and the Special issue guest editor for their thorough reviews and helpful suggestions. Financial support was provided by FQRNT (Programme des actions concertées) through a research grant to C.M., M.B. and colleagues, and by NSERC through a scholarship to H.H.

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