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WHITE PINE WEEVIL ATTACK ON WHITE SPRUCE: A SURVIVAL TIME ANALYSIS

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Abstract. The survival time of a white spruce tree (*Picea glauca* (Moench) Voss) with respect to the attack by the white pine weevil (*Pissodes strobi* (Peck)) was defined as the number of years until an attack occurred. In this context, resistant trees are those capable of delaying attacks rather than preventing attacks. This study investigated the patterns of survival times of resistant and susceptible trees in a progeny trial of white spruce in the interior of British Columbia, Canada. By doing so, we demonstrated that survival time analysis, a technique specifically developed for dealing with clinical medicine and industrial reliability tests, was a very useful approach in analyzing resistance of hosts to herbivore attack. The results suggested that survivorship of resistant trees was significantly different from that of susceptible trees, as expected. The median survival time of susceptible trees was ~12 yr after seeding, while it was 21 yr for resistant trees. The survival times of white spruce trees were identified adequately following a lognormal distribution. Based on the estimated hazard functions of the lognormal distribution, the most severe weevil infestation was predicted to occur at 19 yr for susceptible trees, and at 26 yr for resistant trees. Infestation level was affected by several factors, such as tree height, seasonal temperature, and precipitation. An accelerated failure time model was used to evaluate the effect of these factors on survivorship. The identification of resistant or susceptible trees by survival times is to be incorporated into an integrated pest management program for the white pine weevil in British Columbia.

Key words: accelerated failure time model; censored observations; lognormal distribution; modeling survivorship and hazard rates; pest management; Picea glauca; Pissodes strobi; *survival time analysis; survivorship; time-to-attack; white pine weevil; white spruce.*

INTRODUCTION

Survivorship analysis has been of interest in population ecology for several decades (Morris 1959, Caughley 1977, Southwood 1978), but it is only recently that the statistical methods used to analyze survival data of patients in clinical trials and reliability of products in engineering have attracted attention of ecologists (Muenchow 1986, Pyke and Thompson 1986, Dixon and Newman 1991, Fox 1993, Newman and McCloskey 1996). Ecologists are progressively realizing that many phenomena in biology and ecology can be described by the "time until a given event occurs," for instance, the time until a flower is visited by a pollinator (Muenchow 1986), time to emergence of a seed or flowering of a plant (Fox 1993), time to respond to a toxicant effect (Newman and McCloskey 1996), or stand growth until a fire or since a fire (Johnson and Gutsell 1994). These varieties of time data share some common properties, e.g., nonnegativity, strongly skewed distribution, and censoring. Therefore, "classical" statistical methods (e.g., ANOVA) do not readily accommodate these types of data, or their estimation and inferences can be highly biased. A more proper treatment of these data may be to apply statistical methods specifically developed for survival time (failure time, time-to-failure, time-to-event) analysis (Kalbfleisch and Prentice 1980, Lawless 1982, Cohen and Whitten 1988, Lee 1992), as these may allow us to study a problem from a new angle and enhance our understanding of a phenomenon. An excellent introduction for the application of survival time statistics in ecology can be found in Fox (1993) and Dixon and Newman (1991).

The white pine weevil, *Pissodes strobi* (Peck), is an important North American pest of pine and spruce regeneration (see Plate 1). The insect, which has one generation per year, oviposits on the apical shoot or leader, and the larvae, feeding on the shoot phloem, girdle and kill the leader (Alfaro et al. 1995). Affected trees sustain growth losses and deformity. Resistance or susceptibility of a plant to herbivore attack is usually considered a dichotomous characteristic, by which a plant is either attacked or not attacked. However, in studying spruce (*Picea* spp.) resistance to the white pine weevil in British Columbia, Canada, we have noticed that several factors can affect the probability of weevil attack on a spruce tree, e.g., the resistance level of the trees, the dispersal and spatial patterns of the pest, tree height, and stand density (VanderSar and Borden 1977, Alfaro and Omule 1990, Kiss and Yanchuk

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PLATE 1. An adult white pine weevil, *Pissodes strobi*. Photograph by René Alfaro.

1991, He and Alfaro 1997). Resistance varies widely by host family or tree, with some trees being nearly immune in the field, whereas others are relatively susceptible (Alfaro et al. 1996). The presence or absence of attack, or the number of attacks on a tree, is usually used as a measure of resistance or susceptibility of a spruce tree. However, this single measure is not reliable. For example, moderately resistant trees can also be attacked when weevil food is in short supply; susceptible spruce leaders have been destroyed when the pest population is high. Thus, a resistant tree may not remain free from attack, but will have delayed attacks, i.e., a resistant tree will remain unattacked longer than a susceptible one. The difference between resistant and susceptible spruce trees can be conceived as the difference in the period free from attacks. Biologically, this attack-free time should more appropriately describe the resistant or susceptible status of a host to a pest.

By translating time-to-event into time-to-attack, in this study we apply the techniques of survival time analysis to describe attack rates by the white pine weevil on white spruce (*Picea glauca* (Moench) Voss). The time-to-attack, or survival time, is defined here as the number of years a spruce tree will grow until an attack occurs. Survival time analysis can be useful in pest management, because it may help to predict probability of plantation failure, understand the conditions that increase plantation risk, and determine the benefits of planting resistant stock. Specifically, the objectives of this study are to study the statistical properties of the survival times of white spruce trees attacked by white pine weevils, to compare survivorships between resistant and susceptible trees, and to identify hazard factors for white spruce. A data set of weevil attack in a white spruce progeny trial in British Columbia, Canada, is the basis of the study.

STUDY SITE AND MATERIALS

In the late 1970s, a large genetic survey of white spruce was conducted to identify desirable trees for progeny testing and propagation in British Columbia. In the spring of 1984, a plantation at elevation 1000 m near Clearwater, British Columbia, Canada (51°42′ N, 120°03′ W) was established with three-year-old seedling offsprings of 142 open-pollinated white spruce parents. Thirty-two seedlings from each family (forming a maternal sibship) were planted with ~3 m planting distance between trees. Excluding seedlings that died right after planting, 139 families (4330 trees) were left for subsequent attack observation. The first white pine weevil attack in the plantation occurred in 1986, when seedlings were five years old. In this plantation, the infestation rate was relatively low before 1991, but then gradually increased. In 1995, the attack rate increased sharply, when 22% of the 4330 trees were attacked (Fig. 1). This epidemiology pattern is typical of the white pine weevil: it rarely attacks <5-yr-old trees, then population increases in an oscillatory manner reaching maximum levels, then declines thereafter. Infestation can last >50 yr, but peak infestation

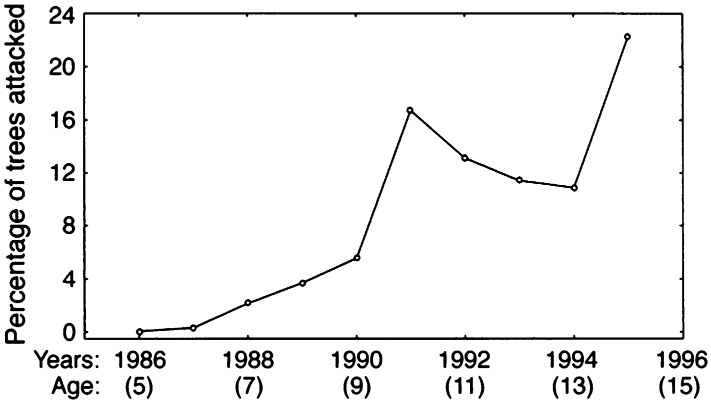

FIG. 1. Outbreak of the white pine weevil in a white spruce family trial at Clearwater, British Columbia, Canada. Weevil attack started in 1986 when the trees were 5 years old.

occurs when stands are 20–30 years old (Alfaro and Omule 1990). In this experiment, we believe the plantation is entering the high infestation period.

In 1995, retrospective surveys determined the number of weevil attacks in each year during 1986–1995, as well as variables that represented attack intensity (e.g., the number of weevil attacks on trees), attack severity (e.g., mean length of stem killed) and tree tolerance to weevil attack (e.g., tree stem form). These variables were used in an earlier report to derive a resistance rank for each of the 139 families based on a principal component scores (Alfaro et al. 1996). The scores were used to group families into resistant, intermediate, and susceptible categories, by defining those in the first quartile and the third quartile of the rank distribution as resistant and susceptible families, respectively; other families were labeled as intermediate. The resistant families include 1135 trees, and the susceptible families, 1146 trees. Survival times (time-to-attack) of the resistant and susceptible trees were recorded.

Climatic data from a nearby weather station (at elevation 720 m) were recorded during 1986–1995. The mean daily seasonal air temperature during January–March (TEMP1) and April–June (TEMP2), and the mean monthly precipitation during January–March (RAIN1) and April–June (RAIN2) were used, together with tree height in 1986 (HT86), as explanatory variables to evaluate how these measurements affect the survival times of spruce trees. These seasonal climatic data were used, because they are important in the weevil biological cycle. The January–March period is when maximum overwintering mortality occurs, while the April–June period is when the weevils emerge from overwintering and select the trees for attack.

SURVIVORSHIP AND HAZARD RATE FOR WHITE SPRUCE TREES

Censored survival times

Survival time of an individual, denoted by T, is subjected to random variation. An important feature of survival time is that it can be exact or censored. Censored time occurs when a tree has been lost or died, or when the experiment has been terminated before the occurrence of an attack. For the censored time, we do not know if an attack would occur in the future, but we do know that the minimum survival time is equal to the observation period. In this study, the resistant group had 259 exact observed times and 876 censored times, while the susceptible group had 829 exact times and 317 censored times. Survival time, T, is considered as a continuous random variable, counted from 1982 (the time of seeding). The pattern of T can usually be characterized by the three functions we now describe.

Probability density, survival, and hazard functions of survival times

The probability density function (pdf), f(t).—The pdf of T is defined as the probability p that a white spruce tree is attacked by a white pine weevil in interval t to $t + \Delta t$:

$$f(t) = \lim_{\Delta t \to 0} \frac{p(t \leq T < t + \Delta t)}{\Delta t}. \qquad (1)$$

The distribution of $f(t)$ is usually skewed. Exponential, Weibull, gamma, and lognormal distributions are commonly used to describe survival times (Lawless 1982, Cohen and Whitten 1988, Lee 1992).

Survival function, S(t).—This function is defined as the probability that a tree lives longer than t without an attack:

$$S(t) = p(T > t). \qquad (2)$$

Hence,

$$S(t) = 1 - p(T \leq t) = 1 - F(t) \qquad (3)$$

where $F(t)$ is a cumulative probability function.

$S(t)$ is a nonincreasing function. When $t = 0$, $S(t) = 1$, which is the case at the beginning no trees are attacked; when $t \to \infty$, $S(t) = 0$, i.e., if time lasted long enough, all trees would be attacked.

Hazard function, h(t).—The hazard function is a conditional failure rate that is defined as the probability that a tree is attacked during interval t to $t + \Delta t$, given that the tree has survived to time t. It is expressed as follows:

$$h(t) = \lim_{\Delta t \to 0} \frac{p(t \leq T < t + \Delta t \mid T \geq t)}{\Delta t}. \qquad (4)$$

The function $h(t)$ is an instantaneous or age-specific failure rate, which characterizes failure risk during the aging process. It can be expressed as a function of $F(t)$ or $S(t)$:

$$h(t) = \frac{f(t)}{1 - F(t)} = \frac{f(t)}{S(t)}. \qquad (5)$$

These three functions are mathematically equivalent (by knowing any one of them, we can derive the others), but they describe different aspects of survival times. If a parametric model can be identified for survival times, the three functions can be explicitly expressed by t, otherwise, these functions should be evaluated by nonparametric approaches in which no explicit forms could be given. A nonparametric analysis is usually applied before a parametric model is identified, for it can provide useful information in choosing a parametric model.

Nonparametric method: product limit estimate

If there are no censored observations, survivorship can simply be estimated by calculating the proportion of trees without attack by time t. However, when censored observations occur, the procedure can overestimate the survivorship, because the exact survival time of the censored observations is unknown. When censored observations are involved, the product limit (PL)

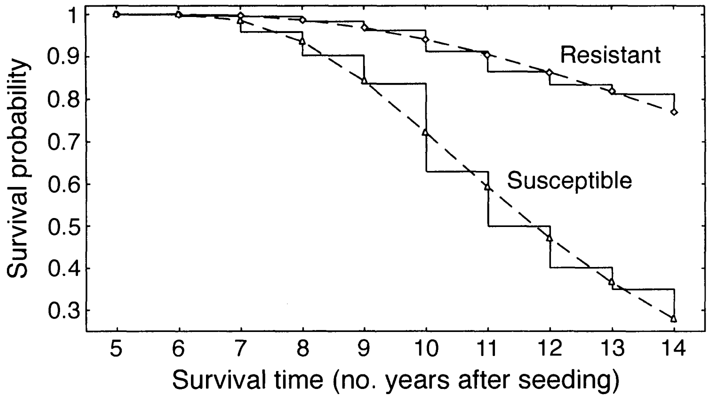

FIG. 2. Survivorship of resistant and susceptible white spruce trees in a plantation near Clearwater, British Columbia. Survival time is the age of a spruce tree when the initial weevil attack occurs, i.e., the number of years after seed germination. The step lines represent the product limit estimates (nonparametric method), while the dashed smooth lines are the estimates of survival functions based on the lognormal distribution (parametric method).

estimate of survival function must be used (Kaplan and Meier 1958). The PL method estimates the survival function $S(t)$ as a product of t conditional observed survival probabilities:

$$S(t) = p_1 \times p_2 \times \ldots \times p_t \qquad (6)$$

where 1, 2, . . . , t are distinct times at which attacks occur; p_i is the proportion of trees surviving the ith year after they have survived $i - 1$ years, which is calculated as $p_i = (n_i - d_i)/n_i$; where n_i is the number of trees at risk at time t_i, i.e., the number of trees alive and uncensored just prior to t_i; d_i is the number of attacks at t_i. Unless otherwise indicated, all the calculations in this study were done using S-plus (MathSoft 1995).

The PL estimates of the survivorships for resistant and susceptible trees are shown in Fig. 2. As expected, the survivorships of resistant and susceptible trees were significantly different (Lee 1992:109–112; log-rank test: $\chi^2 = 599$, df = 1, $P < 0.001$). The median survival time for the susceptible trees was ~12 yr, with half of the susceptible trees attacked 12 years after being seeded; whereas <15% of the resistant trees were attacked at that time. The median survival time for the resistant trees was 21 yr.

Parametric method: lognormal distribution

A parametric model is more efficient than nonparametric counterparts in survival pattern description, parameter inference, process identification, and generating hypotheses. However, choosing a particular parametric model is essentially an empirical task and should be better based on biological experience. The lognormal distribution is widely used as a survival time model in various situations (Nelson and Hahn 1972, Whittemore and Altschuler 1976). The hazard function of the lognormal distribution initially has the value $h(t = 0) = 0$, increases to a maximum with increasing time, and then decreases to zero as t becomes large. This feature has been considered as an undesirable property in many survival time analyses, because the hazard function will generally not approach zero at large time, since all the objects will eventually fail (Lawless 1982). However, it is this "unpleasant" property that renders this model suitable in describing the attack survival times of white spruce trees, because weevil infestation on spruce follows a low–high–low pattern (Alfaro and Omule 1990). Another model with a similar hazard shape is the log-logistic distribution (Lawless 1982). With our data, we found that the fitting of the log-logistic was indistinguishable from the lognormal distribution, although the latter was marginally better in terms of the log-likelihood test. Therefore, only the lognormal distribution is reported here.

TABLE 1. Maximum likelihood estimates of the two parameters of the lognormal distribution that models survival times for resistant and susceptible white spruce trees.

Parameter	Resistant	Susceptible
$\hat{\mu}$	2.7602	2.0468
$\hat{\sigma}$	0.6212	0.4362
−2 log-likelihood	1196.19	1551.67

Note: The "hat" over the parameters μ and σ indicates that estimated values are given.

The lognormal distribution function used here is a three-parameter model with time lag = 4 (1982–1985, inclusive), indicating that spruce trees were not attacked until they were 5 years old, i.e., in 1986. The pdf and the survival function of lognormal distribution are as follows, for $t > 4$:

$$f(t) = \frac{1}{(2\pi)^{1/2}\sigma(t-4)} \exp\left[-\frac{1}{2}\left(\frac{\log(t-4)-\mu}{\sigma}\right)^2\right] \qquad (7)$$

and

$$S(t) = 1 - \Phi\left(\frac{\log(t-4)-\mu}{\sigma}\right) \qquad (8)$$

where Φ is the standard normal distribution function. The hazard function $h(t)$ is related to $f(t)$ and $S(t)$ through Eq. 5.

The parameters μ and σ were estimated for resistant and susceptible groups, respectively. The maximum likelihood estimates (MLE) calculated using S-Plus are listed in Table 1. The log-likelihood tests (χ^2 test; df

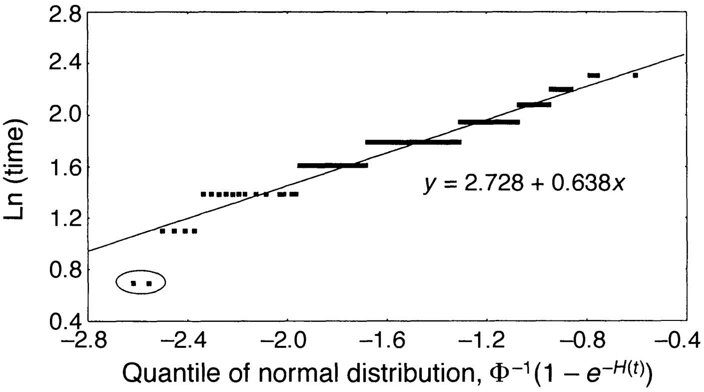

FIG. 3. Hazard plot for the lognormal distribution of the survival times of resistant trees. The two trees (circled) at the lower left corner are the least resistant trees in the resistant group, which cause some curvature in the plot; otherwise the linearity is very reasonable. The linear function is $\ln(T) = \mu + \sigma\Phi^{-1}(1 - e^{-H(t)})$, where $H(t)$ is the cumulative hazard rate (Lee 1992), and Φ^{-1} is the inverse of the standard normal distribution function Φ.

= 2) suggest that the lognormal distribution constitutes an adequate model for the survival times of the white spruce trees (Table 1).

Graphical methods for checking model adequacy can be very effective and helpful, particularly when used in conjunction with numerical analysis. Therefore, they are now advocated in survival analysis (Lee 1992). A hazard plot is a major plotting method in survival analysis that is similar to the probability plot. It, however, plots the observations against the cumulative hazard values, instead of cumulative probability values as in probability plot. A straight line in the hazard plot suggests the adequacy of a model. Model parameters can approximately be read from the slope and intercept of the line. Hazard plots can easily handle censored data. The hazard plot for the resistant group of spruce trees is presented in Fig. 3 (for the detailed procedure of hazard plotting, see Lee [1992]:173–182). No serious departure of the hazard plot from linearity was detected, although there is some curvature at the left corner of Fig. 3, caused by two trees that were attacked at age 6 yr (in 1987 and three years after the seedlings were planted). We knew these two trees belonged to the least resistant family in the resistant group. They may be considered as outliers taking into account the fact that there are 1135 trees in the resistant group. Therefore, we considered it reasonable to accept the lognormal distribution as the underlying model for the survival times of the spruce trees. The intercept (2.728) and slope (0.638) of the line in Fig. 3 are the graphical estimates of the mean and variance of the lognormal distribution that agree very well with the MLEs. The hazard plot of the susceptible trees had a similar linearity.

The survivorship estimates of the lognormal model for the resistant and susceptible spruce trees are shown in Fig. 2. This model fits fairly well the survival data of the spruce trees in this study. The estimated hazard functions of the resistant and susceptible trees are very different (Fig. 4). As expected, susceptible trees had much higher hazard rates than resistant trees. Resistant trees not only had lower hazard rates, but delayed attacks as well. The highest hazard rate, extrapolated from the fitted lognormal distribution, for susceptible trees, occurred at age 19 yr with an estimated hazard rate = 0.298 (i.e., 29.8% of healthy susceptible trees being attacked in that year), whereas for the resistant trees it occurred at age 26 yr with an estimated hazard rate = 0.085 (i.e., 8.5% of healthy resistant trees being attacked in that year). The projection of the hazard function for susceptible trees beyond the observation period (Fig. 4) describe an epidemiology pattern very similar to the one observed by Alfaro and Omule (1990). On susceptible trees, the weevil infestation in-

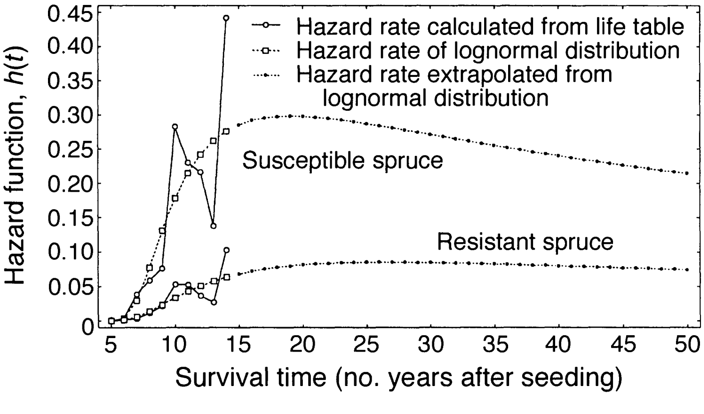

FIG. 4. Hazard rates of spruce trees resistant and susceptible to white pine weevil. The smooth dashed lines were calculated from the hazard function of lognormal distribution. The solid lines were calculated using the life-table method (SAS version 8.09, procedure LIFTEST). Weevil attacks were observed for the first 14 yr. Beyond that, the hazard rates were extrapolated from the estimated hazard functions of the lognormal distribution.

creased quickly at the start of the outbreak, then remained at a high attack rate for several (15–30) years, in a stage of relative equilibrium; thereafter attacks gradually declined. On resistant trees, attacks rose gradually and remained at relatively constant low levels in the duration of the outbreak.

IDENTIFICATION OF RISK FACTORS

It is of high interest to identify factors that affect or explain the survival times of spruce trees to weevil attack. This can be done using conventional regression techniques, relating survival time, or a transformation of survival time, which are dependent variables, to other explanatory variables. An appropriate approach for our data is an accelerated failure time model, in which the explanatory variables multiplicatively affect failure time of a tree, or linearly affect the natural logarithm of a failure time, $\ln(T)$ (Lawless 1982, Fox 1993, Newman and McCloskey 1996). This model is written in the form

$$\ln(T) = \mathbf{X}\boldsymbol{\beta} + \sigma\varepsilon \tag{9}$$

where $\mathbf{X}$ is an $n \times p$ matrix of explanatory variables for n observations and p variables, $\boldsymbol{\beta}$ is a $p \times 1$ vector of unknown parameters, σ is a scale parameter, and ε is a $n \times 1$ vector of random errors from a specified survival distribution that is independent of $\mathbf{X}$. In our case, because T follows a lognormal distribution, ε is a standard normal distribution. $\boldsymbol{\beta}$ is estimated using maximum likelihood methods.

Five explanatory variables were included in the regression: RS (resistance status, an indicator variable; RS = 0 for resistant trees, RS = 1 for the susceptible); HT86 (the tree height when weevil attack started in the plantation in 1986), TEMP1 and TEMP2 (the mean daily temperature of first season and second season, respectively), RAIN1 and RAIN2 (the mean monthly precipitation of first and second season, respectively). The maximum likelihood estimates (MLE) of the coefficients β show that all variables except TEMP2 contribute significantly to the survival time of the spruce trees (Table 2).

Because T and $\ln(T)$ have a monotonic relationship, the interpretation of Table 2 can be directly made on T. The resistance status (RS) of a tree as defined a priori had significantly negative effect on the survival time of spruce trees (Table 2; resistance [RS = 0] had longer survival time than the susceptible [$RS = 1$]). Tree height in 1986 (HT86, a height before attack) also had a significantly negative association with survival times, since shorter trees survived longer. This is consistent with the observation that weevils have a preference for fast growing trees (VanderSar and Borden 1977), probably because slow growing trees have slim phloem in the leaders on which weevils feed. The mean temperature in January–March were all <0°C (i.e., TEMP1 had negative values) except for 1992, in which the mean temperature was 1.33°C. The negative coefficient for TEMP1 in Table 2 indicates that the cold temperature of the first season increased the survival time of spruce trees. The reason may be that cold weather in the first season killed overwintering weevils, thus reduced the weevil populations. No significant effect was found for the mean temperature during April–June (TEMP2) on survival time of spruce trees in the regression (Table 2). Increasing precipitation in the first and second seasons increased survival time of spruce trees, suggesting that wet weather reduces weevil population in the overwintering stage and may delay oviposition, thereby reducing the hazard of weevil attacks.

TABLE 2. Maximum likelihood estimates of the coefficients β for different risk factors in the accelerated failure time model in Eq. 9.

Variable	$\hat{\boldsymbol{\beta}}$	Standard error	z	P
Intercept	1.4152	0.2589	5.48	>0.0001
RS	−0.0808	0.0083	−9.76	>0.0001
HT86	−0.0049	0.0007	−6.54	>0.0001
TEMP1	−0.0507	0.0062	−8.13	>0.0001
TEMP2	−0.0012	0.0235	−0.05	0.958
RAIN1	0.0571	0.0015	37.45	0.0001
RAIN2	0.0061	0.0010	5.86	0.0001

Notes: RS is an indicator variable (0, resistant trees; 1, susceptible trees). HT86 is tree height in 1986, at the beginning of outbreak. TEMP1 and TEMP2 are the mean daily temperatures for January–March and April–June, respectively. RAIN1 and RAIN2 are the mean monthly precipitation in the same periods. The parameters were evaluated using command "survreg" of S-plus. The scale parameter $\sigma = 0.274$ in Eq. 9, and -2 log-likelihood = 858.35. The "hat" over the vector $\boldsymbol{\beta}$ indicates that estimated values are given.

DISCUSSION

The application of survival time analysis to describe the resistance of a host plant to an insect pest is a novel approach in pest management. Under this framework, tree resistance is interpreted as delayed attacks, not lack of attack. This approach is particularly consistent with the principle of integrated pest management, in which the goal is not to eliminate the weevils from the ecosystems, but to reduce the population below an economical threshold (Alfaro et al. 1995). In this study, by defining resistance of spruce trees in terms of time-to-attack rather than the number of attacks, we demonstrated that survival analysis could be a useful approach to achieve this pest management goal. The methods not only allow us to more precisely describe the response patterns of hosts to herbivore attack in temporal dimension, but to readily and directly quantify the effects of covariates on time-to-attack. Therefore, it provides us with essential information for pest control: under what conditions and when outbreaks may occur, which covariates are epidemiologically important, and how to control them by direct manipulation or judicious site selection; the common goal is the maintenance of a pest population below a certain level. Based on this study, expected survival times of resistant and susceptible stock, which may vary by site, could be specified at the time of planting of a particular stand. Thus, pest management actions and contingency plans could be prepared well ahead, avoiding plantation failure.

In this study, we showed that survival times of the resistant and susceptible spruce trees were significantly different, as expected because the two groups were predefined in another report (Alfaro et al. 1996), and the survival time followed a lognormal distribution. This distribution can be used to forecast the weevil hazard level for trees and families with different genetic resistance. This study only included resistant and susceptible trees, defined by the two extremes in the resistance rank distribution for the Clearwater families (top and bottom 25% of the distribution; Alfaro et al. 1996). If intermediate trees were also included, then there would be a continuous spectrum for the survival times from susceptible (short survival time) to intermediate (intermediate survival time) to resistant (long survival time). This property does not invalidate the method, but reflects the continuous nature of the resistance distribution observed.

Although tree height, temperature, and precipitation were found to have significant effects on time-to-attack (Table 2), the survival time of a spruce tree is really an outcome of the interaction of ecological factors and the tree's resistant mechanisms. Known spruce defenses include variation in the chemical composition of feeding stimulants and deterrents (Alfaro et al. 1980), differences in resin canal density (Tomlin and Borden 1994, Alfaro et al. 1997), and production of traumatic resin (Alfaro 1995, Tomlin et al. 1998). These mechanisms often occur simultaneously, each one playing some role, but the relative importance of each defense system varies in different spruce genotypes under different ecological conditions. Some of these factors and mechanisms (e.g., resin canal density) are easily included in the accelerated failure time model (although data were not available in this study), but some are not (e.g., chemical composition). However, it should be kept in mind that survival time is a measurement of a host-resistant ability originating from the biology and ecology of both the host and pest populations.

Many ecological processes can be appropriately treated following the survival time concept (Muenchow 1986, Dixon and Newman 1991, Fox 1993), for instance, the time for an individual to die or for a tree to fall down (forming a gap), the time until a seed is consumed by a predator, and the time until the recapture of a marked animal. However, in other situations, the measurement of interest may not necessarily be time, but rather a nonnegative variable, such as the sampling area until a given species is encountered or cumulative physiological temperature until a flower blossoms. This latter case is of particular interest, because it takes area or cumulative temperature as a random variable, which was otherwise considered fixed in traditional studies. In addition, in ecological studies, censored observations can frequently occur because of loss of experimental subjects, or because of the relatively short observation time relative to the natural occurrence of a process. Therefore, survival time analysis should be a useful approach in ecology.

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LITERATURE CITED

Alfaro, R. I. 1995. An induced defense reaction in white spruce to attack by the white pine weevil, *Pissodes strobi*. Canadian Journal of Forest Research **25**:1725–1730.

Alfaro, R. I., J. H. Borden, R. G. Fraser, and A. Yanchuk. 1995. The white pine weevil in British Columbia: basis for an integrated pest management system. The Forestry Chronicle **71**:66–73.

Alfaro, R. I., F. He, G. Kiss, J. King, and A. Yanchuk. 1996. Resistance of white spruce to white pine weevil: development of a resistance index. Forest Ecology and Management **81**:51–62.

Alfaro, R. I., F. He, E. Tomlin, and G. Kiss. 1997. White spruce resistance to white pine weevil related to bark resin canal density. Canadian Journal of Botany **75**:568–573.

Alfaro, R. I., and S. A. Y. Omule. 1990. The effect of spacing on Sitka spruce weevil damage to Sitka spruce. Canadian Journal of Forest Research **20**:179–184.

Alfaro, R. I., H. D. Pierce Jr., J. H. Borden, and A. C. Oehlschlager. 1980. Role of volatile and nonvolatile components of Sitka spruce bark as feeding stimulants of *Pissodes strobi* Peck (Coleoptera: Curculionidae). Canadian Journal of Zoology **58**:626–632.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, London, UK.

Cohen, A. C., and B. J. Whitten. 1988. Parameter estimation in reliability and life span models. Marcel Dekker, New York, New York, USA.

Dixon, P. M., and M. C. Newman. 1991. Analyzing toxicity data using statistical models for time-to-death: an introduction. Pages 207–242 *in* M. C. Newman and A. W. McIntosh, editors. Metal ecotoxicology: concepts and applications. Lewis Publishers, Chelsea, Michigan, USA.

Fox, G. A. 1993. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. Pages 253–289 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

He, F., and R. I. Alfaro. 1997. White pine weevil (Coleoptera: Curculionidae) attack on white spruce: spatial and temporal patterns. Environmental Entomology **26**:888–895.

Johnson, E. A., and S. L. Gutsell. 1994. Fire frequency models, methods and interpretations. Advances in Ecological Research **25**:239–287.

Kalbfleisch, J. D., and R. L. Prentice. 1980. The statistical analysis of failure time data. Wiley, New York, New York, USA.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association **53**:457–481.

Kiss, G. K., and A. D. Yanchuk. 1991. Preliminary evaluation of genetic variation of weevil resistance in interior spruce in British Columbia. Canadian Journal of Forest Research **21**:230–234

Lawless, J. F. 1982. Statistical methods and model for lifetime data. Wiley, New York, New York, USA.

Lee, E. T. 1992. Statistical methods for survival data analysis. Second Edition. Wiley, New York, New York, USA.

MathSoft 1995. S-Plus, version 3.4. Seattle, Washington, USA.

Morris, R. F. 1959. Single-factor analysis in population dynamics. Ecology **40**:580–588.

Muenchow, G. 1986. Ecological use of failure time analysis. Ecology **67**:246–250.

Nelson, W. B., and G. J. Hahn. 1972. Linear estimation of a regression relationship from censored data. Part II—best linear unbiased estimation and theory. Technometrics **15**: 133–150.

Newman, M. C., and J. T. McCloskey. 1996. Time-to-event analyses of ecotoxicity data. Ecotoxicology **5**:187–196.

Pyke, D. A., and J. N. Thompson. 1986. Statistical analysis of survival and removal rate experiments. Ecology **67**:240–245.

Southwood, T. R. E. 1978. Ecological methods. Second edition. Methuen, London, UK.

Tomlin, E. S., R. I. Alfaro, J. H. Borden, and F. He. 1998. Histological response of resistant and susceptible white spruce to simulated white pine weevil damage. Tree Physiology **18**:21–28.

Tomlin, E. S., and J. H. Borden. 1994. Relationship between leader morphology and resistance or susceptibility of Sitka spruce to the white pine weevil. Canadian Journal of Forest Research **24**:810–816.

VanderSar, T. J. D., and J. H. Borden. 1977. Visual orientation of *Pissodes strobi* Peck (Coleoptera: Curculionidae) in relation to host selection behaviour. Canadian Journal of Zoology **55**:2042–2049.

Whittemore, A., and B. Altschuler. 1976. Lung cancer incidence in cigarette smokers: further analysis of Doll and Hill's data for British physicians. Biometrics **32**: 805–816.