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

studied stumps, we made notes on the position and nature of each infection found on the two excavated buttress roots in an attempt to describe the variety of infection characteristics and stages that were present. Additionally, we did not record exact heights of dominant sprouts, reasoning that since diameter growth is a much lower priority for photosynthate allocation than height growth (Waring et al., 1998), it would reflect vigor status of sprouts at the 7-year mark with more sensitivity than would a height measurement.

As part of the qualitative assessment of *Armillaria* infections on stumps, we considered active infections to exhibit any of the following characteristics or structures: necrotic lesions associated with rhizomorphs or mycelium; white mycelial fans or small mycelial tongues; or watersoaked, stringy to spongy decay with numerous black pseudosclerotial plates and, in later stages, a dry, brittle, honeycomb-like decay consisting of remaining undecayed primary cell walls. We did not consider the presence of epiphytic rhizomorphs or lesions unaccompanied by obvious signs of *Armillaria* to constitute active infections, although the presence of epiphytic rhizomorphs, in particular, was noted.

2.2.4. 50-year clearcut

This site, <2 km distant, along the same road, and within the same forest type as the 2005 clearcut, was harvested in 1963, and beginning in the late 1970s the USDA Forest Service Northern Research Station established permanent plots within which regenerating and competing trees were thinned to various residual densities for ongoing study. This site provided a convenient example for study of an older clearcut with similar soils for comparison with the younger clearcut. At this site, we investigated 100 white oak, black oak (*Q. velutina*), and scarlet oak (*Q. coccinea*) trees, avoiding established research plots and choosing only trees of obvious stump-sprout origin (i.e., with two or more trunks connected at the base, generally with obvious stump remnants or indications). In order to inspect trees growing on a variety of aspects, we randomly chose a starting tree and an azimuth and then assessed ten trees on a transect along the randomly chosen azimuth. Then we moved to a different location within the clearcut and chose a new random starting tree and azimuth for a new transect. At each tree along each transect we recorded dbh and species of the dominant sprout, the number of sprout stems (living and dead) remaining, and the decay class of dead sprout stems. We then followed the same procedure for detection of *Armillaria* as in the younger clearcuts, choosing two large structural roots for excavation out to at least 1 m from the tree bole and making qualitative observations on any infections that we detected.

2.3. Data analysis

2.3.1. Armillaria detection

We used logistic regression to examine the influence of tree age at time of harvest and basal area of dead trees within a 10 BAF-radius plot on the probability of *Armillaria* detection in 2006 and 2012. We used the chi-square test of independence to determine whether prevalence of *Armillaria* infection (i.e., detect/no detect) varied among oak species (white, black, or scarlet oak). We examined the influence of aspect for only the 50-year-old clearcut, since it was situated on a variety of aspects, whereas the 150 stumps in the younger clearcut were all located on roughly the same aspect. For the 50-year-clearcut, we reduced the variety of aspects recorded for trees along the transects we examined to the four aspect classes used in Bruhn et al. (2000): Protected (341–70°), Neutral East (71–160°), Exposed (161–250°), and Neutral West (251–340°), plus a fifth "Flat" aspect. We then used the chi-square test of independence to determine whether the likelihood of *Armillaria* detection was independent of aspect.

2.3.2. Sprout numbers

Since a histogram of the numbers of sprouts surviving on individual stumps exhibited a non-normal distribution, we used the nonparametric Kruskal-Wallis analysis of variance to examine the effect of *Armillaria* presence and of pre-harvest canopy position on the numbers of sprouts surviving on individual stumps in both 2006 and 2012. The non-normal distribution of surviving sprouts per stump resembled one resulting from a Poisson process, so we initially used Poisson regression to analyze the relationship between numbers of sprouts living one year after harvest and the basal area of dead trees within a 10 BAF-radius plot. The analysis revealed overdispersion in the response data, so we subsequently used negative binomial regression to analyze this relationship, since this kind of error structure accounts for such overdispersion (Bolker, 2008). Finally, we used negative binomial regression to examine the relationship between the height of the dominant sprout (for 2006) or dominant sprout dbh (for 2012), as indicators of stump vigor, and the numbers of surviving sprouts.

2.3.3. Stump circumference gaps

We recorded differences in the greatest length of stump circumference without sprouts (stump circumference gaps) for each stump between 2006 and 2012 and tallied the proportions of gaps that shrank, enlarged, or stayed the same. For 2006 and 2012 observations separately, we analyzed the effects of dominant sprout vigor (height for 2006, dbh for 2012), *Armillaria* presence or absence, and the interaction of the two on size of stump circumference gap by constructing a mixed-effects model with those three variables specified as fixed effects and "tree" specified as a random effect.

We conducted all statistical tests in R (R Development Core Team, 2014). We used functions *glm* for logistic and Poisson regression (R Development Core Team, 2014), *lme* for mixed-effects modeling (Pinheiro et al., 2014), and *glm.nb* (Venables and Ripley, 2002) for negative binomial regression.

3. Results

3.1. Armillaria presence

One year after harvest, *Armillaria* was detected on 82/150 (55%) of stumps. Seven years after harvest, 48 of the original 150 (32%) stumps bore no living sprouts; *Armillaria* mycelium or diagnostic decay was found on 100% of these stumps. Of the remaining 102 stumps with living sprouts, 63 (61.8%) supported active *Armillaria* infection. Including the original 48 stumps that did not sprout, the seven-year figure increases to 74%. However, many of these were not the stumps on which *Armillaria* was originally detected in 2006: 39 stumps reported uninfected in 2006 were found infected in 2012, whereas 20 stumps reported infected in 2006 had no detectable infection in 2012. All three *Armillaria* species known to be present in Missouri were recovered from the clearcut (Table 1). In the 50-year-old clearcut, 21/100 (21%) of examined sprout-origin stem clumps were found infected with *Armillaria.*

Logistic regression detected a significant effect of tree age at the time of harvest on *Armillaria* infection in both 2006 ($p = 0.002$) and 2012 ($p = 0.036$). Expressed as odds ratios, this means that the risk of a tree's having an *Armillaria* infection detectable by our methods increases with age: the odds for a 25-year-old tree's being infected are roughly 1 in 2, while the odds for a 50-year-old tree are roughly 1 in 1.5 and those for a 75-year-old tree are roughly 1 in 1.25. The amount of mortality within a 10-BAF-radius plot displayed no relationship to the probability of *Armillaria* infection ($p = 0.832$).

Chi-square tests of independence found no relationship between tree species and likelihood of *Armillaria* detection in the one-year

Table 1
Armillaria species recovered at study site one year after clearcutting. Percentages do not add up to 100, because both *A. mellea* and *A. gallica* were recovered at three stumps.

Species	Number of stumps	%
A. gallica	5	8
A. mellea	50	79
A. tabescens	2	3
Undetermined	9	14

clearcut in 2006 ($p = 0.894$), in the same (7-year) clearcut in 2012 ($p = 0.360$), or in the 50-year clearcut ($p = 0.096$). Aspect was only examined in the 50-year clearcut, and there all aspects except neutral east were sampled by the random procedure for locating transects. Once again, chi-square analysis detected no statistically non-independent relationship, although a weak trend appeared ($p = 0.070$), as more detections were found on neutral west aspects than any other category. However, sample size ($n = 21$) is too small to lend any statistical power to this observation.

3.2. Sprout numbers

The mean number of living sprouts per stump in 2006 (one year after harvest) was 12 (range: 1–44). The mean number of living sprouts per stump in 2012 (seven years after harvest) was 3 (range: 1–8). There was no significant effect of *Armillaria* infection on the numbers of sprouts regrowing one year after harvest ($\chi^2 = 0.034$, df 1, $p = 0.85$). However, the analysis revealed a weak effect of *Armillaria* infection on the numbers of sprouts regrowing 7 years after harvest ($\chi^2 = 3.7328$, df = 1, $p = 0.053$). The non-normal distribution of surviving sprouts makes this difficult to assess from a visual analysis of the data (Fig. 1). The analysis did not detect a significant effect of parent tree canopy position on number of surviving sprouts per stump in either 2006 ($\chi^2 = 5.83$, df 3, $p = 0.12$) or 2012 ($\chi^2 = 5.39$, df 3, $p = 0.15$). However, the number of sprouts was related to tree size: neither very small nor very large trees tended to produce many sprouts (Fig. 2). Negative binomial regression detected a very weak (inverse) trend between amount of mortality around a stump and numbers of sprouts one year after harvest ($p = 0.07$), but the effect size was small (coefficient = −0.0791). Moreover, when stumps that failed to sprout at all were removed from the data set, no relationship was detected ($p = 0.15$).

According to analysis using negative binomial regression, numbers of living sprouts in 2006 were positively associated with sprout height ($p < 0.001$). The same relationship was found to hold true, with a similar level of significance, for numbers of living sprouts in 2012 when related to dominant sprout dbh (Fig. 3).

3.3. Stump circumference gaps

The distribution of stump circumference gap sizes was approximately normal. Using the amount by which largest gap size on each stump changed from 2006 to 2012 as a response variable, and keeping in mind that some gaps decreased, the mixed model procedure detected a significant effect of dominant sprout diameter on shrinking gaps ($p = 0.009$; Fig. 4), as well as a marginally significant effect of *Armillaria* infection ($p = 0.054$), with no interaction effect ($p = 0.092$). Since dominant sprout diameter and *Armillaria* infection in 2012 were highly correlated ($r = 0.75$), models using either of these perform as well as the model with both covariates. When *Armillaria* detections in 2006 and 2012 were combined into one measure of detection, covariate effects on gap size change (again, positive effects were on *shrinking* gap size) were more significant (effect of dominant sprout size: $p = 0.003$; effect of combined *Armillaria* detection: $p = 0.01$; effect of interaction between the two: $p = 0.021$). The random effect of individual tree (sd = 75.66) was highly pronounced, being nearly three times as large as the residual unexplained variation (sd = 28.37).

3.4. Qualitative observations of Armillaria infection

The greatest number of samples recovered from the clearcut comprised *A. mellea* mycelia (Table 1). Consistent with the presence of all three *Armillaria* species, and with the time elapsed since harvest, we observed a complete spectrum of *Armillaria* infection symptoms on the 7-year-old clearcuts, from vigorous and apparently uninfected sprouting stumps to those in which *Armillaria* was present as actively spreading infections and advanced decay. Following is a list covering the variety of signs and symptoms observed (see Fig. 5).

1. *Armillaria* undetectable; sprouts sound; old stump completely surrounded by new, actively growing sapwood.
2. Sprouts sound; old stump surrounded by new sapwood; *Armillaria* present as epiphytic rhizomorphs on exterior bark.
3. New sapwood extending from part of sprout system partly around old stump; *Armillaria* detected on part of old stump not yet surrounded, or on old stump tissues inside the ring of new wood.

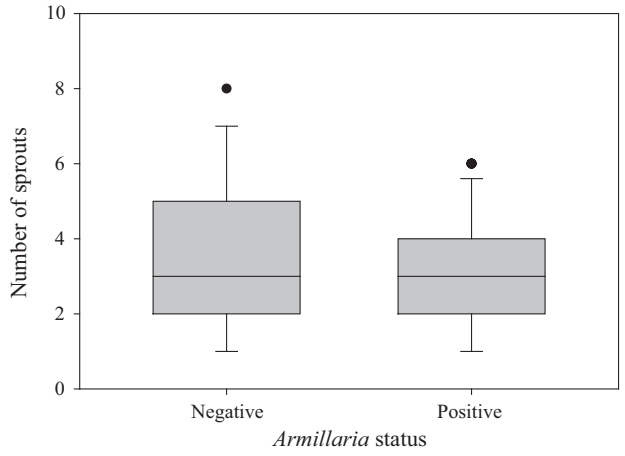

Fig. 1. Comparison of numbers of living sprouts between *Armillaria*-infected (positive) and uninfected (negative) stumps in 2012.

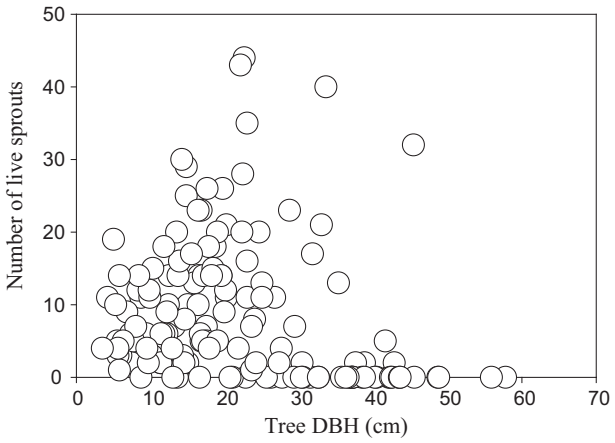

Fig. 2. Numbers of living sprouts on stumps in 2006 by parent tree diameter at breast height (dbh) (measured one year earlier).

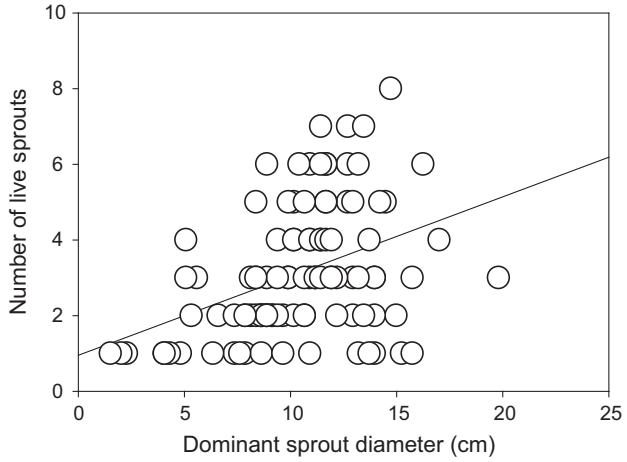

Fig. 3. Relationship between numbers of living sprouts and dominant sprout dbh in 2012.

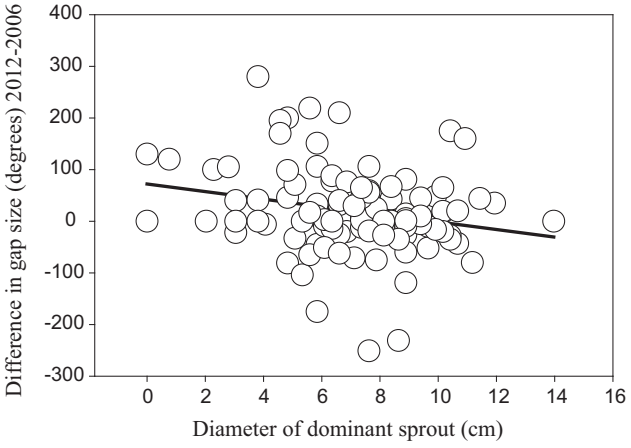

Fig. 4. Relationship between change in size of largest sproutless gap around stump circumference (positive values indicated gap enlarged between 2006 and 2012; negative values indicate gap shrank) and dominant sprout dbh in 2012.

4. *Armillaria* present as mycelial flakes or inward-growing rhizomorphs in outer bark tissues/between bark scales ("infection wedge").
5. Newly formed xylem around parts of old stump mostly healthy, but in places displaying lesions associated with *Armillaria* mycelium and/or rhizomorphs.
6. Newly formed xylem around parts of old stump mostly healthy; *Armillaria* mycelium found in interior of dead sprouts.
7. *Armillaria* mycelial fans clearly blocking advance of new healthy tissue around perimeter of stump system; decay at edges of this tissue as well as in dead sprouts.
8. *Armillaria* easily detectable as mycelium and advanced decay in stump and actively killing sprouts.
9. No sprouts present; stump with advanced decay caused by *Armillaria*.

4. Discussion

This set of stump/sprout observations over time offers a deeper understanding of both ecological and management-oriented aspects of the relationship between *Armillaria* and oak coppice systems in this region of North America. In ecological terms, we see that individual stumps react in some ways as individual biological units and in other ways as modular units composed of individual sprouts, both in terms of general growth and in terms of response to *Armillaria*. In turn, this influences our conception of which management strategies are likely to be successful in fostering and tending oak coppice reproduction.

Using "detection/no detection" as an exclusive response variable can complicate attempts to understand the ecological and physiological roles of *Armillaria*. First, detecting *Armillaria* on an infected root system is notoriously tricky. On any given tree, many possible roots could harbor infections, and excavating all roots is usually impractical. In many cases, *Armillaria* infection is confined to the undersides of roots (Fig. 5F) or to the central structural root. These kinds of infections, especially in the case of *A. gallica*, can be initially undetectable but cause damaging decay over many years (Roth and Sleeth, 1939; Roth and Hepting, 1943). Although we employed a statistical sampling scheme to attempt to accommodate this concern, the results are only partially satisfactory. Second, *Armillaria* infections of different tree tissues cause or at least signal different levels of impact. Infections observed here ranged from those confined completely to bark tissues (usually an indicator of impending cambium infection—Redfern, 1978; Rykowski, 1981) to extensive root infections characterized by advanced decay or large, easily detected mycelial fans.

Nevertheless, root excavation is probably the most meaningful way to estimate infection prevalence. For example, it is interesting to contrast the infection estimates in this study with one that estimated infection prevalence by looking at periodic sprout mortality and basidiome presence in a coppiced oak woodland (Rishbeth, 1991). Estimated infection rates here, in the excavation-based study of Stanosz and Patton (1987), and in the complete root excavations of Filip (1986)—which together range from 21% to 77% in a variety of stand ages—far surpass the Rishbeth (1991) estimate of 4.5%. This contrast could be owing, as noted here, to detection methodology, but also to differences between forest/soil types and climates, to differences in host and *Armillaria* species, or to all of the above.

The current study resembles the work of Stanosz and Patton (1987) in terms of the increase of infection rates with stand age. In cut aspen (*Populus tremuloides*) stands, the former observed a monotonic increase in infection incidence with stand age, at least up to 15 years, the limit of their study. The same monotonic increase with stand age was observed by Rishbeth (1991) in ancient coppiced woodland. In our study, we observed an initial surge of infection on cut stump systems that continued to increase during the next seven years. Moreover, the locations of infection within our stump transects shifted over this time. Again, this could be because of the difficulties of detecting *Armillaria* on root systems; if even some of the stumps positive in 2006 but not 2012 actually still harbor infections, this drives the infection prevalence figure even higher than 74%.

In the 50-year stand, infection prevalence on stump systems was much lower (21%). This may suggest that as oaks reach maturity and approach one to two stems per original sprout clump, they can more effectively defend against *Armillaria* infection. It is also probable that some *Armillaria* infections on these vigorously growing 50-year-old trees were located much deeper on the root systems than our limited excavations could uncover. Finally, the lower infection rate in the older clearcut may also reflect an *Armillaria*-supported shift from red oak (highly susceptible) to white oak (moderately susceptible) dominance in these stands. Voelker (2004) substantiated this trend by sampling in-growth and other mid-story trees on both heavily declining and unaffected plots in the Ozarks and observing that the growth and survival attributes that contribute to white oak's longevity, moderate growth rate, and high shade tolerance relative to other oaks and hickories make it more likely to regenerate successfully and to survive disturbances such as oak decline in Ozark forests currently

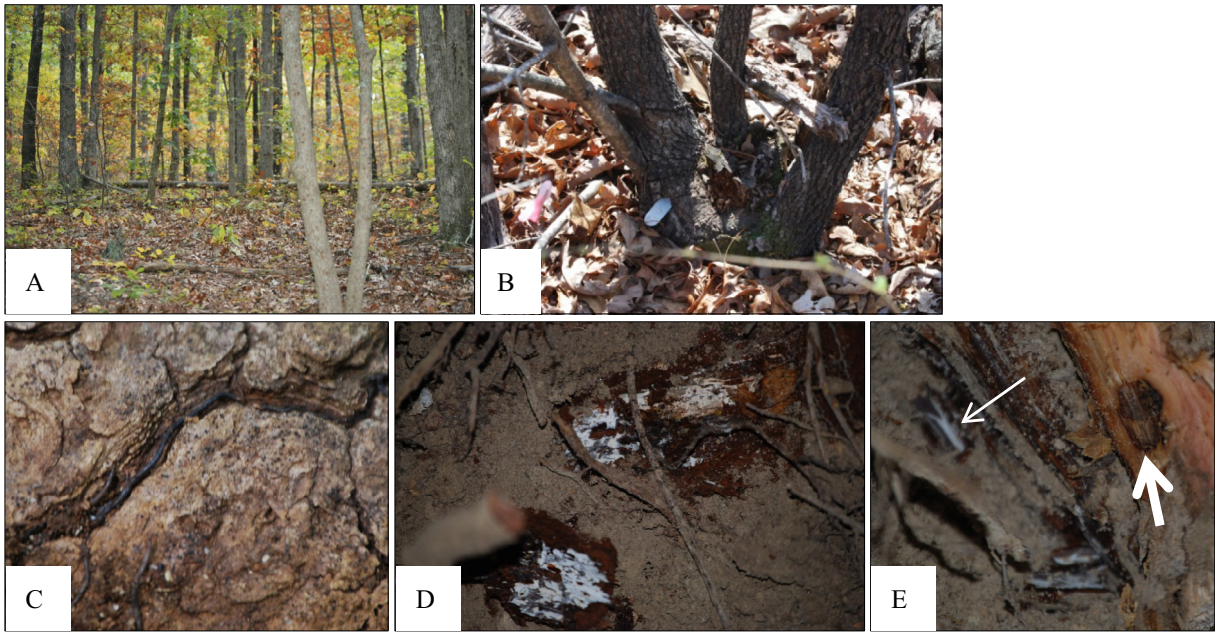

Fig. 5. Examples of *Armillaria* signs and symptoms observed on oak stumps in Missouri clearcuts. (A) 50-year-old clearcut representative of general Missouri mixed-oak forest type. (B) 7-year-old sprout clump that has grown new wood completely around old stump. (C) Rhizomorph following bark fissure. (D) *Armillaria* mycelium growing between root bark and wood. (E) Lesion on underside of root (thick arrow; root has been turned over) in association with mycelium on decayed root (thin arrow).

dominated by red oak group species. It is important to note the high level of infection prevalence in these stands because Missouri is subject to periodic drought events that subject trees to severe water stress, reduce tree resistance, and lead to large-scale episodes of red oak mortality (Dwyer et al., 1995; Jenkins and Pallardy, 1995; Voelker et al., 2008). It is not surprising that in a landscape saturated with *Armillaria* individuals, especially *A. mellea*, this aggressive root pathogen plays an important role in these mortality episodes. Except for a moderate drought in 2007 (and leaving out the 50-year-old clearcut), this study was conducted during an inter-drought period.

The apparent shifts in infection prevalence and location within 1- and 7-year old stump-sprout systems could be attributed to the dynamics of pathogen compartmentalization by oak species and individuals exhibiting varying levels of vigor. This subject begs further study at finer temporal scales for better understanding. Nevertheless, our findings regarding the relationships between *Armillaria*, sprout numbers, and sprout diameters provide evidence supporting this speculation.

Our first hypothesis, that *Armillaria* infection has a detectable impact on numbers of surviving stump sprouts, received only equivocal support from our longitudinal study data. No impact was detected on initial numbers of sprouts, which is to be expected given that other factors such as amount of light have also been observed to impact these initial numbers very little (Dey and Jensen, 2002). By the seven-year mark, it is still difficult to see a difference between mean numbers of sprouts on infected and uninfected stumps, even though statistical analysis detects a weak one (Fig. 1). In any case, this question is clouded by the dynamics of stump resprouting and the micro-spatial scale of fungal invasion: once the pathogen kills a sprout, one or more may develop during the next year from adjacent buds in not-yet-invaded tissue.

It is interesting that dominant sprout diameter in 2012, a proxy for stump vigor, was correlated with *Armillaria* infection, and that *Armillaria* infection was associated with stump circumference gaps that actually shrank (i.e., filled in with new sprouts) between 2006 and 2012. This leads us to reject our second hypothesis, that *Armillaria* infection would be associated with slower-growing/less vigorous sprouts. This seems perplexing in light of the common conception of *Armillaria* as a pathogen that takes advantage of weakened trees (Wargo and Harrington, 1991). Several researchers working with *Armillaria solidipes* (=*Armillaria ostoyae*) in the interior Western U.S. have noted that this species, which is as virulent to conifers as *A. mellea* is to hardwoods, actually appears to infect (Fuller, 1979) and/or kill (Rosso and Hansen, 1998) a greater proportion of high-vigor than low-vigor trees; but others have observed early thinning to increase apparent tree vigor and reduce subsequent *A. solidipes*-caused mortality (Filip et al., 2009). It is hard to address the question of pre-existing tree vigor and host susceptibility to *Armillaria* spp. partly because it is hard to differentiate transient episodes of stress that depress tree growth for varying periods of time from longer-term, background tree vigor status.

It is also likely that a temporal element is relevant in this case. Given the complexity of the infection process, which was evident from the variety of qualitative observations of infection stages we observed, seven years may be insufficient time to observe the effects of *Armillaria* on the vigor of infected oak stumps or on the ultimate fate of sprouts. This likely stems both from the slow development and quiescence of the infection and compartmentalization process (Schwarze et al., 2000) and also from the three-dimensional spatial aspect of infection as the pathogen invades at numerous points on roots and stump circumference. At certain points, it may be that *Armillaria* is actively degrading outer bark or phloem but has not yet reached the xylem tissues that are connected to newly growing dormant buds, so that vigorous stumps continue to produce new sprouts even if infected by *Armillaria*.

In some cases, shrinking gap sizes can be attributed to increasing size of the dominant sprouts over the seven years as they take up more and more stump circumference space. In some of these cases, *Armillaria* is indeed actively killing sprouts around the stump circumference, and carbohydrate resources formerly supporting those sprouts are then redirected to the dominants. Future inspection of these dominants may reveal whether *Armillaria* is eventually able to infect them as well, or if these increased resources enable them to continue to defend themselves successfully. Brazee (2011) points out that in many instances, rather than

pre-existing *Armillaria* actively killing sprouts after a tree is cut, the process works the other way around: sprouts die because they are outcompeted for resources, or perhaps from other causes, and they then serve as infection courts for *Armillaria* to infect the stump much later on.

It is also highly likely that *Armillaria* infection is a stress event that stimulates the production of new sprouts. This phenomenon has not been directly documented for sprouts, but it has been for adventitious roots (Kile, 1980; Rishbeth, 1985). Once again, the effects of individual stump vigor appear to outweigh, or at least complicate our understanding of, the effects of fungal infection in the short term. If the process of cambial killing or colonization of functional sapwood takes decades, then further sprout demographic studies between year 7 and year 50 may be able to document this process.

The correlation between dominant sprout diameter and *Armillaria* infection shows that our third hypothesis was founded on incorrect assumptions. The second part, that sprout diameter/stump vigor and gaps around the stump circumference would be inversely correlated, was not rejected based on the evidence from this study. However, the first part, that *Armillaria* presence and circumferential gaps would be positively correlated, was not supported by the data. Once again, this seems to show that stump vigor influences sprout growth more strongly than does fungal infection, at least at the 7-year mark.

In this study, stumps featuring dominant sprouts with the greatest diameter growth also had the largest numbers of sprouts (Fig. 3), re-emphasizing an intuitive connection between numbers of sprouts and stump vigor. Many researchers have tested the natural importance of intra-stump competition by performing experiments to release individual sprouts, generally finding that an optimal thinning regime varies according to species and to desired objectives, such as timber versus biomass production (e.g., Lamson, 1988; Lowell et al., 1989; Groninger et al., 1998; Espelta et al., 2003; Chatzhiphilippidis and Spyroglou, 2004; Keyes et al., 2008; Liu et al., 2011). Our observations emphasize the additional importance of inter-stump competition to sprout growth, since stump spacing and capture of site resources dictate individual stump vigor and subsequent growth of dominant sprouts. Apparently, vigor of the whole stump is important to production of vigorous sprouting units, and more vigorous stumps may gather, store, and allocate sufficient resources to both support thriving populations of sprouts and deal with ubiquitous invading *Armillaria*.

Espelta et al. (2003) noted that the benefits of releasing individual sprouts through thinning are often balanced by the growth of new waves of sprouts in subsequent years. Our study confirms this, as we observed oak stumps to be dynamic systems in which dying sprouts create gaps around the stump circumference that are then filled in by new sprouts. Similarly, *Armillaria* appeared to move on and off individual stump systems over time, or to invade then be compartmentalized, although this appearance may be owing to the difficulties of detection on root systems. The overall effect is one of a shifting constellation of infected stumps and sprouts over a stand's rotation, with (to judge from comparison with the 50-year-old stand) gradual recession of *Armillaria* in prominence at some point. Then, presumably, increasing rates of infection combine with other stress events such as drought or insect outbreaks to lead to mortality as a given cohort grows even older. This trajectory is likely heavily modified by site characteristics such that, for example, stands on high ridgetops and southwest-facing slopes experience the onset of collective mortality events at an earlier average age than more protected sites (Starkey and Oak, 1989).

This information, along with the weakness of the distribution of prior tree mortality in predicting stump condition and sprout numbers, reinforces the notion that susceptibility to *Armillaria* depends as much upon individual stump (tree) vigor as upon prior pathogen distribution and epidemiology. This is not new information, but it is important to keep these two elements conceptually in balance. As an indigenous, ecologically important pathogen, *Armillaria* pervades tree rhizospheres and is always advancing upon its hosts, testing their defenses. This is especially true of *A. gallica*, which may only manifest its pathogenic potential in times of tree stress but occurs widely nonetheless, as shown by the dense networks of epiphytic rhizomorphs (not counted as *Armillaria* infection for this study) present around the majority of stumps and trees in these forests. For management of these kinds of pathogens, cultivating individual tree vigor through density or light management presents itself as one way to alleviate pathogen-caused losses. For shade-intolerant oaks, this may tip the scales of management toward an even-aged approach in some situations (Dey and Jensen, 2002). On sites with nutrient-poor, rocky, or drought-prone soils, it may provide an argument for wider spacing even though this could lead to a reduction in timber quality (cf. Savill and Spilsbury, 1991).

Studies of tree spacing and mortality during episodes of oak decline have obtained conflicting results. Kabrick et al. (2004), for example, found no relationship between tree spacing and likelihood of mortality during one such decline episode, while Voelker et al. (2008) found that stands affected heavily by oak decline were overstocked. When considering whether to reduce stand density on the most vulnerable sites, forest managers should also recall that *Armillaria* spp. rapidly colonize new stumps, using them as food bases for augmented foraging and growth in the stand and potentially increasing future disease risk (Rishbeth, 1972). However, the results of our study provide some evidence that young, vigorous oaks can largely contain this risk at least until an intense stress event incites a new wave of decline.

In contrast to the findings of Chatzhiphilippidis and Spyroglou (2004), who reported many poorly formed trees in long-untended coppice stands, and Lamson (1988), who warned of bole sweep, forking boles, and root rot in unthinned sprout clumps, the trees in the 50-year-old Missouri clearcut generally exhibit straight growth habits and good form—although as previously mentioned, root rot caused by *Armillaria* is present. In the study of Lamson (1988), red oak did not respond to thinning with increased diameter growth in the same way the other studied species did, although Lowell et al. (1989) reported positive results from both red and white oak species sprout thinning in the same region as the current study. However, Lowell et al. (1989) were seeking to maximize diameter growth over a 30-year rotation, which may not match all landowners' coppice management objectives.

Although there is no evidence from this study to suggest that *Armillaria* infection prevalence varies according to oak species, evidence from other studies suggests that white oak species are less susceptible to fatal parasitic infection than red oak species (Bruhn et al., 2000; Shifley et al., 2006). Sampling of the 50-year-old clearcut lends some support to this. Random transects through the clearcut encountered far more white oak trees of sprout origin than red oak species, and it cannot be ruled out that *Armillaria* may be responsible for the elimination of much of the red oak stump-sprout regeneration over the past half-century. Abundant single-stem, seedling-origin red oak stems were present on this clearcut. Recent death of suppressed and intermediate single stems (both white and red oak species), along with *Armillaria* mycelial fans on the roots, was readily apparent throughout the stand.

In general, the observations in this study provide evidence consistent with two general hypotheses about oak stump-sprout ecology and management: (1) *Quercus* species are well able to regulate the rate of sprout self-thinning and protect residual stems by vigorous compartmentalization of *Armillaria* infection, regardless of oak species or aspect; and (2) despite this, *Armillaria* can gain a foothold early in the life of a regenerating stand and contribute

to further sprout mortality and shifts in species dominance over a long time horizon, through the back-and-forth of pathogen invasion and subsequent tree compartmentalization of infection. The evidence further supports numerous earlier observations that even though *Armillaria* is exceptionally well-established in these stands—including large numbers of *A. mellea* individuals—lethal infection may require at least some degree of compromised host vigor incited by other stresses, largely depending on individual tree vigor. Future studies of sprout demography, especially those that span periodic drought events, will further illuminate our understanding of these relationships.

Acknowledgements

We are grateful to the following individuals for help with access, materials, and methods: John Kabrick and Texas Nall (USDA Forest Service); Jeanne Mihail, Susan Taylor, Jim English, Ricardo Holdo, and Sharon Reed (University of Missouri); the USDA Forest Service Northern Research Station; and the University of Missouri Life Science Fellowship and Research Council Grant programs. We thank Johann Bruhn and Kathy Kromroy for originating this study and performing the first phase including species identifications.

References

Baumgartner, K., Rizzo, D.M., 2001. Ecology of *Armillaria* spp. in mixed-hardwood forests of California. Plant Dis. 85 (9), 947–951.
Beck, D.E., Hooper, R.M., 1986. Development of a southern Appalachian hardwood stand after clearcutting. South. J. Appl. For. 10, 168–172.
Bolker, B.M., 2008. Ecological Models and Data in R. Princeton UP, Princeton, NJ.
Brazee, N., 2011. Armillaria in Massachusetts forests: ecology species distribution and population structure with an emphasis on mixed oak forests PhD dissertation. University of Massachusetts-Amherst.
Bruhn, J.N., Dey, D.C., Kromroy, K.K., Mihail, J.D., Kabrick, J.M., Wetteroff Jr., J.J., 2005. Armillaria root disease affects oak coppice regeneration in upland Ozark forests. In: Manka, M., Lakomy, P. (Eds.), 11th National Conference on Root and Butt Rots. August Czieskowski Agricultural University, Poznan, Poland, pp. 279–285.
Bruhn, J.N., Mihail, J.D., 2003. Opportunistically pathogenic root rot fungi: *Armillaria* species. In: Hanson, P.J., Wullschleger, S.D. (Eds.), North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes. Springer-Verlag, New York, pp. 337–346.
Bruhn, J.N., Wetteroff Jr., J.J., Mihail, J.D., Kabrick, J.M., Pickens, J.B., 2000. Distribution of *Armillaria* species in upland Ozark Mountain forests with respect to site, overstory species composition and oak decline. Eur. J. Forest Pathol. 30, 43–60.
Castello, J.D., Leopold, D.T., Smallidge, P.J., 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience 45 (1), 16–24.
Chatzhiphilippidis, G., Spyroglou, G., 2004. Sustainable management of coppice forests in Greece. In: Andersson, F., Birot, Y., Paivinen, R. (Eds.), Towards the Sustainable Use of Europe's Forests-Forest Ecosystem and Landscape Research: Scientific Challenges and Opportunities. European Forest Institute, Tours, France, pp. 51–60.
Dey, D.C., Jensen, R.G., 2002. Stump sprouting potential of oaks in Missouri Ozark forests managed by even- and uneven-aged silviculture. In: Shifley, S.R., Kabrick, J.M. (Eds.), Second Missouri Ozark Forest Ecosystem Project Symposium: Post-Treatment Results of the Landscape Experiment. USDA Forest Service, St. Louis, MO, pp. 102–113.
Dwyer, J.P., Cutter, B.E., Wetteroff, J.J., 1995. A dendrochronological study of black and scarlet oak decline in the Missouri Ozarks. Forest Ecol. Manage. 75, 69–75.
Edmonds, R.L., Agee, J.K., Gara, R.I., 2000. Forest Health and Protection. Waveland Press, Long Grove, IL.
Espelta, J.M., Retana, J., Habrouk, A., 2003. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. Forest Ecol. Manage. 179 (1–3), 401–414.
Fan, Z., Kabrick, J.M., Spetich, M.A., Shifley, S.R., Jensen, R.G., 2008. Oak mortality associated with crown dieback and oak borer attack in the Ozark Highlands. Forest Ecol. Manage. 255 (7), 2297–2305.
Filip, G.M., 1986. Symptom expression of root-diseased trees in mixed conifer stands in central Washington. West. J. Appl. For. 1 (2), 46–48.
Filip, G.M., Fitzgerald, S.A., Chadwick, K.L., Max, T.A., 2009. Thinning ponderosa pine affected by *Armillaria* root disease: 40 years of growth and mortality on an infected site in central Oregon. West. J. Appl. For. 24 (2), 88–94.
Fuller, L.R., 1979. Infection of stressed ponderosa pines by Armillariella mellea from indigenous and artificial inoculum sources PhD dissertation. Oregon State University.
Garbelotto, M., 2004. Root and butt rot diseases. In: Burley, J., Evans, J., Youngquist, J.A. (Eds.), The Encyclopedia of Forest Sciences. Elsevier, Oxford, pp. 750–758.
Goheen, D.J., Otrosina, W.J., 1998. Characteristics and consequences of root diseases in North America. In: Frankel, S.J. (Ed.), User's Guide to the Western Root Disease Model. USDA Forest Service, Washington, DC, pp. 3–8.
Götmark, F., Berglund, Å., Wiklander, K., 2005. Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. Scand. J. Forest Res. 20, 223–234.
Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2002. Regenerating mixed oak stands in Pennsylvania: a quarter-century perspective. In: Van Sambeek, J.W., Dawson, J.O., Ponder, F., Jr., Loewenstein, E.F., Fralish, J.S. (Eds.), 13th Central Hardwoods Forest Conference. USDA Forest Service North Central Research Station, St. Paul, MN, pp. 254–258.
Groninger, J.W., Stein, H.D., Zedaker, S.M., Smith, D.W., 1998. Growth response and cost comparisons for precommercial thinning methods of Appalachian oak stump sprout clumps. South. J. Appl. For. 22 (1), 19–23.
Guillaumin, J.J., Anderson, J.B., Korhonen, K., 1991. Life cycle interfertility and biological species. In: Shaw, C.G.III., Kile, G.A. (Eds.), Armillaria Root Disease. USDA Forest Service, Washington, DC, pp. 10–20.
Jenkins, M.A., Pallardy, S.G., 1995. The influence of drought on red oak species growth and mortality in the Missouri Ozarks. Can. J. Forest Res. 25, 1119–1127.
Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The Ecology and Silviculture of Oaks, second ed. CABI Publishing, New York, NY.
Kabrick, J.M., Shifley, S.R., Jensen, R.G., Larsen, D.R., Grabner, J.K., 2004. Oak forest composition, site quality, and dynamics in relation to site factors in the southeastern Missouri Ozarks. In: Spetich, M.A. (Ed.), Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. USDA Forest Service, Fayetteville, AR, pp. 94–101.
Keyes, C.R., Matzka, P.J., Wright, K.C., Glebocki, R., Han, H.-S., 2008. Early precommercial thinning of redwood sprout clumps: evaluation of four techniques. Int. J. Forest Eng. 19 (2), 28–36.
Kile, G.A., 1980. Behaviour of an *Armillaria* in some *Eucalyptus obliqua-Eucalyptus regnans* forests in Tasmania and its role in their decline. Eur. J. Forest Pathol. 10, 278–296.
Lamson, N.I., 1988. Precommercial thinning and pruning of appalachian stump sprouts–10-year results. South. J. Appl. For. 12 (1), 23–27.
Li, Q., Ma, K., 2003. Factors affecting establishment of *Quercus liaotungensis* Koidz. under mature mixed oak forest overstory and in shrubland. Forest Ecol. Manage. 176, 133–146.
Liu, Z., Fang, S., Liu, D., Yu, M., Tang, L., 2011. Influence of thinning time and density on sprout development biomass production and energy stocks of sawtooth oak stumps. Forest Ecol. Manage. 262 (2), 299–306.
Lowell, K., Garrett, H., Mitchell, R., 1989. Potential long-term growth gains from early clump thinning of coppice-regenerated oak stands. New Forest 3 (1), 11–19.
Morrissey, R.C., Jacobs, D.F., Seifert, J.R., Fischer, B.C., Kershaw, J.A., 2008. Competitive success of natural oak regeneration in clearcuts during the stem exclusion stage. Can. J. Forest Res. 38, 1419–1430.
National Oceanic and Atmospheric Administration, 2015. Historical Palmer Drought Indices. <http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/>. (Accessed December 2, 2015).
Natural Resources Conservation Service, 2016. Official Soil Series Descriptions. USDA Natural Resources Conservation Service, Washington, DC, https://soilseries.sc.egov.usda.gov/osdname.asp.
Nigh, T.A., Schroeder, W.A., 2002. Atlas of Missouri Ecoregions. Missouri Department of Conservation, Jefferson City, MO.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team. 2014. _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-118. <http://CRAN.R-project.org/package=nlme>.
Pulido, F.J., Díaz, M., 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. Ecoscience 12 (1), 92–102.
Pyttel, P.L., Fischer, U.F., Suchomel, C., Gärtner, S.M., Bauhus, J., 2013. The effect of harvesting on stump mortality and re-sprouting in aged oak coppice forests. Forest Ecol. Manage. 289, 18–27.
R Development Core Team, 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. (ISBN 3-900051-07-0, Retrieved October 2015).
Redfern, D.B., 1978. Infection by *Armillaria mellea* and some factors affecting host resistance and the severity of disease. Forestry 51 (2), 121–135.
Redfern, D.B., Filip, G.M., 1991. Inoculum and infection. In: Shaw, C.G.III., Kile, G.A. (Eds.), Armillaria Root Disease. USDA Forest Service, Washington, DC, pp. 48–60.
Rishbeth, J., 1972. The production of rhizomorphs of *Armillaria mellea* by stumps. Eur. J. Forest Pathol. 2, 193–205.
Rishbeth, J., 1985. Infection cycle of *Armillaria* and host response. Eur. J. Forest Pathol. 15, 332–341.
Rishbeth, J., 1991. *Armillaria* in an ancient broadleaved woodland. Eur. J. Forest Pathol. 21, 239–249.
Rosso, P., Hansen, E., 1998. Tree vigour and the susceptibility of Douglas fir to *Armillaria* root disease. Eur. J. Forest Pathol. 28, 43–52.
Roth, E.R., Hepting, G., 1943. Origin and development of oak stump sprouts as affecting their likelihood to decay. J. Forest. 41 (1), 27–36.
Roth, E.R., Sleeth, B., 1939. Butt Rot in Unburned Sprout Oak Stands. US Department of Agriculture Technical Bulletin No. 684, Washington, DC.
Rykowski, K., 1981. The influence of fertilizers on the occurrence of *Armillaria mellea* in Scots pine plantations I. Evaluation of the health of fertilized and non-fertilized plantations and the variability of *A. mellea* in the areas investigated. Eur. J. Forest Pathol. 11 (1–2), 108–119.

Savill, P.S., Spilsbury, M.J., 1991. Growing Oaks at Closer Spacing. Forestry 64 (4), 373–384.
Schwarze, F.W.M.R., Engels, J., Mattheck, C., 2000. Fungal Strategies of Wood Decay in Trees. Springer, New York.
Shifley, S.R., Fan, Z., Kabrick, J.M., Jensen, R.G., 2006. Oak mortality risk factors and mortality estimation. Forest Ecol. Manage. 229 (1–3), 16–26.
Stanosz, G.R., Patton, R.F., 1987. Armillaria root rot in aspen stands after repeated rotations. Can. J. Forest Res. 17, 1001–1005.
Starkey, D.A., Oak, S.W., 1989. Site factors and stand conditions associated with oak decline in southern upland hardwood forests. In: Rink, G., Budelsky, C. (Eds.), Proceedings of the 7th Central Hardwood Forest Conference; 1989 March 5–8; Carbondale, IL. USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, pp. 95–102.
USDA Forest Service, 2008. Sinkin Experimental Forest. <www.nrs.fs.fed.us/ef/locations/mo/sinkin>. (Accessed December 4, 2015).
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics With S, fourth ed. Springer, New York.
Voelker, S.L., 2004. Causes of Forest Decline and Consequences for Oak-pine Stand Dynamics in Southeastern Missouri PhD dissertation. University of Missouri-Columbia.
Voelker, S.L., Muzika, R.-M., Guyette, R.P., 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. Forest Sci. 54 (1), 8–20.
Wargo, P.M., Harrington, T.C., 1991. Host stress and susceptibility. In: Shaw, C.G., III, Kile, G.A. (Eds.), Armillaria Root Disease. USDA Forest Service, Washington, DC, pp. 48–60.
Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 18 (2), 129–134.
Weigel, D.R., Peng, C.-Y.J., 2002. Predicting stump sprouting and competitive success of five oak species in southern Indiana. Can. J. Forest Res. 32, 703–712.