Forest Ecology and Management 374 (2016) 211–219

Contents lists available at ScienceDirect

Forest Ecology and Management

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

# Oak stump-sprout vigor and *Armillaria* infection after clearcutting in southeastern Missouri, USA

Christopher A. Lee [a,*], Daniel C. Dey [b], Rose-Marie Muzika [a]

[a] Department of Forestry, School of Natural Resources, 203 ABNR Building, Columbia, MO 65211, United States
[b] USDA Forest Service, Northern Research Station, 202 ABNR Building, Columbia, MO 65211, United States

ARTICLE INFO

*Article history:*
Received 21 December 2015
Received in revised form 5 May 2016
Accepted 9 May 2016
Available online 18 May 2016

*Keywords:*
Root disease
Tree vigor
Sprout competition
Infection
Compartmentalization
Regeneration
Disease management

ABSTRACT

*Armillaria* spp. occur widely in Missouri mixed-oak ecosystems. In order to better understand the ecology and management of this pathogen and its effects on oak coppice, we observed a transect of 150 stumps after clearcutting in southeastern Missouri, noting *Armillaria* infection and oak sprout demography one year and seven years after harvest. Additionally, we visited a 50-year-old clearcut in the same area to sample oak root systems of stump-sprout origin for comparison with the seven-year-old clearcut. One year after harvest, 55% of stumps supported *Armillaria* infections, while 62% of stumps were infected after seven years. In the 50-year-old clearcut, 21% of examined root systems were infected. Logistic regression analysis of the younger clearcut related likelihood of infection to tree age at time of harvest. Whereas *Armillaria* infection displayed weak to absent relationships with numbers of sprouts surviving over time, dominant sprout height and diameter on individual stumps—proxies for stump vigor—were positively associated with numbers of survivors. These measures of vigor also had more influence over the magnitude and development of sproutless gaps around the circumference of the stump than did *Armillaria* infection. Moreover, the random effect of the individual tree on the development of such gaps was large. These results point to an important role for individual stump vigor in regulating sprout self-thinning rates, potentially through compartmentalization of invading *Armillaria*.



## 1. Introduction

*Armillaria* species, like other root pathogens, play important ecological and economic roles in North American forests. In their various roles as saprophytes and parasites, they contribute to large-scale nutrient recycling and forest succession (Castello et al., 1995; Goheen and Otrosina, 1998; Edmonds et al., 2000; Garbelotto, 2004), and they also complicate management of forest and agricultural products by killing woody crop plants, with damage levels varying according to the individual agrosystem (Baumgartner and Rizzo, 2001).

In the Ozark Highlands of the central USA, *Armillaria* species have contributed to episodic red oak decline that is shifting the overstory composition of oak-hickory forests from dominance by species in *Quercus* subsection *Erythrobalanus* (red oaks) toward dominance by white oak (*Quercus alba*) (Voelker, 2004). A variety of studies have resulted in various management recommendations designed to enhance red oak health. Many of these recommendations center on reducing density in overstocked stands (e.g., Fan et al., 2008; Voelker et al., 2008). Development of methods to enhance oak regeneration in stands affected by red oak decline represents another research need.

The sources of oak reproduction include new seedlings, advance reproduction and stump sprouts. By far the most competitive and fastest growing type of oak reproduction are stump sprouts (Johnson et al., 2009). Advance reproduction, however, has been long identified as the key to sustaining oak stocking in future forests because not all oak stumps sprout. Oak regeneration failures and declines in oak stocking in regenerating stands are commonly reported worldwide, and are largely attributed to lack of sufficient density of large, competitive advance reproduction (Li and Ma, 2003; Götmark et al., 2005; Pulido and Díaz, 2005; Johnson et al., 2009).

Consequently, the large proportion of dominant oak in regenerating stands are of stump sprout origin (Beck and Hooper, 1986; Gould et al., 2002; Morrissey et al., 2008). Stump sprouting ability in oak is a function of initial tree diameter and age at time of cutting, is modified by site quality, and varies by species (Weigel and Peng, 2002; Johnson et al., 2009; Pyttel et al., 2013). The probability of producing a sprout decreases with increasing tree diameter and age. *Armillaria* species have the potential to interfere with the

* Corresponding author at: Department of Forestry, University of Missouri, 203 ABNR Building, Columbia, MO 65119, United States.

*E-mail addresses:* calyt3@mail.missouri.edu (C.A. Lee), ddey@fs.fed.us (D.C. Dey), muzika@missouri.edu (R.-M. Muzika).

http://dx.doi.org/10.1016/j.foreco.2016.05.014
0378-1127/

production of sprouts; however, how this potential manifests itself on oak stumps is poorly understood.

Three *Armillaria* species (*Armillaria mellea*, *Armillaria gallica*, and *Armillaria tabescens*) are prominent in Missouri oak-hickory and pine-oak forests (Bruhn et al., 2000) and have gained particular attention as contributing mortality agents to red oak decline. These fungi comprise an important sector of the indigenous forest biota. They maintain extremely long-lived, genetically individual bodies (genets) of varying sizes both underground and within trees, over large portions of a given forest, for hundreds of years in some cases (Bruhn and Mihail, 2003). *A. gallica* plays primarily a saprophytic role and requires compromised tree physiology, usually in response to abiotic stress, to overcome living trees, while the other two species are moderately to severely pathogenic even on living, healthy trees (Redfern and Filip, 1991; Bruhn et al., 2000). Bruhn et al. (2005) found all three species on resprouting stump systems following both uneven-aged and even-aged management in the Ozarks and hypothesized that sprout mortality corresponded to *Armillaria* infections active around the circumference of the stump system. The stumps they studied represented a highly infested system; 40–80% of inspected stumps supported active *Armillaria* infections. Stanosz and Patton (1987) found similar infection prevalence on aspen suckers in Wisconsin. Both studies concluded that *Armillaria* may pose a threat to continued coppice or sucker regeneration on affected sites.

In order to better understand the ecology and management of oak coppice systems in Missouri oak-hickory forests inhabited by this pathogen, we compared *Armillaria* infection of sprouting stumps one year after clearcut harvest with infection of the same stumps 7 years after harvest. We also compared the infection status of these stumps with infection on stems that originated from a clearcut in 1963 at a nearby site. In these comparisons, we were guided by three sets of hypotheses using three response variables:

- Incidence of *Armillaria* infection will be positively associated with tree age at time of harvest, surrounding mortality at time of harvest, tree species in the red oak group, and southern and western aspects.
- Sprout quality, as estimated by dominant sprout height/diameter—a proxy for stump vigor—will be inversely associated with *Armillaria* infection and with surrounding tree mortality at time of harvest and positively associated with better parent tree canopy positions.
- The sizes of gaps in sprout distribution around the circumferences of stumps will be positively associated with *Armillaria* infection and inversely associated with sprout quality.

The general assumptions, derived from previous literature and observations, behind these hypotheses were that the observed pattern of *Armillaria* infection would depend to some extent on (1) the pattern of previous *Armillaria*-caused mortality, (2) stump/parent tree vigor, and (3) the age and species of the parent tree stem as well as environmental drivers (e.g., aspect). As a secondary objective, we sought to clarify the etiology of stump infection and stump-pathogen antagonism by making qualitative observations of the positions and characteristics of *Armillaria* mycelium, rhizomorphs, and lesions in infected stumps.

## 2. Methods

### *2.1. Study site*

The 1659 ha (4100-ac) Sinkin Experimental Forest, located approximately 40 km (25 mi) southeast of Salem, Missouri, is within the Current River Hills subsection of the Ozark Highlands (Nigh and Schroeder, 2002). This subsection, located on the southeastern flanks of the Ozark Uplift, features a variety of topography and parent materials: less dissected, more rolling landscapes are underlain by acidic sandstones of the Roubidoux formation, while more rugged landscapes expose the limestone and dolomite of the Gasconade and Eminence formations. Soil type varies according to topographic position, with significant fractions of cherty gravel on many backslope soils in the region and root-restricting fragipan layers in interfluvial positions (Nigh and Schroeder, 2002). Soils in the study area exist as complexes within the Nixa, Clarksville, Coulstone, and Bender soil series: all are formed from alluvium over residuum weathered from limestone and have high gravel fractions and poor water-holding capacity (Natural Resources Conservation Service, 2016). Average annual precipitation in the Sinkin EF is 1118 mm, falling mostly as rain under a temperate climate with hot summers and cool, dry winters (USDA Forest Service, 2008). The area, along with the rest of the Ozark Highlands, is subject to periodic moderate-to-severe drought. Significant droughts throughout the twentieth century included those in the 1930s, 1950s, early 1960s, early 1980s, and 2000. A recent moderate drought occurred in 2007 (National Oceanic and Atmospheric Administration, 2015).

### *2.2. Data collection*

#### *2.2.1. Original clearcut area*

The choice of study site arose because of its interest as a heavily impacted red oak decline area, with the intention of investigating how oak stump sprout regeneration responded to *Armillaria* presence in subsequent years. A 2.83 ha (7 ac) area (lat 37.50°, long −91.28°) was selected for complete tree removal, and in 2005 150 oak trees were selected within this area to provide a balanced representation of all oak species on-site and to cover both heavily declining trees and those relatively unaffected by decline. Pretreatment data consisted of the following information collected for selected trees: species, diameter at breast height (dbh), canopy position (suppressed, intermediate, codominant, dominant), an assessment of crown dieback on a 1–4 scale (1 = least amount of branch dieback, 4 = greatest amount of dieback), the number of dead trees within a 10-basal-area-factor (BAF) variable-radius plot around the subject tree, and tree age (obtained by counting stump rings immediately after felling).

#### *2.2.2. Post-clearcut 1-year revisit*

One year subsequent to felling (in 2006), we revisited the clearcut, marked stumps with aluminum tags, and collected the following information: number of live sprouts, number of dead sprouts, the largest gap free of sprouts around the circumference of the stump (measured in degrees), stump basal diameter, and height and azimuth (with reference to stump center) of the dominant sprout. Upon this visit, we excavated two large structural roots as near as possible to opposite sides of each tree for up to 1 m from the root crown to examine them for signs of *Armillaria* spp. Where mycelial fans or infecting rhizomorphs were found, we sampled them, re-covered the excavated roots with soil, and isolated the fungus on water agar. Subsequently, we transferred cultures to 2% malt extract agar and purified them of bacterial and fungal contaminants before subjecting them to compatibility tests with known tester strains according to the method described in Guillaumin et al. (1991) to determine species.

#### *2.2.3. Post-clearcut 7-year revisit*

In 2012, we revisited the initial study site and located all 150 stumps for further study. The procedure for this resurvey generally followed the original study protocol, with the following exceptions. Instead of simply recording presence or absence of *Armillaria* on