USING DECOMPOSITION RATES TO INFER HOW FAR BACK TREE POPULATIONS CAN BE RECONSTRUCTED

S. A. RICHARDS 1 AND E. A. JOHNSON 2

Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4 Canada

Abstract. To study forest dynamics without relying on the space-for-time substitution, one must be able to follow a population or stand of trees back or forward in time. The method of stand reconstruction looks back in time by aging all the live trees and aging and dating the time of death of dead standing and fallen trees. However, dead trees are lost by decomposition so the record becomes increasingly incomplete with passage of time. Here we present a model of the passage of trees from dead standing to dead decomposed but still datable to completely decomposed and thus undatable or lost. We then generalize a method for calculating the falling rate of dead trees originally proposed in 1985 by A. P. Gore, E. A. Johnson, and H. P. Lo. We do this by removing the assumption that no trees are lost by decomposition, i.e., by using the decomposition rate. Finally, in the most important result, the model allows estimation of how far back a good estimate of the numbers in the population can be made if the decomposition rates are known.

Key words: dead tree falling rate; dendrochronology; forest reconstruction; log decay rate; stand history; stand reconstruction; succession; tree populations.

INTRODUCTION

Stand reconstruction is a method for determining the history and population dynamics of a particular forest stand. It was developed by H. M. Raup (Johnson and Raup 1947) and refined by E. Stephens (Stephens 1955, Henry and Swan 1974, Oliver and Stephens 1977). These early forest reconstructions dealt primarily with live trees and tip-up mounds and other forest-floor characteristics that indicated disturbances (Stephens 1955). These forest-floor characteristics were then dated by aging the live trees growing on them.

Johnson and Fryer (1989) and Johnson et al. (1994) added to the repertoire of stand-reconstruction methods by reconstructing tree populations using dendrochronological techniques to date the live, dead standing, and dead downed trees. This population-reconstruction method allows tree succession to be recovered without a time-for-space substitution. However, trees that were too decomposed to date or were missing could not be included in the reconstruction.

Dead trees not overturned or broken by a disturbance usually remain standing for many years before falling to the ground (Hinds et al. 1965, Raphael and Morrison 1987, Morrison and Raphael 1993, Harrington 1996, Storaunet and Rolstad 2004). In general, dead standing trees decay much slower than fallen boles because they are drier (Dahms 1949, Lyon 1977, Rayner and Todd 1979, Cline et al. 1980, Boddy 1983, Carpenter et al. 1988, Johnson and Greene 1991, Zabel and Morrell 1992). If the goal of stand reconstruction is to estimate the tree population dynamics, simply counting standing and fallen boles that died X years ago could give an underestimate of the true number of deaths in that interval because of loss of datable stems. The error in the number of estimated deaths will be greater for earlier dates and for smaller boles. The error may be large for stands where the rate of tree fall or the rate of decomposition is high.

Gore et al. (1985) developed a technique for estimating falling rates of dead boles divided into cohorts by size or by time since recruitment into the dead-bole population. The technique used counts of current standing and fallen boles and assumed the survivorship of standing dead boles is a negative exponential following empirical evidence (Keen 1955, Hind et al. 1965, Lyon 1977, Cline et al. 1980, Raphael and Morrison 1987). The technique did not account for
boles that had fallen and decomposed to a point where they could not be dated. Johnson and Greene (1991) used the technique to estimate fall rates of Pinus contorta London var. latifolia Engelm. and Picea engelmannii Parry ex Engelm. boles for a cohort of trees recruited in the first five years after a stand-replacing fire in subalpine forests in the southern Canadian Rocky Mountains. Estimates of fall rates for both species ranged from 0.020 to 0.064 falls/yr, which was consistent with other studies (see Johnson and Greene 1991).

The purpose of this paper is to develop a better understanding of how to think about and deal with the trees that have been lost from the stand reconstruction so that we have a better determination of the limitations of studies of tree population dynamics based on stand reconstruction. We show that under certain conditions the Gore et al. (1985) technique may underestimate fall rates if fallen boles quickly decay to a stage where their ages cannot be determined. We also show how this bias can be corrected if estimates of bole decomposition rates are available. Correcting for the bias by estimating the number of uncounted boles allows us to more accurately estimate past rates of tree death. We also present an approach for determining how far back in time death rates can be reliably estimated. The model presented is simple and assumes that the population is divided into relatively homogenous cohorts defined by age at recruitment or size.

A Model of Dead-Bole Dynamics

Suppose data are collected on all the dead boles in a stand at some point in time (t = 0). For each bole, its state (standing or fallen) is recorded, as well as the number of years since death. Let X be the number of years since the death of an individual (to the nearest year). For the remainder of this paper we refer to the age of a bole as “the number of years since tree death.”

The falling rate after death is denoted \( \varphi \) and in our model this rate is assumed to be constant. A constant falling rate results in a negative-exponential age distribution of standing trees and is consistent with empirical data (Keen 1955, Cline et al. 1980, Johnson and Greene 1991).

The rate of bole decomposition (i.e., breakdown to a non-datable state) once it is on the ground is denoted \( \mu \) and this rate is assumed to be known. The probability that a bole that has been on the ground \( t \) time units and cannot be aged due to decomposition (D) is

\[
D(t) = 1 - \exp\left(-\int_{a=0}^{t} \mu(a)\,da\right) \tag{1}
\]

where \( a \) is an integration variable representing the time the bole has been on the ground. We may expect \( \mu \) to be an increasing function of time on the ground for boles because it takes time for microbes and fungi to cause substantial bole decomposition (Zabel and Morrell 1992).

Consider a tree that died \( X \) years ago (i.e., at time \( t = X \)). By time \( t = 0 \) the tree is either: (1) still standing, (2) on the ground but able to be aged, or (3) on the ground and non-datable or missing. We use the subscripts \( s, g, \) and \( d \) to refer to variables associated with these three states, respectively. For the first two states it is possible to date the time of death \( t = X \), whereas for the last state it is not. The probabilities that the bole is in these three states at time \( t = 0 \), given that it is of age \( X \), are

\[
p_s(X) = \exp(-\varphi X) \tag{2}
\]

\[
p_g(X) = \int_{\xi=0}^{X} \varphi \exp(-\varphi \xi)[1 - D(X - \xi)]d\xi \tag{3}
\]

and

\[
p_d(X) = \int_{\xi=0}^{X} \varphi \exp(-\varphi \xi)D(X - \xi)d\xi. \tag{4}
\]

Suppose at the time of sampling (\( t = 0 \)), \( n_s(X) \) standing boles and \( n_g(X) \) fallen boles of age \( X \) were counted. The number of trees that died \( X \) years ago but were not datable or missing due to decomposition can be estimated from the number of standing or grounded boles using

\[
n_d(X) = \frac{p_d(X)}{p_s(X)}n_s(X) = \frac{p_d(X)}{p_s(X)}n_g(X). \tag{5}
\]

In order to apply Eq. 5 we have to be able to calculate the state probabilities \( p_s, p_g, \) and \( p_d \), which we can only do if we know the falling rate \( \varphi \). Unfortunately, the falling rate is typically unknown for most stands.

Next we show how \( \varphi \) and \( n_d(X) \) can be estimated. First we assume that the rate of decomposition is constant (i.e., independent of time on ground). In this case, the probability of bole decay and the state probabilities are

\[
D(t) = 1 - \exp(-\mu t) \tag{6}
\]

\[
p_s(X) = \exp(-\varphi X) \tag{7}
\]

\[
p_g(X) = \frac{\varphi \exp(-\mu X)}{(\varphi - \mu)} \left[1 - \exp[(\mu - \varphi)X]\right] \tag{8}
\]

and

\[
p_d(X) = 1 - \exp(-\varphi X) - \frac{\varphi \exp(-\mu X)}{(\varphi - \mu)} \left[1 - \exp[(\mu - \varphi)X]\right]. \tag{9}
\]

Plots of the three state probabilities \( p_s(X) \), \( p_g(X) \), and \( p_d(X) \), are presented in Fig. 1A with values of \( \varphi \) and \( \mu \).
consistent with *Pinus contorta* (Johnson and Greene 1991).

Alternatively, suppose the rate of bole decomposition increases linearly with time on the ground, i.e., \( \mu(t) = \mu_0 + \mu_1 \tau \), where \( \mu_0 \) and \( \mu_1 \) are constant parameters. In this case, the probability that decomposition prevents a bole being dated is

\[
D(\tau) = 1 - \exp\left(-\mu_0 \tau - \frac{\mu_1}{2} \tau^2 \right). \tag{10}
\]

The probabilities \( p_\varphi(X) \) and \( p_d(X) \) need to be evaluated numerically using Eqs. 3 and 4. Fig. 1B shows an example of state dynamics for this case. In both examples, increasing (decreasing) the falling and decomposition rates singly or together will increase (decrease) the loss of datable boles.

**ESTIMATING THE FALL RATE OF DEAD BOLES**

Suppose the total number of boles that died in the stand within the last \( T \) years is \( N \). The state of the stand at time \( t = 0 \) can be described by the number of boles in each of the three states (s, still standing; g, on the ground but able to be aged; and d, on the ground but non-datable or missing) for each bole age class, \( X (1 \leq X \leq T) \). Let the vectors \( n_s, n_g, \) and \( n_d \) denote the sets of bole counts, for each age class (i.e., \( N = \Sigma[n_s + n_g + n_d] = \Sigma_3[n_s(X) + n_g(X) + n_d(X)] \)). The probability that the stand would be in state \( (n_s, n_g, n_d) \), given that boles fall at rate \( \varphi \), is given by the multinomial equation

\[
\Pr(n_s, n_g, n_d|\varphi) = \prod_{X=1}^{T} \left\{ \frac{[n_s(X) + n_g(X) + n_d(X)]!}{n_s(X)!n_g(X)!n_d(X)!} p_s(X, \varphi)^{n_s(X)} \right. \\
\left. \times p_g(X, \varphi)^{n_g(X)} p_d(X, \varphi)^{n_d(X)} \right\}. \tag{11}
\]

The likelihood that boles fell at rate \( \varphi \) and we did not observe the set of \( n_d \) decayed boles, given the observations \( n_s \) and \( n_g \), is

\[
L(\varphi, n_s, n_g) = \Pr(n_s, n_g, n_d|\varphi). \tag{12}
\]

The most likely fall rate and number of unobserved boles in each age class are the values of \( \varphi \) and \( n_d(X) \) that maximize Eq. 12, which we denote \( \hat{\varphi} \) and \( \hat{n}_d(X) \). The 95% confidence interval for each of these unknowns can be estimated using the likelihood profile method presented in Venzon and Moolgavkar (1988). In this case, the likelihood profiles are non-smooth because the estimates \( \hat{n}_d(X) \) must be integers. The above-mentioned method is equivalent to the method presented in Gore et al. (1985) when decayed boles are ignored (i.e., the \( n_d(X) \) are all set to zero).

**AN EXAMPLE AND DISCUSSION**

To show how the technique works, we simulated bole dynamics for 20 boles in each of 10 age classes, assuming fall rate \( \varphi = 0.05 \) falls/yr and decomposition rate \( \mu = 0.02 \) yr\(^{-1}\). For each simulation we estimated the fall rate and historical bole numbers. Bole simulations were repeated 20 times to determine uncertainty and bias in our estimates. We considered three scenarios that differed in our assumption about the decomposition rate: (1) decomposition was assumed to not have occurred \( [\mu = 0 \text{ yr}^{-1}] \), (2) the correct decomposition rate was assumed \( [\mu = 0.02 \text{ yr}^{-1}] \), and (3) the decomposition rate was overestimated by 50% \( [\mu = 0.03 \text{ yr}^{-1}] \).

Fig. 2 shows that knowing the decomposition rate resulted in an unbiased estimate of the fall rate, whereas not including the decomposition rate resulted in an underestimate of the fall rate, and an overestimate of decomposition rate resulted in an overestimate of fall.
rate. Knowing the decomposition rate resulted in unbiased estimates of bole numbers for all age classes (Fig. 3). Having an overestimate of decay rate resulted in overestimates of bole numbers and ignoring bole decay resulted in underestimates. Although knowledge of a correct decay rate resulted in unbiased estimates of bole numbers for all age classes, uncertainty in the estimates increased quickly after 20 years since tree death, which is the time when significant numbers of boles begin to decay and become non-datable (Fig. 1). However, the variation in estimated bole numbers was relatively bounded for boles older than 20 years (Fig. 3). On the other hand, when decay rate was overestimated the variation in estimated bole numbers continued to increase with age since death.

An estimate of the number of decayed boles can only be made for age classes with boles either observed to be standing or on the ground (i.e., for $X$ where $n_s(X) > 0$ and/or $n_g(X) > 0$). Thus, there is a limit as to how far back population estimates can be made. If the falling and decomposition rates ($\mu$ and $l$, respectively) are approximately known, then $v = (1/\phi + 1/\mu)$ gives an estimate of how long a bole will be datable. In our case, $v = 70$ years (see Fig. 1). Our results show that provided a good estimate of the decay rate is known then
reasonable estimates of bole numbers can be made for time periods of at least $v$ (Fig. 3), even when less than 20 boles are datable in an age class. This result is consistent with empirical findings by Johnson and Fryer (1989). These results also demonstrate how larger sample sizes can significantly improve estimates, as in our example younger age classes, on average, had more datable boles.

The calculations above were made for a population where each tree was assumed to have the same falling rate and decay rate. For populations in which the smaller (younger) and larger (older) trees have different falling and/or decay rates, then one could run the model separately for each group. Alternatively, one could propose various relationships between bole size and decay and/or fall rate and seek the most parsimonious relationship using model-selection techniques.

ACKNOWLEDGMENTS

This research was supported by the Natural Sciences and Engineering Research Council of Canada, Discovery Grant (E. A. Johnson) and G8 Legacy Chair (E. A. Johnson). We also thank two referees.

LITERATURE CITED


