Forest Ecology and Management 409 (2018) 372–377

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Not dead yet: Beech trees can survive nearly three decades in the aftermath phase of a deadly forest disease complex

Jonathan A. Cale[a,*], Stacy A. McNulty[b]

[a] Department of Renewable Resources, University of Alberta, Edmonton, AB, Canada
[b] Adirondack Ecological Center, State University of New York College of Environmental Science and Forestry, Newcomb, NY, USA

ARTICLE INFO

Keywords:
Invasive species
Fagus grandifolia
Beech bark disease
Neonectria
Cryptococcus fagisuga
Survival analysis

ABSTRACT

Management efforts often focus on preventing the arrival of destructive insects and pathogens or mitigating damage in forests experiencing heavy mortality. This need for management often abates after the mortality event due to reduced causal agent presence. However, the persistence of causal agents in beech bark disease (BBD)-impacted forests typically results in repeated tree mortality; this cycle has cascading impacts on forest biota and timber regeneration. We analyzed remeasurement data on BBD severity and tree death collected from 1988 to 2016 in disease aftermath stands in the Adirondack Mountains of New York to quantify the survival of BBD-affected trees over time. We found that while BBD severity has a strong influence on the yearly probability of tree survival, affected trees can survive for at least 28 years. However, the probability a tree will survive this long declined with more severe initial disease status regardless of how BBD severity changed over time. These findings could help inform management efforts to ameliorate the indirect impacts of BBD on forest wildlife populations, plant community diversity, and the regeneration of desirable timber species over time. Furthermore, our results underscore the continued need to manage BBD-induced beech mortality and disease-associated agents in aftermath stands.

1. Introduction

Forest ecosystem functions and services can be disrupted by destructive forest insects and diseases (Boyd et al., 2013; Lovett et al., 2016; Luyssaert et al., 2008). Such disturbances can cause billions of dollars in annual economic damages to private timberlands as well as public lands managed by governments in the United States (Aukema et al., 2011; Lovett et al., 2016). These damages are substantial but may be exceeded by concomitant losses of non-market forest values indirectly resulting from heavy tree mortality (Holmes et al., 2009). Collective economic and non-market losses and the need to triage damaged stands are naturally of significant concern to forest stakeholders. Managing destructive forest insects and diseases and their impacts can represent a substantial cost, with US federal and local government expenditures estimated to be more than $1.7 billion annually in some cases (Aukema et al., 2011). Management efforts resulting from such expenditures are often focused on preventing or slowing the arrival/spread of the damaging agent or mitigating damage in forests experiencing the resulting heavy mortality (Cale et al., 2017; Herms and McCullough, 2014; Lovett et al., 2016; Schoettle and Sniezko, 2007).

Managing the causal agent and/or tree death after the heavy mortality period has ended typically receives less attention. With many forest insect and disease systems, such a lack of attention is reasonable as the outcome of pest-induced mortality might not necessitate continued pest management. This is because forest insects and pathogens often are extirpated or substantially decline when the status of susceptible hosts is reduced to rare or occasional in a given stand (Berryman, 1987; Geils et al., 2010; Herms and McCullough, 2014). One exception to this associated decline is with beech bark disease (BBD; Cale et al., 2017; Houston, 1994).

Beech bark disease is a decline disease of American beech (*Fagus grandifolia*) populations throughout northeastern North America (Cale et al., 2017; Houston, 1994). The disease can involve non-native and native scale insects (*Cryptococcus fagisuga* [beech scale] and *Xylococculus betulae*, respectively) that predispose healthy beech infection by the pathogenic fungi *Neonectria ditissima* and *N. faginata* (Cale et al., 2015; Ehrlich, 1934; Houston, 1994). Though annually-accumulating bark necroses from *Neonectria* spp. infections kill the aboveground portions of affected trees, the roots remain alive to produce clonal sprouts (Houston, 2001, 1975). Thickets comprised of young beech of clonal and seed origins fill the understories of many forests in the aftermath of heavy BBD-induced overstory mortality (Garnas et al.,

* Corresponding author.
E-mail address: Jacale@ualberta.ca (J.A. Cale).

https://doi.org/10.1016/j.foreco.2017.11.044
Received 10 September 2017; Received in revised form 21 November 2017; Accepted 22 November 2017
0378-1127/

Table 1
The number of mature American beech (*Fagus grandifolia*) trees entering the study each sampling year (numbers) for each northern hardwood forest stand sampled in the Adirondack Mountains of New York. An "X" indicates years in which the stand was sampled.

Stand	Measurement year													Total trees
	1988	1991	1994	1997	1998	2005	2009	2010	2011	2013	2014	2015	2016	
EF	15	22	X	X	X	X	8	X	X	X	X		X	45
BB						15		X	X	X		X	X	15
CL	15	X			X	X								15
AD	10	X			X	X								10
SL	10	X			X	X								10
SM	10	X			X	X								10

2011; Giencke et al., 2014; Houston, 1975). These beech-dominated understories are then colonized by BBD agents transmitted by older disease-affected trees (Giencke et al., 2014). Thus, heavy BBD-induced mortality of overstory beech increases the abundance of susceptible trees, which in turn allow beech scale and *Neonectria* spp. to persist and kill beech trees for decades after the period of heavy mortality (Cale et al., 2017; Shigo, 1972).

Such aftermath conditions occur throughout the majority of geographical range impacted by BBD (Cale et al., 2017; Morin and Liebhold, 2015). Indeed, BBD-related organisms have persisted and continued to cause mortality in New York, New England and the Canadian Maritimes for over forty years (Kasson and Livingston, 2012; Morin and Liebhold, 2015). Despite the persistence and prevalence of aftermath conditions across much of the geographical range of beech, how BBD affects beech survival in aftermath stands is largely unknown. Understanding tree survival is critical to managing the cascading effects of BBD-induced mortality. Two such effects are (1) the reduction of understory plant diversity and (2) desirable tree regeneration; both result from the heavy shade cast by dense understories of clonal beech largely originating from the root systems of dead, mature trees (Cale et al., 2013; Collin et al., 2017; Giencke et al., 2014; Hane, 2003; Nyland et al., 2006). Beech bark disease reduces the capacity of mature trees to produce nuts, a highly nutritious food for wildlife (Costello, 1992; Rosemier and Storer, 2010). Thus, BBD-induced mortality likely has a profound influence on many animals, such as black bears (*Ursus americana*) and martens (*Martes americana*), for which beechnuts either represent an important component of the diets or influence prey numbers and availability (Jakubas et al., 2005; Jensen et al., 2012).

We investigated the survival of BBD-affected beech in aftermath forests using tree-level remeasurement data on BBD severity collected from 1988 to 2016 in stands of the central Adirondacks of New York. We used survival analysis methods to investigate two research questions: How does the proportion of surviving beech change over time in aftermath stands? and How does BBD severity affect the yearly probability of beech survival? Furthermore, we discuss how our results can be used to inform (1) the management of understory beech thickets in order to promote understory plant diversity and the regeneration of desirable tree species, (2) provision for wildlife that depend on beechnuts for food, and (3) retention of quality mature beech that contribute genetic and ecological value to the northern hardwood forest.

2. Materials and methods

2.1. Site description

The study was conducted in the Huntington Wildlife Forest (HWF) and adjacent state Forest Preserve in the towns of Newcomb (Essex County) and Long Lake (Hamilton County) located in the Adirondack Mountain region of New York. The HWF is a 6000 ha research forest in Newcomb, NY in the central Adirondack Mountains (44°00′N, 74°13′ W) and operated by the State University of New York College of Environmental Science and Forestry. Regional topography is mountainous, with elevations ranging from 457 m to 823 m above sea level. Average annual precipitation is 1010 mm, and the mean annual temperature is 4.4 °C. Soil types are largely spodosols consisting of glacial till. Dominant forest covertypes include northern hardwood (*Fagus-Acer-Betula*; 72%), mixed hardwood-conifer (18%), and coniferous (10%) types. Common forest tree species include: American beech, sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britton), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), northern white cedar (*Thuja occidentalis* L.), and eastern white pine (*Pinus strobus* L.). Beech bark disease caused heavy morality in this region beginning around 1967, and the stands have been in aftermath conditions for over 40 years (Morin and Liebhold, 2015; Sage, 1996).

2.2. Tree selection and disease rating

A total of 105 mature beech trees (18.0–63.5 cm in diameter at breast height [1.3 m; DBH]) were selected in six northern hardwood forest stands. Study trees in five of the stands (four stands [EF, CL, AD, and SM] in the HWF and one [SL] in a state forest preserve adjacent to HWF) were selected and initially sampled in 1988, whereas trees in another HWF stand (BB) were added to the study and initially sampled in 2005 (Table 1). To offset the loss of study trees due to early mortality, additional trees in stand EF were added to the study in 1991 and 2009 (Table 1). The number of study trees in each stand as well as the year these trees were initially sampled are shown in Table 1. Study trees were at least 10 m apart, marked with a permanent identification tag, and evaluated for BBD severity using a qualitative rating scale based on beech scale and *Neonectria* spp. canker presence and abundance. Trees without BBD were rated a "0," with light beech scale infestation a "1," with heavy scale infestation a "2," with light *Neonectria* spp. infection a "3," with heavy *Neonectria* spp. infection a "4," and with heavy *Neonectria* spp. infection as well as cracked and peeling bark a "5" (Burns and Houston, 1987). This rating scale was used to reassess BBD severity 3–11 times from the time of initial assessment to 2016 (Table 1). This variation was due to a substantial loss of study trees (50–90% mortality) by 2005 in stands CL, AD, SL, and SW, whereas study trees in stands EF and BB succumbed more slowly to BBD. Tree status (alive or dead) was recorded during each reevaluation period. All trees were free of signs of other damaging diseases or insects when initially sampled.

2.3. Data analysis

The survival of beech trees in the sampled stands was investigated using survival analysis. An extended Cox proportional hazards model was used to determine the effect of BBD rating and initial tree DBH on tree time-until-death in order to predict the probability of tree survival and death (i.e., hazard) over time. This type of model was chosen over other probabilistic methods because it (1) is designed to predict survival and hazard probability from a time-to-death response variable, (2)