MORTALITY OF TREES IN LOBLOLLY PINE PLANTATIONS

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Abstract—The annual probability of mortality for planted loblolly pine (*Pinus taeda* L.) trees was estimated using a set of permanent plots covering the entire native range of the species. The recorded causes of death were infestation by the southern pine beetle (*Dendroctonus frontalis* Zimmermann) and other insects, lightning, and unknown reasons. It was found that mortality from these causes does not change with age of trees, which allowed us to calculate an overall mean annual mortality probability for each density-independent factor. Two sets of these estimates are provided: one for all plots and another for the plots that in the past were affected by a given factor. A model was constructed to analytically separate density-dependent from density-independent factors of mortality recorded as “other causes.” The average annual probabilities of mortality are 0.8 percent and 0.6 percent for density-independent and density-dependent causes, respectively. Our analysis also covers the events that wipe out entire plots such as flood, fire, and catastrophic insect infestation. This neglected kind of mortality, referred to as indiscriminate, eliminates four times as many trees as density-dependent mortality and three times as many as density-independent mortality.

INTRODUCTION

Stand dynamics of even-aged stands consists of two basic processes, tree growth and mortality. These processes are related because the growth of some trees necessitates the death of others. This relationship between growth and mortality becomes more pronounced as stand density increases. In addition to this density-dependent mortality (also called regular or noncatastrophic), trees die from other causes unrelated to density, such as lightning. Too often, studies of population dynamics neglect the events that obliterate entire plots, resulting in indiscriminate mortality (fire, flood, tornado, and land development). Modeling stand dynamics requires detailed knowledge and estimates of all kinds of mortality. Because of the importance of loblolly pine (*Pinus taeda* L.) plantations to the national economy, this forest type is the object of the reported study.

GOAL AND OBJECTIVES

The goal of the study was to estimate the annual probability of mortality for planted loblolly pine from all recorded physical, biological, social, and random factors. Our objectives were to analyze various causes of mortality, to develop a method for mortality calculation, to construct a model that separates density-dependent from density-independent mortality, and to provide estimates of mortality on the stand and the region-wide levels for the entire native range of loblolly pine from the Atlantic coast to eastern Texas.

DATA

Long-term observations of loblolly pine plantations maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Polytechnic Institute and State University (Burkhart and others 1985) were used in this investigation. They constitute one of the largest data sets on pine growth. The plots were established from 1980 to 1982 on 186 locations which were selected in cutover, site-prepared plantations, originated from woods-run (unimproved) seedlings. There are three plots at each location: control (unthinned), lightly thinned (about one-third of basal area removed at each thinning), and heavily thinned (approximately one-half of basal area removed). Since some plots did not survive to the last measurement, the total number of plot measurements is 2,502. The plots were measured five times at 3-year intervals. The total range of age is 29 years, from 9 to 38 years. Summary statistics for the initial measurement are given in table 1. The dataset contains information on tree vitality and causes of death: lightning, insect damage, and unknown causes (codes 1, 2, and 3, respectively). Other relevant information is provided by status code because, among other factors, it identifies plots attacked by the southern pine beetle (SPB) (*Dendroctonus frontalis* Zimmermann).

MORTALITY ESTIMATES

This study characterizes mortality by annual probability, *M*. Because plots are rarely measured annually, it is not always possible to obtain M directly. Usually, *M* is calculated as:

Table 1—Basic statistics of the loblolly pine dataset at the first measurement (559 plot measurements)

	Statistics		
Variable	Minimum	Mean	Maximum
Age from seed, years	9	16	26
Number of trees per ha	339	1,459	2,746
Arithmetic mean height (m)	4.2	11.6	22.2
Diameter (cm)	6.5	14.8	25.6
Basal area (m^2/ ha)	2.1	18.3	60.0
Stand density index of pine trees	147.5	570.9	1,094.3
Stand density index of hardwoods	0.64	22.05	150.25

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$$M = \frac{N_0 - N_t}{N_0 t} \tag{1}$$

where

N_t and N_0 = numbers of trees/ha at the end and the beginning of the period, and

t = the time between plot measurements.

Because number of trees does not change linearly with age, this formula underestimated annual mortality by 19 percent for a 3-year period and more for longer periods. To improve the estimates, we tried the expression of relative growth rate commonly used in growth studies (Harper 1977):

$$M = \frac{\ln(N_0) - \ln(N_t)}{t} \tag{2}$$

This method errs in the opposite direction by about half as much.

To find a better expression, we assumed that the annual probability M does not change during the period, t. Then the number of trees at the end of a period can be expressed in terms of initial number of trees, N_0, and t as follows:

$$N_t = N_0 (1 - M)^t \tag{3}$$

which leads to:

$$M = 1 - \left(\frac{N_t}{N_0} \right)^{\frac{1}{t}} \tag{4}$$

This equation predicts mortality better than the others and was accepted for subsequent calculations.

In the stands already infested by insects, mortality is often higher than that in the entire data set. Similarly, lightning strikes trees in some locations more often than in others. This shows that density-independent mortality is not totally random. To reflect this fact, we will provide two sets of mortality estimates, one for all plots and another for the plots affected in the past by a given mortality factor.

INITIAL MORTALITY

For 222 plots out of the total 559 plots, the dataset contained the number of planting spots. By comparing this number with the number of trees at the first measurement, one could estimate the initial mortality of trees, defined as annual mortality for the period between planting and the first inventory. During this period (lasting on average 14.7 years) volunteer pines often appeared among planted trees. When the data were analyzed, those tagged at the first measurement could not be distinguished from planted trees, which may have biased our estimates of initial mortality. Most likely, the initial mortality was more intensive during the first 2 or 3 years after planting. Because annual information was not available, we computed the initial mortality using equation (4). The mean initial annual mortality is 0.0219. In other words, about 2 out of every 100 planted trees died each year prior to the first measurement.

MORTALITY CAUSED BY THE SPB

The SPB was found on 22 (out of 186) plot locations. Eighty two (out of 2,502) plot measurements were affected by the beetle, with some plots attacked repeatedly. Annual probability of mortality was calculated using equation (4) with a 3-year time interval between measurements. It was found that neither age (slope = -0.0017 ± 0.0022, $R^2 = 0.0220$) nor stand density (slope = -0.0002 ± 0.0027, $R^2 = 0.0065$) were statistically significant predictors for SPB attack, so we could use an overall mean probability to predict the annual mortality of pine trees on SPB-infested plots. This annual probability of mortality was obtained from the weighted mean of annual mortality probability. The total number of trees in each age class was used as weight. We also studied the effect of previous beetle attacks and calculated the mortality probability for plots where at least one tree died from the SPB (table 2). This probability of mortality was about 40 times higher than the average of all plots (0.0398 versus 0.0010).

MORTALITY CAUSED BY OTHER INSECTS

Plots having a status code other than 1 (which indicates SPB infestation) were considered for estimation of the mortality caused by other insects. There were 580 dead trees with an insect damage code (cause of death = 2). When the annual mortality caused by this factor was regressed on age, the slope was -0.00005 ± 0.0017 ($R^2 = 0.0000$), which indicates that the mortality is not related to age. Calculations showed that the probability of mortality on all plots was 0.0011, which was 10 times less than on plots containing at least 1 tree that died from the same cause in the past (0.0011 versus 0.0095). This ratio is four times smaller than the ratio for the SPB, indicating that the SPB is more contagious than other insects (table 2).

MORTALITY FROM LIGHTNING

Records indicate that lightning killed 27 trees from 17 plot measurements, with age varying from 10 to 30 years. The weighted annual probability of trees killed by lightning is 0.0001. The linear regression of the probability of lightning mortality on age was not statistically significant. The slope was 0.0002 with standard error 0.0029 ($R^2 = 0.0002$). The ratio of the mean diameter of the trees killed by lightning to the mean diameter of live trees is 1.12 with the standard

Table 2—Annual probability of mortality on sample plots for density-dependent and density-independent causes. Affected plots are plots with at least one dead tree in the past from the listed reason

	Annual mortality probability		
Cause	Affected plots	All plots	Ratio of probabilities
Lightning	0.0063	0.0001	56
Insects	0.0095	0.0011	9
SPB	0.0398	0.0010	40
Density-independent component of unknown causes	0.0062		
Total density-independent mortality	0.0618	0.0084	7
Density-dependent mortality	0.0060		

deviation of 0.24611. Although the ratio confirms the common knowledge that lightning kills larger trees, it does not differ from 1 significantly.

MORTALITY FROM OTHER CAUSES: ANALYTICAL SEPARATION OF DENSITY-DEPENDENT FROM DENSITY-INDEPENDENT MORTALITY

There were 2,925 trees that died from the reasons recorded as "other causes." It is known that competition among trees is a leading cause of death, at least in dense stands. If so, the probability of mortality should increase with stand density. As a measure of stand density, we used Reineke's (1933) stand density index. To facilitate comparisons with other species, the index was normalized by dividing it by the maximum value for the studied species. Reineke reported that for loblolly pine such a value was 450 or in metric units 1,112. As a result, the normalized stand density index, *I*, is equal to:

$$I = \frac{N}{1112}\left(\frac{D}{25.4}\right)^{r} \qquad (5)$$

where

N = the number of trees per ha,

D = the quadratic mean of diameter in cms, and

r = a parameter.

The points representing plots with $I < 0.5$ did not show any density-related increase as would be expected from mortality caused by competition. This finding indicated that the unknown causes included not only density-dependent but also density-independent mortality. To estimate the mortality caused by density-dependent factors, it is necessary to separate it from density-independent mortality. In reality, both groups of factors are blended, which makes physical separation impossible. In this study, the separate estimates were obtained by constructing a model that includes both kinds of mortality.

Number of Trees and Their Average Size

The relationship between *D* and *N* is well-known in forestry as Reineke's (1933) equation:

$$N = kD^{-r} \qquad (6)$$

where

k and r = parameters.

Parameter k

In growth modeling we often predict number of trees, N_2, at some future moment when the current diameter, D_1, number of trees, N_1, and future diameter, D_2, are known. From

$$N_1 = kD_1^{-r} \qquad (7)$$

one can express *k* as:

$$k = \frac{N_1}{D_1^{-r}} \qquad (8)$$

Now it is possible to present N_2 without using *k*:

$$N_2 = kD_2^{-r} = N_1\left(\frac{D_2}{D_1}\right)^{-r} \qquad (9)$$

Parameter r

Reineke's relationship holds true only for fully stocked stands. It can be applied to managed plantations with their changing canopy closure by making *r* variable. When trees do not compete with each other, their number changes little. Equation (9) is still applicable if $r = 0$. If the plantation remains unthinned and trees are allowed to compete, stand density builds up and *r* gradually tends to a certain stationary value. Using unreported intuitive methods, Reineke estimated *r* as 1.605. When MacKinney and others (1937) reanalyzed the data using standard statistical methods, they arrived at the power equal to 1.7070. Thus, as density increases, Reineke's parameter changes from 0 to 1.7. To model density-dependent mortality, we need to express *r* as a function of density, *I*.

Reineke's Parameter as a Function of Density

This function should satisfy the following requirements: (1) When trees are located far away from each other, they do not compete and their increment and mortality do not depend on density. Therefore, when *I* is below some threshold value of I_0, *r* should be zero: $r(I\ I_o) = 0$. (2) When density is maximal and $I = 1$, r should reach its maximum value, 1.7: $r(I=1)=1.7$. (3) When $I = 1$, the tangent of the relationship between *r* and *I* should equal zero: $r'(I=1)=0$, where r' is the first derivative. The following model satisfies these requirements:

$$r = 1.7\left(1 - e^{-b\frac{I-I_0}{1-I}}\right) \qquad (10)$$

Density-Dependent Mortality

If trees died only from density-dependent factors, the number of surviving trees, N_2, could be calculated by the following equation:

$$N_2 = N_1\left(\frac{D_2}{D_1}\right)^{-1.7\left(1-e^{-b\frac{I-I_0}{1-I}}\right)} \qquad (11)$$

where

N_1 and D_1 = initial number of trees,

diameter D_2 i = the diameter of trees at the next remeasurement, and

b = a parameter to be estimated from data.

Combined Mortality

Equation (11) cannot be applied to our dataset because it records trees that died from a combination of density-dependent and density-independent factors. Assuming that density-independent mortality is proportional to the initial number of trees, we can include into the equation (11) a term c is the mortality probability that a tree dies from density-independent causes during the studied period:

$$N_2 = N_1\left[\left(\frac{D_2}{D_1}\right)^{-1.7\left(1-e^{-b\frac{I-I_0}{1-I}}\right)} - c\right] \qquad (12)$$

The parameters *b* and *c* were estimated using the data on mortality from unknown causes except for the plots infested by the SPB (b = 0.1920 ± 0.0299 and c = 0.0187 ± 0.0030). To obtain the annual probability of mortality from density-independent factors, the estimate of c was divided by three (the time between remeasurements). The equation (12) predicts the number of trees with an R^2 higher than 0.97.

The accuracy of this model can be compared with those using the same variables, such as the model by Harrison and Borders (1996). For the interval of 3 years from age 15 to 18 years, the difference between their prediction and the data was 32 trees/ha. For a 6-year interval, it was 45 trees/ha. The corresponding errors of our model were 19 and 14 trees/ha.

INDISCRIMINATE MORTALITY

Some plots were lost during the study because of various disturbances (table 3). Unlike mortality on the tree and stand levels, the mortality caused by hurricanes, fire, or road construction that wipes out the whole plot is indiscriminate. The annual probability of this kind of mortality was obtained for each recorded cause by dividing the number of lost plots by the total number of plots and the time between remeasurements (3 years).

DISCUSSION

In this study, the mortality of trees in loblolly pine plantations was assessed for each recorded cause of death. We also inferred the rate of initial mortality by comparing the number of trees at the first measurement with the number of planting spots. The actual mortality is likely to be higher than the estimate of 0.0219 because the number of trees at the first measurement includes large number of volunteers. All other estimates relate to the period after the first inventory. One of the major causes of mortality is insects. On the intact plots, each year they kill 2 out of every 1000 trees. The SPB is responsible for half of this mortality. Mortality from unknown causes was split analytically into two components, accounting for density-dependent and density-independent factors. Because the plantations are relatively young and not fully stocked, this component is less damaging than it would be in older, unmanaged stands. Still, the density-independent component of mortality from unknown causes is three times as great as the insect damage. The combined annual probability of mortality from all density-independent causes is 0.8 percent. Plugging in average diameter, its increment, and stand density into equation (11), it is possible to assess the average annual probability of mortality from density-dependent causes for all plots, which is 0.6 percent, slightly less than the probability of mortality from density-independent causes.

Table 3—Annual probability of mortality in loblolly pine plantations from all causes

	Mortality level		
Cause	Region (indiscriminate)	Plot	Total
Lightning		0.0001	0.0001
Flood	0.0003		0.0003
Fire	0.0004		0.0004
Ice	0.0004		0.0004
SPB	0.0076	0.0010	0.0086
Other Insects		0.0011	0.0011
Unknown	0.0148	0.0062	0.0210
Competition		0.0060	0.0060
Total	0.0235	0.0144	0.0379

Not all recorded causes provide a true picture of mortality because it is not easy to disentangle primary and proximate causes of death. Recorded mortality from lightning is small. One out of 10,000 trees dies annually from this cause. This number is probably underestimated because there are indications that fully 70 percent of trees killed by insects were predisposed by lightning strikes (Wahlenberg 1960).

This investigation showed that mortality from lightning and insects was not related to stand characteristics such as age and stand density, etc. As a result, it was possible to provide the overall annual mortality probabilities for these causes, independent of age. Mortality from lightning was affected by tree size but not significantly. Among patterns of mortality documented by this study was the effect of stand history. Usually, stands with previous records of mortality from a given cause suffer heavier losses than do other stands. For example, the SPB damage in previously affected stands was 40 times higher than that for the entire data set. To reflect this fact, we provided two sets of mortality estimates, one for all plots and another for plots affected in the past by a given mortality factor. The connection between past and future mortality from unknown causes (which include competition mortality) is reflected by equation (12).

So far, relationships between number of trees and their size were developed only for unmanaged fully stocked stands (Reineke 1933, Yoda and others 1963). This study attempted to relate these variables for managed stands that are far from full density. Our approach was to present the constant parameter of Reineke's equation as a variable that changed with density from 0 to the maximum value of 1.7 [equation (10)]. Trying to uncover the ecological interpretation of the model parameters, we identified parameter I0 as the density at which trees start competing with each other and suggested a technique for its estimation. This model was extended to cover density-independent mortality on the assumption that this kind of mortality is proportional to current number of trees.

These estimates refer to mortality within the observed plots. They are smaller than the wholesale mortality that forced abandoning entire plots. The indiscriminate mortality caused by fire, flood, and land conversion destroys about four times as many trees as density-dependent mortality and three times as many as density-independent mortality (tables 2 and 3). On average, for the entire region about 4 (3.8) out of 100 planted trees die every year from all causes. This information may be useful in projecting growth and yield of loblolly pine.

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